Passerine Birds of Ontario

Habitat Requirements, Limiting Factors, & Status

Al Sandilands

Illustrated by Ross James

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Yellow-throated Vireo, photographed by Ross James

Cover photograph Blue-headed Vireo, photographed by Ross James.

HOW TO USE THIS BOOK

To access a topic, click on it in the Contents, which follow on the next page. On every page, there is an icon of a Blue-headed Vireo in the upper left corner. If you click on this icon, it will return you to the Contents. The entire document can be downloaded. The book is more than 2,400 pages long so it is recommended that one prints only those files that are of most interest. As can be seen in the Contents, the bulk of the book is devoted to accounts of the 145 passerine species that have nested in Ontario.

Literature Cited

Bookmarks are provided in the Literature Cited section. The bookmarks panel is closed in the online version but can be opened by clicking on the icon in the navigation toolbar. Once you have opened the bookmarks panel, ">Literature Cited" will be displayed. Click on > to reveal the letters of the alphabet. The list of references is 222 pages long, so bookmarks are provided for the first reference starting with each letter of the alphabet to reduce the amount of scrolling that may be required to find a reference. So, for example, if you are looking for an article authored by "Caffrey", you can click on the "C" bookmark to get close to the reference. In this example, the bookmark takes you to "Cabe".

I have provided hyperlinks to references that occur only online. Clicking on a hyperlink should take one directly to the paper that is cited. Over time, some of these may cease to function because of updates and other changes. This is most likely to occur in the *Birds of the World* species accounts. These accounts are constantly being updated and the references are changed with each revision. There are a few cases where a website has already been taken down. In these cases, I have not provided a hyperlink.

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Barn Swallow
Cliff Swallow
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Bohemian Waxwing
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Hermit Thrush
Wood Thrush
American Robin
House Sparrow
American Pipit
Evening Grosbeak

Pine Grosbeak
House Finch
Purple Finch
Redpoll
Red Crossbill
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Pine Siskin
American Goldfinch
Lapland Longspur
Smith's Longspur
Snow Bunting
Grasshopper Sparrow
Lark Sparrow
Chipping Sparrow
Clay-colored Sparrow
Field Sparrow
Fox Sparrow
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Vesper Sparrow
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Song Sparrow
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Canada Warbler
Wilson's Warbler
Scarlet Tanager
Northern Cardinal
Rose-breasted Grosbeak
Blue Grosbeak
Indigo Bunting
Dickcissel

LITERATURE CITED

SCIENTIFIC NAMES OF SPECIES MENTIONED IN THE TEXT

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Cole McLennan designed the website. He provided me valuable information on design options and helped me select the preferred design.

Staff at the University of Guelph library annex were extremely helpful, getting publications out of storage and allowing me to photocopy them on site. Angela Davidson, in particular, was of great assistance. Without their help, I would not have been able to track down many of the older or more obscure references.

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I am indebted to all those citizen scientists that conducted fieldwork for the programs that I used in summarizing status trends for species. These include the Breeding Bird Survey, Christmas Bird Count, Project FeederWatch, Marsh Monitoring Program, Forest Bird Monitoring Program, and Winter Bird-Population Study.

Although many have helped me throughout this process, all errors and omissions are mine.

INTRODUCTION

This book summarizes the life history requirements of 145 species of passerine birds that occur in Ontario. Two previous volumes (Sandilands 2005, 2010) covered the nonpasserine species.

Only species that are normally part of the ecology of the province or that have been confirmed breeding are included in the accounts. Vagrants and extremely rare species are not discussed because they are typically out of their normal range and habitat.

Through strict application of the breeding evidence rules for the Ontario Breeding Bird Atlas, 5 species that I have not included as breeding species are considered breeders by one or both of the atlases (Cadman et al. 1987, 2007). These are the Northern Wheatear, Sprague's Pipit, Worm-eating Warbler, Kentucky Warbler, and Summer Tanager. These species have not been confirmed as breeders in Ontario. Because these species do not occur regularly in the province during other seasons, I have not prepared species accounts for them. The Mountain Bluebird has nested in the province, but only in mixed pairs with the Eastern Bluebird. Because the Mountain Bluebird has not been confirmed nesting conspecifically in the province, no account is presented for it.

Three aspects of bird life histories are the focus in this book: habitat requirements, limiting factors, and status. Where applicable, each species is discussed during the breeding season, postfledging period, migration, and winter. A more detailed explanation of the format of the species accounts follows.

I have omitted many topics typically considered in life history accounts. These include description and identification information, vocalizations, behaviour, parasites other than the Brown-headed Cowbird, and predators. Occasionally, the latter three topics are discussed if they have a direct bearing on habitat use, are a limiting factor, or may affect the status of the species. Details of the materials used in the construction of the nest and its size have been omitted. This information is available in Peck and James (1987). No information is provided on hybrids or misdirected parenting among species except in cases where these pose a significant limiting factor or change the habitat or behaviour of the species involved.

The information in the species accounts is derived almost entirely from published data. The accounts also contain my unpublished personal observations and those of individuals who have provided me with some of their personal knowledge.

The order and nomenclature of the accounts follow the seventh edition of the American Ornithologists' Union (1998) *Check-list of North American Birds* and its supplements through to 2025 (Chesser et al. 2025a). Scientific names of species mentioned in the text are provided in the appendix. Bird species for which species accounts are presented are not included in the appendix.

Definitions of the extent of southern and northern Ontario are identical to those presented by James (1991), and are similar to the delineation used in the Ontario Breeding Bird Atlases (Cadman et al. 1987, 2007). The 47th parallel is used to distinguish between northern and southern portions of the province. Figures 1 and 2 show southern and northern Ontario respectively, along with

municipal boundaries and most localities mentioned in the text. Figure 3 indicates physiographic and forest regions of the province.

The species accounts deal with 4 biological seasons: breeding, postfledging, migration, and winter. Due to the different "biological clocks" of various species, these seasons are only loosely related to the human calendar. For example, February is winter for most species, but breeding season for the Great Horned Owl and spring migration for the Horned Lark.

For each species, approximate dates of major life history events are identified. In many cases, different dates are relevant to northern and southern portions of the province. Ranges of dates of occurrence are often presented along with periods of peak occurrence when they are available.

Winter species usually include only birds that normally occur in the months of January and February. December birds and those reported on Christmas Bird Counts are often late autumn migrants.

Not all species are present during all biological seasons. When a species is consistently absent in a season, or very rare and sporadic, this season is not mentioned in the species account. Breeding requirements are discussed for all species that have nested even only occasionally in the province. All species are present during the postfledging period, but no information is available for some species.

The following sections describe topics that are usually addressed during the 4 seasons. If no information is presented, it is because I could not find any. Although I have undoubtedly overlooked some publications, lack of discussion usually means that no information is available.

FORMAT OF THE SPECIES ACCOUNTS

Breeding Season

Under habitat requirements, 3 topics are discussed in all accounts: nesting habitat, a description of where the nest is likely to be situated, and the territory and/or home range size. Additional information that is presented includes natal philopatry and site fidelity of adults to territories. The information on nesting habitat is often quite detailed. Information is provided on a species' habitat requirements in each of the physiographic regions that it occurs in Ontario followed by details on habitat use in other areas. In addition to the general habitat, information may be provided on landscape-level habitat, microhabitats, differences in habitat at nests and the remainder of the territory, differences between occupied and unoccupied habitat, and comparison of habitat use with other species using the same habitat. For most species, a discussion in provided on where it nests within a habitat patch (on the edge, in the interior, or throughout), and whether it is area sensitive.

Under limiting factors, information is always provided on the time of key events in the nesting period, the annual reproductive effort, mating systems, and diet. Topics discussed about timing include how long it takes to build the nest, when nesting is usually initiated, the egg-laying interval, incubation period, and the nestling period. Factors considered under reproductive effort are number of broods raised, whether renesting occurs, and clutch size. Topics under mating systems include age at first breeding, breeding periodicity if breeding does not always occur every year, the mating strategy (monogamy or polygyny, extra-pair copulations, and intraspecific parasitism), and

mate fidelity within and between seasons. The discussion of diet emphasizes the breeding season. Diet in other seasons is occasionally included here if there are no significant differences among seasons, or if the entire diet can be summarized briefly. Besides a description of food items, information on food-size preferences may be presented, and it is noted whether feeding territories are defended. Feeding techniques and substrate are also described. Information on parasitism by the Brown-headed Cowbird is provided for all species that are hosts. This includes information on how the species responds to parasitism and how it is affected by parasitism.

The section on breeding season limiting factors is frequently the most extensive portion of a species account. In addition to the topics that are always addressed, habitat loss and fragmentation, human disturbance, environmental contaminants, effects of water-level fluctuations, forest management, water and air quality, nest-site availability, interspecific competition, mowing, prescribed burns, livestock grazing, climate change, and many other factors may be discussed. When no additional information is provided, it is because there is no evidence to suggest that adverse effects are occurring or because no information is available. Some minor effects that are not limiting factors, such as entrapment in spider webs or burdocks, are not presented.

For status, a historical perspective of changes since the late 19th century to the present is given. In some instances, the future status of species has been predicted. Occasionally, a distinction is made between status in the northern and southern portions of the province.

The status section is the weakest in the book, simply because status is dynamic and because it varies so much across the province. In addition, many bird species are not routinely monitored throughout the province by any survey program, and there is no reliable information on the status of many species. For status, I have identified differences in abundance over large geographic areas, such as in and south of the Canadian Shield, but I have seldom discussed differing abundance levels within smaller regions. There are numerous excellent publications on birds in different regions of the province and these should be consulted for more detailed information on local status.

The Ontario Breeding Bird Atlas program is an important analysis of breeding bird distribution and status in the province. Two atlases have been completed to date. Fieldwork for the first atlas was completed 1981-85 and results were summarized by Cadman et al. (1987). Fieldwork for the second atlas was conducted 2001-05 (Cadman et al. 2007). These are referred to the "first atlas" and the "second atlas" in this document.

The atlases use the term "probability of observation", and this information is provided throughout the species accounts. The probability of observation is the percentage of squares that a species could be expected to be found in during 20 hours of atlassing effort within the province and the 5 regions that were used in analyzing atlas data. For a full discussion of the methods of calculating changes in the probability of observation between atlases, Cadman et al. (2007) should be consulted. The information on changes in probability of observation of species reported by Cadman et al. (2007) is very useful. In many cases, a species was found in a similar number of squares during the second atlas as during the first, but is identified as significantly decreasing or increasing based on the statistical analysis of the probability of observation. In some cases, I have also provided information on the number of squares that the species was detected in during the 2 atlases. The

third atlas, currently underway 2021-25, will be a much better indicator of change in the probability of observation provided that the same methods for reporting when birds are observed are followed.

Breeding abundance is defined slightly differently than for migration and winter. During the breeding season, species maintain territories or home ranges that disperse birds throughout suitable habitat. For most species, territorial boundaries dissolve in other seasons, allowing concentrations of birds in preferred habitats.

Abundance is difficult to define and has been done in several ways historically. The most frequently used technique is based on how many breeding pairs could potentially be recorded daily. This definition works well for common and abundant species that are readily observed and use widespread habitats. Species that are difficult to detect, have large territories, or have specialized habitat requirements may not be adequately defined by these criteria.

Abundance of species can be greatly affected by the size of their territory and the availability of their preferred habitats. Some raptors have extremely large home ranges and would not be plentiful even if the entire province were suitable habitat. The Peregrine Falcon, in addition to having large area requirements, is limited by the availability of nest sites such as cliffs or skyscrapers. Thus, even under ideal conditions, it would not be a common species in the province.

Even species that do not have specialized habitat requirements are limited by the abundance of their general habitat needs. Southern Ontario species that nest in urban areas, pastures, or old fields are likely to be more common than those that require bogs, simply because the former habitats are much more common.

Among species inhabiting a particular vegetation type, there are usually generalists and specialists. This has been well documented for forests but also applies to wetlands and grasslands. In forest habitats, the generalists are edge species that occur around the periphery of woodlots, and they often use adjacent open habitats for foraging, displaying, or even nesting. When openings are created in forests, these species are able to exploit microhabitats within the woodlot. Specialists require specific microhabitats within the forest. Thus, within any given forest or any other habitat, generalist species are more abundant than specialists.

An attempt has been made to take all of the above factors into account when assigning a status designation to a species. When one or more factors affect abundance, this is usually stated under both limiting factors and status.

A reasonable estimate of abundance is whether the existing habitat is being used to its carrying capacity. A species could be considered common to abundant if all suitable habitat was defended in nesting territories. Although there are some obvious microhabitat preferences, Savannah, Grasshopper, and Henslow's sparrows occupy similar habitats, and may nest together in the same field. Based on their occupancy or use of available habitat within their normal geographic range, they would be classified as abundant, uncommon, and rare, respectively.

With all of the caveats mentioned above, I have used a combination of 2 techniques to define breeding abundance when actual numbers cannot be estimated: (1) amount of available habitat used, and (2) numbers of birds that could be observed in a single day.

The usage of available habitat is difficult to determine for many species because information on their requirements is deficient. For those species for which an appropriate judgment could be made, I used the following definitions:

Abundant — Essentially all suitable habitat is incorporated into a breeding territory or home range. It is certain that the species will be observed in suitable habitat.

Common — Almost all suitable habitat is incorporated into a breeding territory or home range. It is highly probable that the species will be observed in suitable habitat.

Uncommon — Less than 50% of suitable habitat is occupied. It is unlikely that the species will occur in any given area, but it can usually be found by searching several areas of suitable habitat.

Rare — Less than 10% of suitable habitat is occupied. It is highly unlikely that the species will occur in any given area. It is present in isolated portions over a wide geographic range of suitable habitat.

The numerical rating is identical to that used by James (1991). These definitions are based on the number of birds that could be observed during the breeding season away from the periphery of the normal range. The definitions assume that the observer is looking in appropriate habitat and concentrating on that species only.

The following 2 examples indicate how designations of abundance have been tempered. The Savannah Sparrow is considered abundant. In a long day, starting slightly before dawn and ending at nightfall, one could probably find 500 individuals of this species. Admittedly, it would not be easy and the observer might not achieve this, depending on the distance between suitable habitats and the amount of time consumed by walking. On the other hand, if one visited a single suitable habitat patch 500-1,000 ha in area, 500 birds could easily be recorded. The important factors are that whenever suitable habitat is visited, Savannah Sparrows will be present, and that suitable habitat is abundant.

The Lesser Yellowlegs was formerly considered common (James 1991; Sandilands 2010), which means numerically that one should have been able to see between 25 and 500 birds in a day. This species nests in the Hudson Bay Lowland and the northern Boreal Forest Region. The area is fairly inaccessible, but it is likely that 25 could have been observed with the aid of a helicopter. The fact that this species was a widespread breeder in the available habitat lends credence to the fact that it was common. Wherever one sets down in a helicopter in suitable habitat, there was a moderate probability of observing a Lesser Yellowlegs. Since then, this species has declined significantly and is no longer a common breeder.

Following are the numerical definitions of abundance:

Abundant — More than 500 can be seen in 1 day.

Common — Can always be found (well distributed). More than 25 a day is usual, but seldom more than 500.

Uncommon — Can usually be found but numbers seen are likely to be small (6-25 a day).

Rare Usually seen singly (seldom more than 5) and difficult to find on any particular outing (unless a specific location is known).

James (1991) presented definitions of frequency based on the rate of annual occurrence. Frequency generally has not been a concern, because I have focused on those species that are of regular or occasional occurrence in the province. Regular species are usually present every year, while occasional species occur most years and at least once a decade.

Vagrant species have been ignored in this work, except for species that have been documented breeding in the province. From a breeding perspective, the Black-necked Stilt could be considered a vagrant, yet it was included in Volume 2 because breeding has been confirmed. Similarly, I prepared an account in this volume for the Blue Grosbeak because 1 pair with a fledgling was observed, the only breeding record for the province.

Postfledging Period

The postfledging period begins when young leave the nest and lasts until autumn migration takes place. This is a critical period for birds. Young just out of the nest may be subject to high rates of mortality and this is an important time for building up fat reserves prior to migration. Adults may undergo a moult at this time with some species becoming flightless.

Although this is a critical period, limited information is available for the postfledging period. For some species, there is essentially no information. This topic was not dealt with in any detail in the volumes on nonpasserine birds. More research is being done during this period now due to the development of miniature radiotags.

A good understanding of a species' habitat and diet requirements during the postfledging period is essential. Some species may move to a different habitat type after the young leave the nest. A forest that appears to be ideal breeding habitat may be unoccupied if there is no suitable postfledging habitat nearby.

Movement patterns during the postfledging period vary considerably among species. For some species, the fledglings and adults may remain in or near the breeding territory until autumn migration, some remain near the territory until the young are independent and then move to nearby but different habitat, and others may disperse long distances prior to migration.

Topics that may be included in this section are habitat requirements of dependent and independent juveniles and the adults, movement patterns, foraging behaviour and diet, flocking behaviour, and associations with other species. Some species are highly gregarious and gather in large conspecific or multispecies roosts. In these cases, details are provided on the roosting habitat, site fidelity to roosts, and movement patterns among foraging areas and roosts.

Migration

In addition to habitat requirements, limiting factors, and status, migration timing is discussed for spring and autumn. For some species, general information on routes is provided, but only if there is something relevant to Ontario.

Approximate dates of migration are given for each species. Dates are provided for different areas of the province when they are available.

For most species, the discussion of habitat requirements during migration is brief. Many species do not have very specific needs during migration. Others are limited by their microhabitat requirements. In these instances, more detailed discussion is presented.

No limiting factors are apparent for some species during migration. For others, degradation and loss of habitat, diet, territoriality, collisions with human-made structures, climate change effects, and other factors may be discussed.

For status, the numerical definitions of abundance presented in the section on breeding season are used. In some cases, the number of birds observed during the peak of migration at different locations is provided. This information is usually generalized without giving exact numbers by site because these are likely to change with time.

Some species are year-round residents in the province. A few of these exhibit some southward movement in autumn and others disperse from breeding grounds to intermediate habitat prior to going to wintering areas. For resident species that do not remain within the home range all year, habitat requirements and limiting factors are discussed under the heading of autumn. Spring is not treated as a season for these species; most move directly from wintering areas to breeding habitat. The 2 crossbill species may nest almost any time in the province and make extensive movements between breeding areas. These movements are discussed under the heading of nonbreeding season.

Winter

The winter portion of the account for most species is brief. For a few species, the winter season is significant, with very particular habitat preferences. Limiting factors may include habitat availability, snow depth and other weather variables, and food. Winter status is defined numerically.

Mapping

A map is included for all species. For the breeding season, the normal breeding range is shown and extralimital or marginal breeding areas may be indicated. Normal wintering areas and extralimital or marginal wintering areas are depicted.

Extralimital habitat includes areas that are outside the species' normal range, where the species may not occur again or occurs infrequently. Some species establish small populations and these may be considered extralimital if they continue to be isolated from the main population.

Marginal habitat consists of part of the range that is regularly inhabited but at lower than normal density because habitat conditions are less than ideal. For instance, many open-country species nest sparingly in densely forested regions even though these areas may well be within the species' range. I have tried not to confuse low abundance of a species in an area and marginal habitat, but may not have succeeded in some cases. Marginal habitat is habitat that is less than ideal for a species; low abundance of a species may potentially occur in good as well as marginal habitat.

The range maps are general. A species may be locally absent in some areas where the range map indicates that it is present, and isolated records of a species may occur outside the indicated range. Distribution during the breeding season is fairly well known for most species. The winter range is not well defined for many species, including some very common birds. Christmas Bird Counts are typically completed before winter arrives and Project FeederWatch is the only program

that monitors birds over the winter. The northern extent of the winter range of many species has not been determined adequately.

FOREST-INTERIOR BREEDING BIRDS

I have learned much during the compilation of 312 species accounts. Possibly the most important fact is that the existence of obligate forest-interior birds appears to be a myth. I did not find a single forest-breeding species that always avoids edge. A possible exception is the Acadian Flycatcher, but there are few studies that explicitly examine where it nests in relation to forest edge.

The concept of forest-interior species was first introduced in 1981 (Whitcomb et al. 1981) based on point count results with no attempt to determine nest and territory locations relative to edge. Forest breeding birds were put into 1 of 4 categories based upon where they putatively nested in the forest (edge, interior-edge generalists, forest-interior specialists, and field-edge species). This classification system was widely adopted and is still used by some researchers.

After the original concept of forest-interior breeding birds was introduced, much research was undertaken to refine this information. Numerous field studies were undertaken to ascertain where species nested in relation to forest edge. This resulted in some species being moved into different categories, but some of the research appeared to confirm edge avoidance by some species. Much of this research used point counts or transects to detect where bird species occurred within the forest.

Villard (1998) was the first to question the concept of forest-interior birds. Further research has confirmed that individual species identified as forest-interior do not always avoid edge. One of the issues with the earlier fieldwork was that it was completed very early in the morning when birds are actively singing and defending their territories. At this time, birds with a territory bordering on edge sing away from the edge because the interior is the only location where they may have potential competitors. More recent studies using radiotracking techniques indicate that these same birds spend most of the remainder of the day near forest edge because food is usually more abundant there.

From the extensive information I reviewed, it is apparent that forest-breeding birds use 3 criteria to select where they nest in relation to edge. They select areas with the best habitat, the most abundant food supply, and where predators are least abundant. As an example, the Ovenbird is considered a forest-interior species by many authors (Burke and Nol 1998, 2000; Freemark and Collins 1992; Hann 1937), but in 1 Pennsylvania forest it completely avoided forest interior and could not be coaxed into the interior with broadcasts of its song. This was because of a high density of chipmunks in the forest interior, one of the main Ovenbird nest predators (Emmering et al. 2018). Another example is the Winter Wren which appears to prefer forest interior south of the Canadian Shield in Ontario, but commonly nests along edges of rivers, lakes, and wetlands in the Shield. The reason for this is that it prefers to nest where there are large logs and other downed timber, a resource that is most common in forest interior south of the Shield and common on edges in the Shield.

The term "forest-interior breeding bird" cannot be accurately applied to any Ontario bird species.

AREA-SENSITIVE BREEDING BIRDS

In most species accounts, I have discussed whether the species is area sensitive. I have considered area-sensitive species to be those species that require a habitat patch to be much larger than its territory size before inhabiting it. There are numerous examples of species with territory sizes of 1 ha or less that require habitat patches of 20 ha or larger. Birds inhabiting forests, grasslands, and marshes may be area sensitive.

Some authors consider species to be area sensitive if their density increases with increasing patch size. I have included these results in the species accounts, but do not consider this a true indication of area sensitivity. Many of these species inhabit patches that are not much larger than their territory size.

Area sensitivity is complex and results from 1 area are not directly applicable to other areas. The amount of habitat that a given species requires depends on factors such as how common the species is in the general area, whether it is in the core or periphery of its range, and the amount of suitable habitat in the landscape. Where a species is rare or at the periphery of its range, it tends to inhabit the best and largest examples of its preferred habitat. It is unlikely to inhabit smaller patches even if the habitat is ideal. Where suitable habitat is rare or patchily distributed, a species may require large habitat patches. The same species may not exhibit any area sensitivity where its habitat is abundant. In Ontario, some birds may require forests a minimum of about 100 ha in Essex County where there is only 3% forest cover, may only need about 20 ha in Waterloo Region where there is 15% forest cover, and are unlikely to be area sensitive at all along the Niagara Escarpment where there is 80% forest cover.

The reason for area sensitivity in breeding birds may be related to the mating system. Many species engage in extra-pair copulations to enhance the genetic viability of the brood and to ensure fertility. Extra-pair copulations are best facilitated when a habitat patch is large enough to support several pairs of the species, especially in fragmented landscapes. In landscapes where the preferred habitat is common and patches are close together, birds may move among patches to seek extra-pair copulations and the nest patch does not have to be larger than a single territory.

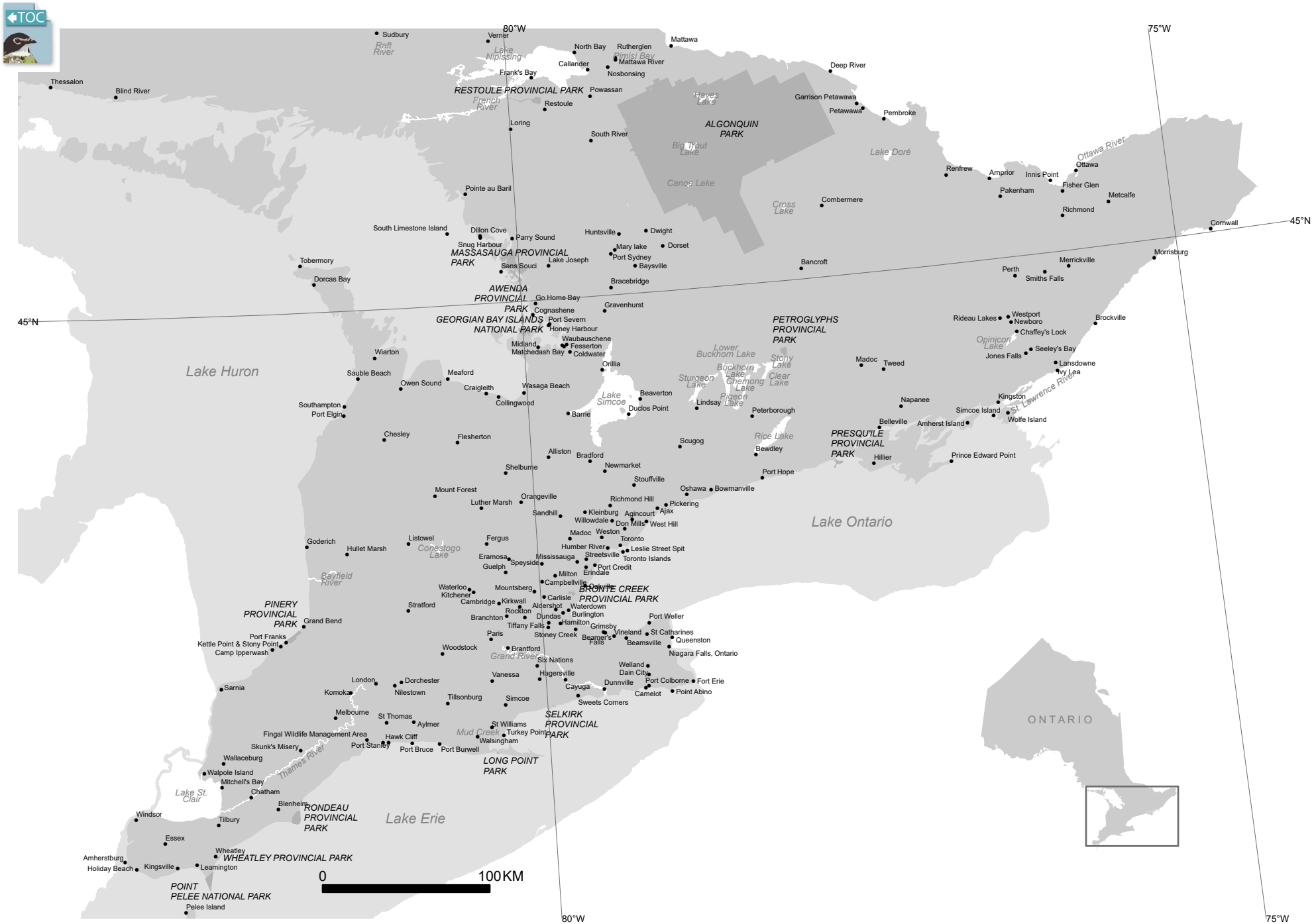


Figure 1 Counties, regional municipalities, districts, urban centres, provincial and national parks, and other localities in southern Ontario

Figure 2 Districts, urban centres, provincial parks, and other localities in northern Ontario.

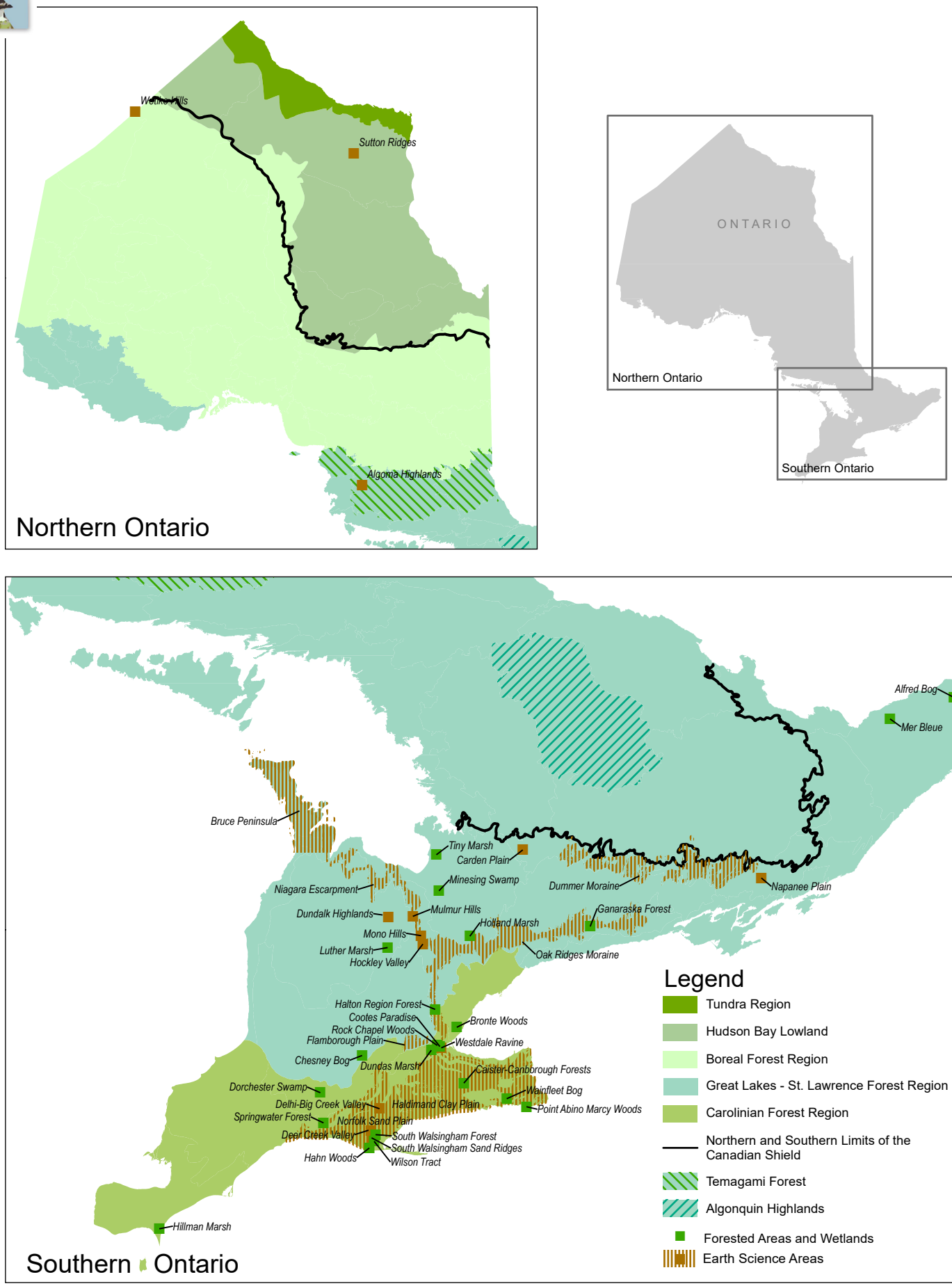
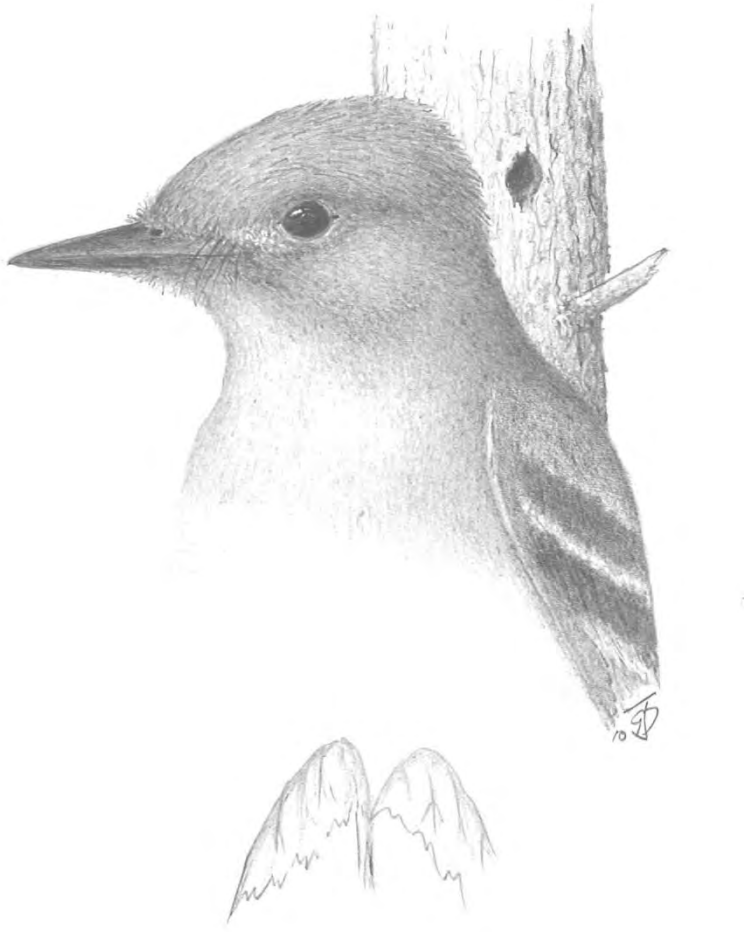


Figure 3 Physiographic and forest regions, and selected forest sections and physiographic features of Ontario.

Great Crested Flycatcher

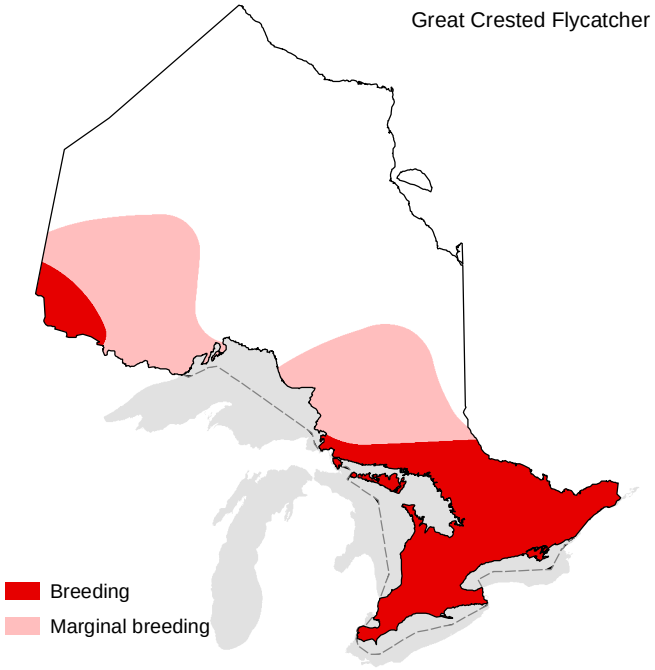
Myiarchus crinitus



BREEDING SEASON

Habitat Requirements

In Ontario, the Great Crested Flycatcher breeds in upland and lowland mixed (13.2% of nests), deciduous (8.6%), and coniferous (1.1%) forests and in unspecified woodlands (13.8%); in agricultural fields and pastures (23.0%); in orchards (6.3%); in beaver ponds, marshes, and bogs with scattered trees (17.8%); in gardens, near cottages, and on golf courses and cemeteries (8.0%); in fencerows and along roads (6.9%); and on sand dunes (1.1%). It prefers dry habitats, but will nest in wetlands with dead trees that provide suitable nest sites (Peck and James 1987). Near Parry Sound, it was absent in pure jack pine forests, but present in semi-open jack pine associated with trembling aspen, white birch, sugar maple, and white pine (James 1979a). In Durham Region, it occurred on 9 of 11 plots surveyed. Highest densities were in a mature beech–sugar maple forest and a mature white



cedar–elm swamp with numerous dead elms and openings (Speirs and Orenstein 1975). There is a record of it nesting in a Toronto backyard (Iron and Pittaway 2001).

In other areas, the Great Crested Flycatcher nests mostly at edges of deciduous and mixed woods; many authors state it prefers wet habitats to dry areas. Presence of suitable nesting sites is probably more important than moisture regime. It tends to favour second-growth woodlots and those that have been selectively cut, and avoids extremes of closed-canopy forests or open savannahs. Breeding has been documented in urban areas and orchards, although it is uncommon in these habitats. In the early 1900s, it was a common breeder in Illinois orchards, but virtually absent in this habitat by the mid-1960s. Most authors agree that it is associated with edge and semi-open canopies, and is much less frequent in forest interior. It appears to have benefitted from forest fragmentation. In Maryland and the mid-Atlantic states, degree of forest isolation was a significant predictor of its presence. It requires forests mature enough to have snags of suitable size (approximately 30 cm diameter at breast height [DBH]) for providing a nesting cavity. In fragmented aspen forests in North Dakota, its abundance was negatively correlated with the number of trees 15-23 cm DBH. In the Appalachians, it was less likely to occur in old-growth forest than in the landscape as a whole. In Kansas, all territories contained woodland edges and fields with scattered groves of trees, but most activity was confined to woodlands. In New Jersey, there was no significant difference in its abundance in oak-pine forests and hardwood swamps (Back 1979; Bent 1942; Blake and Karr 1987; Capen 1979; Evans and Conner 1979; Faanes and Andrew 1983; Fitch 1958; Graber et al. 1974; Haney 1999; Kirk et al. 1996; Lynch 1987; Miller and Lanyon 2020; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991; Noon et al. 1979; Rail in Gauthier and Aubry 1996; Rich et al. 1994; Robbins 1979; Robbins et al. 1989; Samson 1979; Temple et al. 1979).

In southern Ontario, the probability of detection of the Great Crested Flycatcher was negatively correlated with the amount of forest cover 100 m or more from edge, woodlot size, the amount of forest cover within 2 km, and the amount of regional forest cover. All but the latter relationship were significant, although correlations with amount of core forest habitat and amount of forest within 2 km were significant only at the 0.10 level (Austen et al. 2001). Based on these results and the fact that it regularly occurs in small forest fragments, it can be concluded that the Great Crested Flycatcher is not area sensitive in Ontario. Forest size was a significant predictor of abundance in the mid-Atlantic states. Robbins et al. (1989) concluded that it required forests at least 10 ha in area, it occurred in forests as small as 0.8 ha. In Pennsylvania, there was no significant relationship between

its abundance and forest size or degree of habitat fragmentation in the landscape (Keller and Yahner 2007).

At the landscape level, the Great Crested Flycatcher preferred areas that were 59-75% forested in North Dakota and 82-100% forested in New York. There were no areas in North Dakota that had more than 75% forest cover (Cunningham and Johnson 2019). Brennan and Schell (2007) used Breeding Bird Survey (BBS) data from south-central states to determine its landscape-level preferences. It was most abundant in undisturbed areas with a high ratio of edge to interior. Population numbers were higher in densely wooded areas and lower in more sparsely wooded locations.

In a Connecticut woodlot over a 59-year period, there was a progressive shift to larger trees, a sparser shrub layer, and a less diverse tree canopy dominated more by oaks and maples, with a severe decline in the amount of hemlock. There was no significant change in the abundance of the Great Crested Flycatcher (Buchanan et al. 2016). In Pennsylvania, Rohnke and Yahner (2008) conducted bird surveys in a woodland 16 years apart. During this time, the density of tall shrubs increased, but density of short shrubs and overstorey and subcanopy trees declined. The Great Crested Flycatcher decreased by 56% as a result of these habitat changes.

Ontario nests were in dead or living deciduous or coniferous trees, snags, and stumps; in bird boxes, barrels, and gourds; and in fence posts, rails, and utility poles. Over 87% of nests in trees were in deciduous species, and 61.8% of tree nests were in dead or partially dead trees. DBH of 1 nest tree was 20 cm. Nests were in both natural cavities and abandoned woodpecker nests. Nests were 0.6-18.3 m from ground, with most 1.5-4.6 m up (Peck and James 1987). Fairfield and Fairfield (2004) reported a Toronto nest in a nest box.

Elsewhere, the Great Crested Flycatcher appears to prefer natural cavities to old woodpecker nests in deciduous trees, but readily uses cavities excavated by the Red-headed Woodpecker, Red-bellied Woodpecker, Northern Flicker, and Pileated Woodpecker, particularly in conifers. It prefers dead to living trees and deciduous trees to conifers. Nests have been reported in oaks, willows, cottonwood, black locust, ashes, maples, birches, pines, beech, white cedar, tulip tree, pear, elms, apple, sycamore, common hackberry, and red cedar. Nest boxes of a variety of sizes are used, from screech-owl boxes and Purple Martin houses to those of bluebird size, with 5 cm the optimum cavity entrance diameter. Hanging or swinging nest boxes are preferred to fixed boxes. Other nest sites include hollow posts, old wooden pumps, stove pipes, and old tin cans and boxes. Nest heights of 0.6-23 m have been reported, with most 3-7 m up (Bancroft 1984, 1986a; Bent 1942; Engels 1949; Evans and Conner 1979; Gillespie 1924; Graber et al. 1974; Iron and Pittaway 2001; Miller and Lanyon 2020; Mousley 1934a; Rail in Gauthier and Aubry 1996; Stauffer and Best 1982; Taylor and Kerschner 1991; Twedt and Henne-Kerr 2001). In Florida pine habitats, nest density increased where nest boxes were provided, and numbers peaked during the first year after boxes were introduced. Once boxes were installed, some birds moved from the control areas to the nest-box areas, and the overall population increased. Suitable nest sites appeared to be limiting (Miller 2010). Medlin and Risch (2006) used artificial nests and added snake skins to some nests, and to the outside of some nest boxes as well as in those nests. Twenty percent of the control nest boxes were depredated whereas

no nests with snake skins were depredated. Snake skins appear to be effective in deterring mammals from preying on nests; this flycatcher frequently incorporates snake skins into its nest.

Territories are established shortly after arrival, and other Great Crested Flycatchers are vigorously excluded. Territories frequently overlap with those of Eastern Wood-Pewee, Acadian Flycatcher, Least Flycatcher, and Eastern Phoebe (Hespenheide 1971a; Johnston 1971; Peck and James 1987; Taylor and Kerschner 1991). The largest reported territory sizes were from the Kingston area. Until egg laying, 3 territories were 23.8, 38.5, and 15.9 ha. After egg laying, these pairs had territories of 24.6, 13.9, and 2.0 ha, respectively. The third pair made a second nesting attempt and had territory sizes of 9.6 and 3.1 ha before and after egg laying (MacDougall-Shackleton and Robertson 1995). In Quebec, Rail (in Gauthier and Aubry 1996) reported territory sizes of 0.2-3.2 ha, mostly 1.5-2.5 ha. Territories in sugar maple and hemlock stands averaged 1.2 and 1.9 ha, respectively. In 1 Illinois study area, territories were very closely spaced, with all available area claimed. Twenty-six territories were 0.24-1.86 ha (average 1.25 ha). Other territories were 0.6, 1.2, 4.5, and 5.7 ha (Graber et al. 1974). Other reported territory sizes are 1.6 and 3.2 ha in Maryland, and 2.9, 2.7, and 2.3 ha in Kansas (Fitch 1958; Miller and Lanyon 2020). In North Carolina, Engels (1949) found 2 nests in dead trees on a sand dune. Adults of both pairs foraged in an adjacent woodland 153 and 250 m from their nests.

Natal site fidelity appears to be low, although there are few data. None of 61 nestlings returned in subsequent years. Adults exhibit high site fidelity. In Illinois, 9.5% of adults returned 4 years later, probably most surviving birds. One pair nested in the same cavity as 9 years previously. There are numerous records of the same birds using the same nesting area or nest site for 3-5 years, and occasionally as long as 8 or 9 years. The same cavity is usually used for replacement nests, but occasionally a new cavity is used (Bancroft 1984, 1986a; Bent 1942; Graber et al. 1974; Miller and Lanyon 2020; Peck and James 1987; Rail in Gauthier and Aubry 1996; Robinson 1992; Taylor and Kerschner 1991).

Limiting Factors

Eggs have been found in Ontario nests from the third week of May until mid-July, with most present from the second to fourth weeks of June (Peck and James 1987). In Algonquin Park, adults have been observed inspecting potential nest cavities 18-25 May and nests with young occur from 29 June to 7 July (Tozer 2012).The female builds the nest in 2-10 days. Two to 11 days (mean 4.8 days in Florida) may elapse between nest completion and laying of the first egg. These intervals are shorter further north. Eggs are laid at the rate of 1 a day. Incubation usually begins with the laying of the last egg or occasionally the penultimate egg, or on the afternoon before the last egg is laid. The incubation period of 11 Ontario nests was 12-15 days, with eggs in 8 nests hatching in 13 or 14 days. Overall, the incubation period has been reported as 12-15 days. Fledging usually occurs at age 13-15 days, with longer reported fledging periods of 18-25 days being incorrect. Young can fly short distances when they are 9 days old if they are disturbed (Bent 1942; Fairfield and Fairfield 2004; Gillespie 1924; MacDougall-Shackleton and Robertson 1995; Miller and Lanyon 2020; Peck and James 1987, 1997; Taylor and Kerschner 1991).

One brood is raised a season, but renesting is common if a clutch is lost. Second clutches may be initiated 1-7 days after the first is lost, and replacement clutches typically have 1 or 2 fewer eggs than the first. Clutches of 1-7 eggs have been reported in Ontario with most containing 5 or 6 eggs;

the number of clutches containing 5 or 6 eggs was equal. Clutches of 1, 2, 3, and 7 eggs were rare. Elsewhere, clutches of 3-8 eggs have been reported, with 5 eggs most common. Six-egg clutches are common; larger clutches are rare (Bent 1942; Graber et al. 1974; MacDougall-Shackleton and Robertson 1995; Miller and Lanyon 2020; Peck and James 1997; Taylor and Kerschner 1991).

The age at first breeding is 1 year, and the mating system is monogamous. Because of the strong homing tendency, the male and female may reform their pair bond in subsequent years. Some pairs were together at least 3 years. Different mates may also be selected (Bent 1942; Miller and Lanyon 2020; Taylor and Kerschner 1991).

The Great Crested Flycatcher is a canopy species, feeding mostly at heights of 15-21 m, except in edge situations where it may feed near the ground. In Illinois, 72% of foraging occurred in the lower canopy (11-15 m) and upper canopy (above 16 m). It forages mostly from dead perches in the canopy and the outer periphery of trees on edges. It forages significantly higher than the Eastern Wood-Pewee, Least Flycatcher, Acadian Flycatcher, and Eastern Phoebe. In Virginia, food items overlapped 28% with the Least Flycatcher and 25% with the Eastern Wood-Pewee, but the Great Crested Flycatcher selected significantly larger prey. It uses 3 main foraging techniques in equal frequency: sallying from a perch; hover gleaning from leaves, branches, and trunks; and dropping to the ground from a perch to capture prey. In Illinois, it changed foraging techniques depending upon whether it was in open-canopy forest (savannah) or closed-canopy forest. It flycatched significantly more in open habitat and sallied more often in closed-canopy forest. It hovered more frequently in closed-canopy forests and used gleaning and flushing as foraging techniques in open-canopy forest but not in closed-canopy forest (Bent 1942; Hartung and Brawn 2005; Johnston 1971; Miller and Lanyon 2020).

Young are fed mostly insects, including dragonflies, crickets, grasshoppers, spiders, beetles, katydids, stink bugs, flies, and adult and larval butterflies and moths. Fruit may also be brought to young including common elderberry, black cherry, raspberry, and white mulberry. A sample of 265 adult stomachs contained 93.7% animal matter and 6.3% plant material. Lepidopterans comprised 21.4% of the diet; 52 species of 12 families of beetles constituted 16.8%; grasshoppers, crickets, and katydids 15.6%; bugs 14.3%; bees and wasps 13.7%; dragonflies and other miscellaneous insects 4.1%; and spiders 4.0%. There were also traces of eggshells and lizard bones. Fruits eaten included those of mulberry, pokeweed, sassafras, spicebush, blackberry, raspberry, chokecherry, black cherry, Virginia creeper, wild grape, huckleberry, blueberry, and elderberry. Other adult foods include beetles (June, darkling, and lady beetles), cicadas, ants, mosquitoes, juneberries, damselflies, flies (blow, fruit, anthomyiid, and snipe flies), long-horned grasshoppers, and midges. On Pelee Island, 1 captured a Ruby-throated Hummingbird in mid-air and ate it. In Alabama, it fed on maggots in mammal road kills. Insects consumed are 3-40 mm in size, mostly those longer than 10 mm. It has also been documented consuming an Eastern Whip-poor-will egg (Bent 1942; Cink et al. 2020; Gillespie 1924; Graber et al. 1974; Hespenheide 1971b; Holt 1918; Johnston 1971; Miller and Lanyon 2020; Mousley 1934a; Nelson 1997; Sargent and Sargent 1996; Taylor and Kerschner 1991).

The Great Crested Flycatcher is an infrequent host of the Brown-headed Cowbird. Six of 227 Ontario nests (2.6%) were parasitized. Rare records of parasitism have been documented in Illinois,

New York, Massachusetts, Michigan, and Maryland. There is 1 record of a clutch containing a starling egg (Bent 1942; Graber et al. 1974; Miller and Lanyon 2020; Peck and James 1997).

Although the Great Crested Flycatcher initially benefitted from forest fragmentation, habitat loss and alteration may affect populations. Some remnant forests in southern Ontario are being completely removed resulting in direct habitat loss. Forestry practices that cull dead and dying trees and snags may reduce or eliminate nest sites. Total clear-cuts eliminate habitat, but clear-cuts that retain snags and copses of trees may enhance habitat. Aerial spraying of pesticides may be detrimental directly or indirectly through loss of prey (Miller and Lanyon 2020; Stribling et al. 1990). In the Carolinian Forest Region of Ontario, it was more abundant in heavy, diameter-limit cuts than in forests with no recent history of harvesting (Holmes et al. 2004). In Illinois, Robinson and Robinson (1999) clear-cut openings of 0.02-0.4 ha in contiguous forest. There was no difference in its abundance in uncut and cut forest.

Abundance of the Great Crested Flycatcher appears to be unaffected by urban and suburban development. It inhabits a variety of anthropogenic habitats including old orchards, wooded pastures, parks, and other urban areas with numerous large shade trees (Miller and Lanyon 2020). It is absent in recent developments where there are no mature trees. In urban woodlots in Chicago, it decreased as the proportion of buckthorn trees in plots increased (Schneider and Miller 2014).

The Great Crested Flycatcher is positively associated with roadsides and is vulnerable to collisions with vehicles (Miller and Lanyon 2020).

In New Jersey and Pennsylvania over a 15-year period, hemlock declined from representing 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The Great Crested Flycatcher responded positively to hemlock decline and increased (Toenies et al. 2018).

The Great Crested Flycatcher competes for nest sites with many other cavity-nesting species. These include the Red-headed Woodpecker, Red-bellied Woodpecker, Tree Swallow, Northern House Wren, Eastern Bluebird, European Starling, and red squirrel. In Iowa, this flycatcher chose nest sites similar to the 2 woodpecker species and starling, but nested more in dead limbs of live trees than the other species. In the mid-19th century, it commonly nested in crevices around dwellings and outbuildings, but was ousted from these habitats by the starling and House Sparrow. Woodpeckers and the starling are dominant to the Great Crested Flycatcher, but it may dominate the Tree Swallow (Bent 1942; Graber et al. 1974; Miller and Lanyon 2020; Rendell and Robertson 1991; Stauffer and Best 1982). Breeding success in nest boxes is highest in new boxes and declines with time; predators learn to exploit nest boxes (Miller 2002).

In North Carolina pine-oak forests, the Great Crested Flycatcher exhibited no response to fire (Rose and Simons 2016).

DesGranges and Morneau (2010) considered the Great Crested Flycatcher sensitive to climate change in Quebec. Its distribution was correlated predominantly with the mean annual number of degree-days 10°C or more in May, June, and July.

Status

The Great Crested Flycatcher is probably more common in Ontario now than in presettlement days. It was apparently absent in the Kingston area in the 1850s, but was the fourth-most abundant flycatcher during the first atlas. It was more frequent on the Canadian Shield where snags are more abundant (Weir 2008). McIlwraith (1894) considered it a regular breeder in the south and Baillie and Harrington (1937) considered it common north to southern Algoma District and Lake Nipissing. The first atlas confirmed that it nested throughout southern Ontario and the Shield portion of the Great Lakes–St. Lawrence Forest Region. It was almost entirely absent in the Boreal Forest Region except for isolated records in the extreme south of this forest community. It was most abundant along the southern edge of the Shield (Bennett in Cadman et al. 1987). James (1991) considered it a common breeder in the south and uncommon to locally rare north to Red Lake and Timmins.

The second atlas indicated that the range of the Great Crested Flycatcher had remained the same since the first atlas. Its probability of observation declined significantly between atlases. Significant declines occurred in the Great Lakes–St. Lawrence Forest Region both south of and in the Shield. South of the Shield, it was seen in almost every square. Most of the decline occurred in the Algonquin Highland, possibly a result of forest maturation. It was most abundant in a broad band along the southern edge of the Shield. It was less abundant in the more northerly, heavily forested portions of the Shield and the intense agricultural areas in the extreme southwest (McLaren in Cadman et al. 2007).

Long-term (1970-2021) population trends determined by the BBS indicate annual declines of 0.753% in Canada and 0.567% in Ontario. The short-term (2011-2021) trends were annual increases of 0.309% in Canada and 0.459% in Ontario. All estimates were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

After fledging, the family remains together near the nest site for about 3 weeks (Miller and Lanyon 2020).

Akresh et al. (2009) netted birds during the postbreeding season in Michigan upland and riparian forests. Only 2 juveniles were captured, both in riparian habitat. Upland and riparian forests had a similar canopy composition, but riparian forests had a much denser shrub and sapling layer than upland forests.

MIGRATION

Migration is partially nocturnal, but may also occur during day, and the Great Crested Flycatcher travels singly during migration (Miller and Lanyon 2020). It arrives in Ontario in early May, or occasionally late April, with individuals continuing to arrive throughout May, peaking around mid-May. Males arrive on territories 7-12 days before females. Most birds have left the province by mid-September, but typically a few are present until the end of the month. Occasionally, stragglers occur until late October (James 1991; Miller and Lanyon 2020).

While migrating, the Great Crested Flycatcher uses a broader range of wooded habitats than during the breeding season, including shrubby clearings and second growth (Graber et al. 1974; Miller and Lanyon 2020). During spring migration in Wisconsin and Minnesota, it was significantly more abundant in mature floodplain forests than in mature upland forests (Kirsch et al. 2013).

The Great Crested Flycatcher frequently collides with television towers in Florida and probably elsewhere, and may be vulnerable to striking any tall structure during migration (Miller and Lanyon 2020).

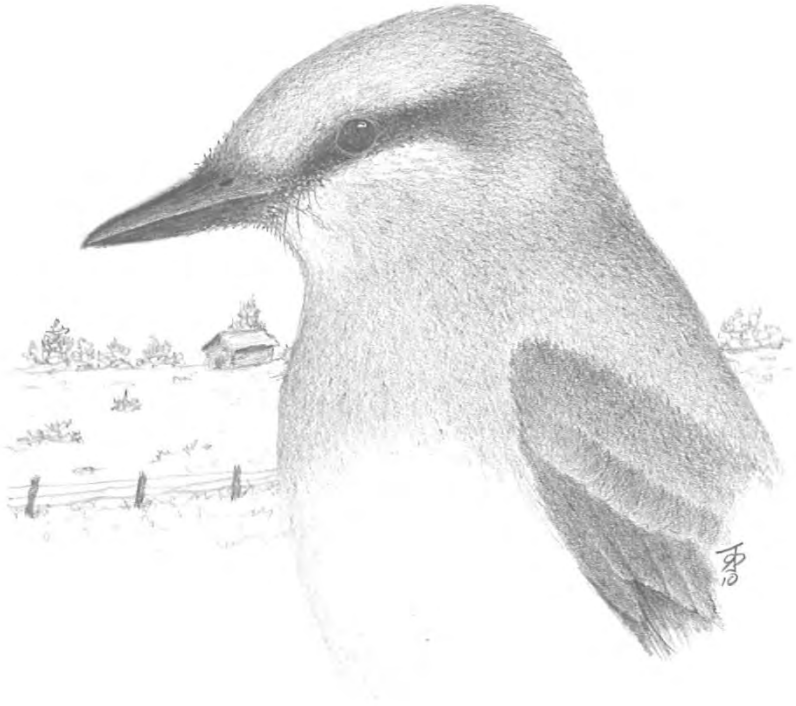
In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and the length of the breeding season for 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming occurred during the second period. The spring arrival date of the Great Crested Flycatcher was significantly earlier during the second period but there were no significant differences in its autumn departure dates or length of the breeding season.

The Great Crested Flycatcher is a common migrant that occasionally wanders as far north as Moosonee (James 1991).

At Long Point Bird Observatory, the Great Crested Flycatcher decreased during the late 1960s and early 1970s, increased in the early to mid-1980s, decreased in the late l980s, and increased in the 1990s, with no significant overall trend (Badzinski 2000; Hussell et al. 1992).

Western Kingbird

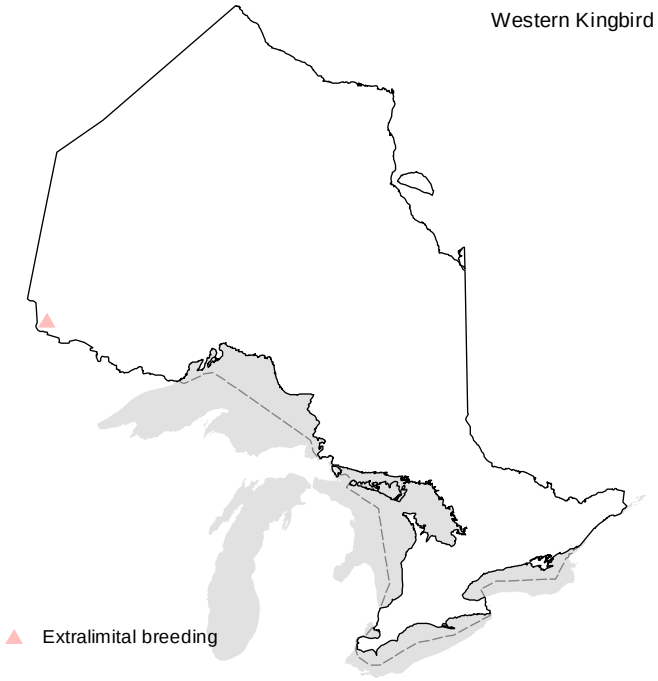
Tyrannus verticalis



BREEDING SEASON

Habitat Requirements

The Western Kingbird nests in open, grassy habitats with scattered trees, hydro poles, or fence posts. Where trees are scarce, it frequently associates with humans, nesting around farmsteads, dwellings, and in shade trees in villages and towns. One Ontario nest was in a farmyard near buildings and another was in a residential area of a small town. In natural habitats, it prefers grassy areas with scattered trees or groves of trees. In Nebraska, it selected sites with fewer but larger trees, resulting in an open canopy with taller ground cover and more shrubs. In addition to savannah-like habitats, it nests in grasslands, deserts, pastures, open riparian strips and patches, shelterbelts around farms, and urban areas. Frequently used habitats in British Columbia include cultivated farmland, orchards, vineyards, and rural and suburban areas. It was extremely adaptable



there, with breeding occurring in 40 habitat types. Over half of nests were associated with roadsides, gardens, and open hillsides. In Texas, it frequently nested at power substations where there were open expanses of grass for foraging and human-made structures for nest sites. Where it overlaps with the Eastern Kingbird, the Western Kingbird selects drier, more open areas with taller trees (Bent 1942; Bergin 1992a; Blancher and Robertson 1984a, 1987; Campbell et al. 1997; Gamble and Bergin 2020; Honig 1992; MacKenzie and Sealy 1981; Peck and James 1997; Rumble and Gobeille 1998; Semenchuk 1992; Smith 1996). In California, the Western Kingbird was significantly more abundant in oak savannahs with grass cover than in oak savannahs with shrub cover, montane hardwoods, and oak woodlands (Wood et al. 2013).

Brennan and Schnell (2007) used Breeding Bird Survey (BBS) data from south-central states to analyze landscape-level habitat requirements of the Western Kingbird. It was strongly associated with edge and was more abundant in areas that were predominantly open. Trees, shrubs, or tall human-made structures are an essential component of its habitat, even though areas that are selected are predominantly open in nature. It is frequently found where 2 or more habitats converge. Human presence is important in many open habitats where shade trees and other structures (power lines and poles) provide perches and potential nest sites (Gamble and Bergin 2020).

The first 3 nests documented in the province were in trees. Nest heights were 3, 6, and 10 m and they were in willow, Manitoba maple, and bur oak. Two were in large forks near the trunk and the other was on a lateral branch (Carpentier 1989; Peck and James 1997). A nest in Rainy River District in 2001 was on a radio tower (Carpentier in Cadman et al. 2007).

Throughout its range, the Western Kingbird prefers to nest in trees. In Manitoba, it preferred green ash and peach-leaved willow for nesting, but selected only the largest trees. Trees with a diameter at breast height (DBH) greater than 30 cm represented 4.6% of available trees but supported 82% of nests. Nests were in taller trees with a larger DBH and higher up than Eastern Kingbird nests. In British Columbia, a wide variety of dead and living coniferous and deciduous trees and shrubs was used for nesting, but 84% of nests were on power poles. Additional trees species it has nested in include elms, sycamore, oaks, hackberry, cottonwood, junipers, apple, locusts, aspens, alders, and rarely pine. It typically nests in the top third of trees, well within the canopy, and usually on a horizontal branch, although nests may be in crotches of upwards-slanting branches. Because trees larger than average are selected, many nest trees are used more than once. Nests from the

previous breeding season may be reused, and it has also used old Northern Flicker, American Robin, and oriole nests. Heights of nests from ground range from 0 to 45 m, with most 3.8-17 m up. Nests are frequently on human-made structures, particularly power poles, fence posts, and buildings. It has nested in a lampshade suspended from a ceiling in an abandoned house, on windmills, in an old woodpecker cavity, on metal girders, in open wooden boxes, on rocky cliffs, on top of hollow stumps, in eavestroughs of houses, on a ledge over a kitchen door that had considerable human use, and on bridges (Bent 1942; Bergin 1992a, 1992b, 1997; Blancher and Robertson 1984a; Campbell et al. 1997; Gamble and Bergin 2020; Honig 1992; Koonz 1982; MacKenzie and Sealy 1981; Ohlendorf 1974; Pinkowski 1982; Whedon 1938).

Shortly after arrival, the male defends a loosely defined territory. After pairing, both sexes defend the territory, but territory size and amount of patrolling decrease after pairing. By mid-incubation, only the nest tree and nest are defended, but this is done very aggressively. Even early in the breeding season, feeding areas are not defended. Some authors state that it is aggressive toward Eastern Kingbirds, but they were tolerated in a Manitoba study area. No information on territory or home range size is available. Occasionally, 2 or 3 pairs nest together with nests separated by as little as 12 m. Rarely, there may be 2 or more nests in a single tree (Bent 1942; Bergin 1992a; Gamble and Bergin 2020; Honig 1992; MacKenzie and Sealy 1981; Ohlendorf 1974).

No information on natal philopatry is available. Some successful breeders have been documented returning in subsequent years, but there are few data. In Oklahoma, geolocators were attached to 40 adults, and 25 of these were recovered the next year for a return rate of 62.5% (Bergin 1997; Gamble and Bergin 2020; Jahn et al. 2013).

Limiting Factors

Clutches have been found in Ontario nests in the first 2 weeks of June (Carpentier 1989; Peck and James 1997). Western Kingbird clutches could conceivably be present in Ontario from mid-May until late July, but most likely throughout June (Peck and James 1987). In Manitoba, the nesting chronology of the Western and Eastern kingbirds highly overlapped, with the Western Kingbird establishing territories slightly earlier (MacKenzie and Sealy 1981). Nest construction takes 4-8 days, and 4 or 5 days may elapse after nest completion before the first egg is laid. Eggs are laid at the rate of 1 a day. Incubation takes 12-20 days; incubation is initiated after the last egg is laid. In the southern portion of the range, the average incubation period was 14 days, but all British Columbia clutches had incubation periods of 18-20 days. Eggs hatch over a 2-day period and nest departure may be spread over several days. Fledging occurs at age 13-19 days, averaging 16 days in the south, but 16-19 days in British Columbia (Bent 1942; Blancher and Robertson 1987; Campbell et al. 1997; Gamble and Bergin 2020).

Usually 1 brood is raised in a season, but double brooding has been confirmed in Arizona, Mexico, and California; there is evidence to suggest that it occurs in British Columbia. Clutches of 2-7 eggs have been reported, normally 3-5 eggs, with 4 eggs most frequent. Clutch size declines with advancement of the breeding season and decreasing insect abundance. Some of the smallest clutches were laid in old oriole nests or other sites where there was not enough room for more eggs (Bent 1942; Bergin 1992b; Blancher and Robertson 1987; Campbell et al. 1997; Gamble and Bergin 2020).

The mating system is monogamous and age at first breeding is 1 year. Breeding typically occurs every year thereafter, but in Arizona, some pairs built nests but did not lay eggs due to a scarcity of insects. Lack of food is unlikely a limiting factor in Ontario (Blancher and Robertson 1987; Gamble and Bergin 2020).

Most foraging is by sallying from an exposed perch after flying insects. The Western Kingbird may also fly down to pick prey from the ground and glean insects from vegetation. It has been observed feeding opportunistically on tiger beetles congregated around a pond, capturing them in flight or flushing them into the open to capture them. It occasionally feeds nocturnally under lights. In Arizona, it fed at heights of 0-50 m, but almost half of foraging flights were at or below 1.5 m. In Kansas, most foraging occurred at heights of 1-2.4 m. At 2 sites in Arizona, 83.6% and 59.2% of prey were captured in the air, 3.6% and 11.2% were gleaned from vegetation, and 12.7% and 25.9% were picked from the ground. In Kansas, prey was gleaned from vegetation more frequently than from the air or ground (Blancher and Robertson 1984a, 1987; Gamble and Bergin 2020; Honig 1992; Schulz 1993).

Nestlings are fed crickets, dragonflies, butterflies, short-horned grasshoppers, bees, wasps, beetles, flying ants, spiders, robber flies and other flies, and bugs. An analysis of nestlings' feces revealed that they had consumed 48.2% grasshoppers and crickets, 18.5% flies, 12.5% beetles, and 11.3% bees, wasps, and ants. In Arizona, the average length of prey consumed by adults was 8-10 mm; the diet consists of 90-99% insects. In Manitoba, it ate mostly midges. Bees, wasps, ants, beetles, grasshoppers and crickets, bugs, flies, and spiders are important in the diet. Other animal foods include millipedes, cicadas, caterpillars, moths, dragonflies, and treefrogs. It occasionally eats fruits of elderberries, hawthorns, and mulberries. In California, the most important items in the diet were bees and wasps (31.4%), grasshoppers and crickets (27.8%), and beetles (17.0%). Forty-eight adults from Texas had consumed 35.7% grasshoppers and crickets, 26.7% beetles, 16.9% bees, wasps, and ants, and 10.0% bugs. At 2 sites in Kansas, beetles (29.5% and 88.2%), hymenopterans (45.9% and 2.9%), and grasshoppers and crickets (8.2% and 3.9%) were most important in the diet (Beal and McAtee 1912; Bent 1942; Blancher and Robertson 1984a; Gamble and Bergin 2020; MacKenzie and Sealy 1981; Ohlendorf 1974). In Texas, a pair feeding near a honey bee colony consumed 149 drone bees and 0 worker bees. They were capable of distinguishing them in flight. Worker bees are distasteful and have stingers; drone bees are palatable and lack stingers (Schmidt and Klotz 2023).

No parasitism of Western Kingbird nests by the Brown-headed Cowbird has been documented in Ontario. Parasitism of this kingbird is rare and it is a known cowbird egg and nestling ejector. Kingbirds defend their nests vigorously against cowbirds (Gamble and Bergin 2020).

DDE was evident in samples collected from eggs, nestlings, and adults in Texas. Despite high concentrations of DDE in eggs, there was no effect upon eggshell thickness or nesting success (Gamble and Bergin 2020).

Status

Four nests have been confirmed in Ontario, all in western Rainy River District. The first nest was found on 9 June 1987, with 1 nest each in 1988, 1989, and 2001. A nest was reported from Kent County in 1943, but photographs and descriptions were inadequate to positively confirm it as a Western

Kingbird nest (Carpentier 1989; Carpentier in Cadman et al. 2007; Peck and James 1987, 1997). In Ontario, the Western Kingbird is a rare and irregular breeder in the Rainy River area. It is likely that it is absent as a breeding species most years, with maximum populations of 1 or 2 pairs annually (Carpentier in Cadman et al. 2007).

Overall, the Western Kingbird has increased significantly and greatly expanded its range. Range expansion was facilitated by tree planting and erection of human-made structures, particularly on the prairies where trees were rare or absent. In Saskatchewan, it usually arrived in a given location 20-30 years after shelterbelts were planted. It is a recent arrival in Manitoba, first occurring around the 1920s. In British Columbia, its range expanded when residential areas and orchards replaced natural open areas, and it also expanded along highway corridors and farm clearings. It has also increased in traditional breeding areas due to proliferation of human-made structures suitable for nesting and perching (Bent 1942; Campbell et al. 1997; Gamble and Bergin 2020; MacKenzie and Sealy 1981; Ohlendorf 1974; Smith 1996). BBS data for Canada indicate an annual increase of 0.113% 1970-2021 and a decrease of 3.07% 2011-21. All results were highly reliable. Due to its rarity in Ontario, there are no BBS data (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young are dependent on adults for 2 or 3 weeks after fledging (Gamble and Bergin 2020).

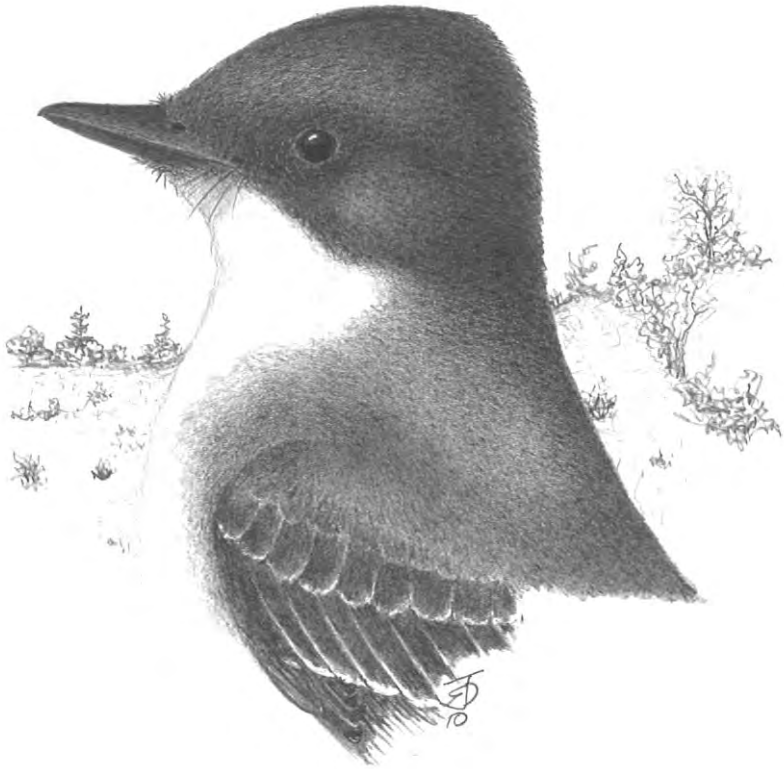
MIGRATION

The Western Kingbird is typically a diurnal migrant, but has also been observed migrating in late evening and early morning. It migrates singly or occasionally in small flocks, but flocks are more likely to occur in the southern states and further south (Gamble and Bergin 2020). Adults undertake a moult migration in the main portion of their range. Most adults leave the breeding grounds before moulting and fly to Mexico and the southeastern states for the moult. Moult migration of adults may begin in mid-July and continue until mid-October. Juveniles remain on the breeding grounds throughout the breeding season and moult after autumn migration (Barry et al. 2009; Gamble and Bergin 2020).

The Western Kingbird is an irregular, rare migrant in Ontario, more of a vagrant than a true migrant. It now occurs annually in the province and may become more regular as a migrant. In spring, males arrive before females. Normally, it appears late in May but occasionally in mid-May. Autumn migration begins in early August and continues until mid-September, with the peak in late August. It has been observed in the province as late as mid-November. During migration, it frequents habitats similar to those used during the breeding season (Gamble and Bergin 2020; James 1991).

Eastern Kingbird

Tyrannus tyrannus



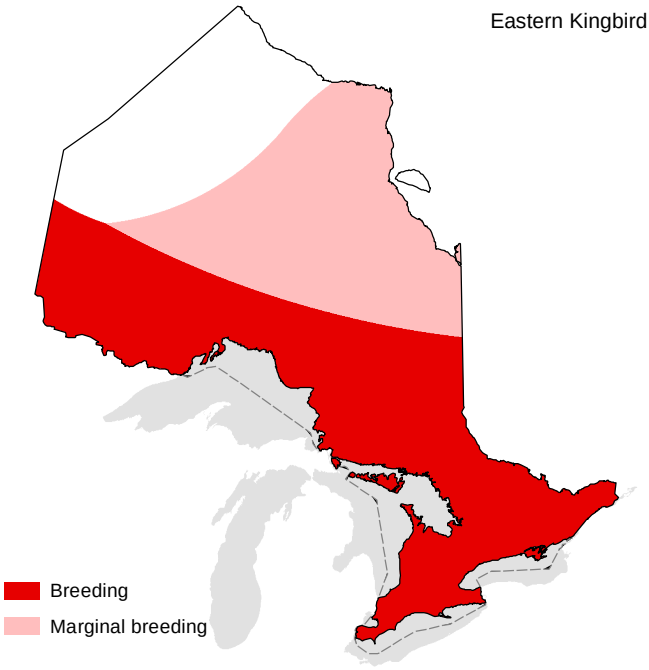
BREEDING SEASON

Habitat Requirements

The Eastern Kingbird nests in a variety of open habitats in Ontario. These include shrubby meadows and pastures, orchards, fencerows, and golf courses (46.7% of nests); beaver ponds, bogs, and marshes with standing trees or snags, and shorelines (27.5%); forest edges and openings (10.3%); treed sand dunes (9.0%); parks, cottage areas, and residential areas (6.4%); and tundra (0.1%). Fifty-two percent of nests were in dry habitats, 18% were in wet areas, and 30% were over water (Peck and James 1987).

Near Cape Henrietta in the Tundra Region, the Eastern Kingbird nested on tundra in willow shrubs bordering a pond (James and Peck 1995b). Near Gogama in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, it was rare in stands dominated by jack pine, occurring where

there were scattered large trees adjacent to very young regeneration with open areas suitable for foraging (James and Peck 1995a). In Algonquin Park, it inhabited bogs with dead stubs and was absent in upland forested habitats (Martin 1960). At Lake Opinicon near Kingston in the Great Lakes–St. Lawrence Forest Region south of the Shield, it showed distinct habitat preferences. Islands were much preferred to mainland areas although the habitat was virtually identical, and small islands were preferred to large islands (Blancher and Robertson 1985a).



In heavily forested areas, the Eastern Kingbird is restricted to natural openings such as swamps, marshes, edges of lakes and rivers, beaver ponds with dead trees and shrubs, bogs and fens with scattered trees or snags, savannahs and alvars or other barrens, sparsely treed sand dunes, and natural disturbances due to forest fire and windthrow. Clear-cuts with residual trees and snags provide good breeding habitat. In natural habitats, it prefers wetlands and often nests over water or in trees and stumps surrounded by water. In human-altered landscapes, it prefers uplands. In British Columbia in altered habitats, 57% of nests were associated with anthropogenic habitats, 37% with woodlands and grasslands, and 6% with wetlands; in natural areas, 48% of nests were in wetlands. Forty-one percent of British Columbia and 50% of Montana nests were close to water. In Michigan, it was common to abundant in a burned forest of jack pine and Hill's oak, but absent in the residual forest of similar species composition. In Kansas, it was common in a heavily grazed pasture, but quickly abandoned it when grazing ceased and grass height increased. In Illinois, it was most abundant in savannahs, followed by marshes, grazed grass, grass mowed for hay, water, shrubs, low-density developments, idle grass, developed open spaces, upland forests, floodplain forests, and soybeans. In agricultural landscapes, it is associated mostly with woodland edges, shrubby meadows, orchards, pastures, shelterbelts, roadsides, hedgerows, riparian strips, airports, city parks, sewage lagoons, and golf courses. In Michigan, it was strongly associated with grassy meadows with coniferous snags rather than meadows with deciduous trees and snags. In North Dakota, its abundance was correlated with the number of ponds available, so it may be adversely affected by drought. In North Dakota mixed-grass prairies, it was significantly more abundant in plots with 30-80% shrub coverage than in plots with 10% or less shrub coverage (Arnold and Higgins 1986; Campbell et al. 1997; Davis 1941, 1955; Fitch 1958; Graber and Graber 1963; Graber et al. 1974; Hamas 1983; Johnson and Igl 2001; MacKenzie and Sealy 1981; Mossman 1988; Mossman et al. 1991; Murphy and Pyle 2020; Niemuth et al. 2008; Riffell et al. 2001; Roy and Choiniere in Gauthier and Aubry 1996; Tyler in Bent 1942; Walk et al. 2011).

At the landscape level, the Eastern Kingbird preferred areas with 5-28% forest cover in North Dakota (Cunningham and Johnson 2019). In North Dakota 400-m landscapes with more than 30% tree cover, its probability of occurrence was 10% with 10% tree cover within 100 m, declining to 0% at 70% tree cover. In landscapes with less than 30% tree cover, its probability of occurrence was highest at 17% with 10% tree cover, declining to 10% at 40-70% tree cover (Cunningham and Johnson 2016).

In North Dakota aspen woodlands, abundance of the Eastern Kingbird was negatively associated with forest size. In aspen groves 1 ha in area, there was a 50% chance of detecting a kingbird. This probability declined quickly with forest size and was only 10% for 10-ha woodlands (Grant and Berkey 1999). In Michigan, its presence was positively associated with increasing size of wet meadows (Riffell et al. 2001).

In Ontario, 90% of nests were in trees, shrubs, or vines; 6% on standing stumps; 1.0% in roots of upturned stumps; 1.0% on fallen tree trunks and branches; 0.2% in a rotted-out woodpecker cavity; and 2% on human-made structures (hydro towers, the end of a small crane, on top of a steel culvert, on a sill, on a beam of a hydro transformer, on telephone-pole insulators, on a bridge, on a pole on a ski hill, and on a fence post). When nesting in trees or shrubs, living ones were much preferred (84% compared with 16% for dead). Most nests were on horizontal branches with a few on up-slanting or almost vertical branches. Most were in crotches or forks away from the trunk, but they were occasionally at the trunk. Distances of nests from the trunk were 0.6-4.6 m, mostly 1.2-2.4 m away. Deciduous trees, shrubs, and vines were preferred (81%) to conifers. Favoured nest trees were hawthorns (30.9% of nests), apple (26.2%), poplars (10.3%), white cedar (9.6%), pines (9.0%), elms (7.4%), and oaks (6.6%). Occasionally old nests were rebuilt or material from an old nest may be reused. Some nests were built on top of old American Robin and Cedar Waxwing nests. Nests were 0.3-21.3 m from the ground, with most 1.8-4.3 m up (Peck and James 1987). At Lake Opinicon, there were significant differences between lakeshore and upland nests. Lakeshore nests were at a mean height of 2.80 m compared with 7.75 m for upland nests. This was unrelated to the height of available trees. Over 61% of lakeshore nests were in the lower half of the tree, which is atypical, compared with 5.7% for upland nests. Over 90% of lakeshore nests were built over water, at an average distance of 3.45 m from shore. More lakeshore nests were in white cedar than expected based on availability. This species has low branches extending over water; most other species do not. Most upland nests were in elm, hawthorn, and apple (Blancher and Robertson 1985a).

Most nests elsewhere are in woody vegetation, but human-made structures are also used. These include eavestroughs on houses, hydro towers, on culverts, in nest boxes, in gourds hung up for Purple Martins, street lights, a rain gauge, utility poles, posts, pilings, abandoned cars, buildings, and water towers. In British Columbia, the Eastern Kingbird also nested on cliffs and banks. In Illinois, it showed a preference for placing its nests in tree branches overhanging water. In upland habitat, it prefers living trees and shrubs for nesting, but in wetlands selects dead vegetation, including stumps. Nests at the tops of stumps or snags are often recessed so that the nest is almost in a cavity. In 1 burn, most nests were in cupped depressions formed by embers burning into the heartwood. In dead wood, it prefers sites where the nest is in a bit of a cavity, but it also nests in dead branches. In trees, most nests are on horizontal or diagonal branches approximately 60% of the distance from

the trunk to the canopy edge. Nest tree preference varies geographically, but overall deciduous trees are greatly preferred. In Manitoba, green ash and peach-leaved willow were actively selected. These same tree species were available in New York and Kansas, but seldom used. Hawthorn and apple are preferred nest trees and are actively selected for nest sites. Other species it has nested in that occur in Ontario include white pine, blue beech, willow, white ash, alder, oak, juniper, locust, Manitoba maple, cherry, rose, mulberry, elm, Norway spruce, cottonwood, aspen, white cedar, sycamore, jack pine, and birch. Overall, nests were 0-33 m from ground, with most 1.5-7 m up. It appears to prefer to nest about 2 m above the surrounding vegetation. As in Ontario, it has nested in old robin, Cedar Waxwing, and oriole nests (Campbell et al. 1997; Davis 1941, 1955; Graber et al. 1974; Hamas 1983; MacKenzie and Sealy 1981; Mayfield 1952; Mousley 1916a; Murphy 1983a; Murphy and Pyle 2020; Murphy et al. 1997; Roy and Choiniere in Gauthier and Aubry 1996; Sprunt 1946; Tyler in Bent 1942; Walk et al. 2011). In Oregon, 35 of 341 nesting attempts (10.3%) were in old nests of Eastern Kingbird and other species, with 8-14% of old nests reused annually. American Robin nests were used most frequently (49% of reused nests) followed by Eastern Kingbird (31%), Brewer's Blackbird (14.3%), and oriole (5.7%) nests. There appeared to be no benefit in reusing nests as there were no differences in egg-laying dates, clutch size, reproductive success, or age of females reusing nests or building their own entirely (Redmond et al. 2007). In Oregon, kingbirds readily used artificial nests built of a mix of mud and grass over a wire frame; these closely resembled robin nests (Cancellieri and Murphy 2014).

The Eastern Kingbird is fiercely territorial, driving away conspecifics and potential predators. Early in the breeding season, a large, ill-defined territory is defended. Once a nest site is selected, it becomes the centre of the territory. Both adults are involved in defence, but the male is at least twice as aggressive as the female. Initially, the territory may be quite large, but shrinks with time until only a radius of about 10 m (0.03 ha) around the nest is defended by mid-incubation then it increases again. Four territories in South Carolina during the nesting period were 5.7, 6.5, 7.3, and 14.2 ha. In Georgia, 1 pair had a territory of 5.7 ha during nest building and incubation, but it shrank to 3.8 ha during the nestling stage. One pair near Guelph foraged as far as 180 m from the nest, suggesting a home range size of about 10 ha. Despite the fierceness of territorial disputes, nests have been found very close together in Ontario. Twice 2 active nests have been found in the same tree and 2 nests were separated by only 0.9 m. Any animal that is perceived as a potential predator is vigorously attacked and often chased for great distances. It is particularly aggressive towards humans, cats, squirrels, chipmunks, and almost all birds its size and larger. Even when not chasing predators, it frequently flies out of the territory. Consequently, the home range is much larger, but there is no information on its size (Blancher and Robertson 1985a; Davis 1941; Dyer 1974; Graber et al. 1974; James 1999a; Murphy and Pyle 2020; Odum and Kuenzler 1985; Peck and James 1987; Redmond et al. 2009; Roy and Choiniere in Gauthier and Aubry 1996; Tyler in Bent 1942).

Natal philopatry is low. At Lake Opinicon, 4 of 259 fledglings (1.5%) returned to breed. The average distance between the natal site and the first breeding area was 2.85 km for those that returned (Blancher and Robertson 1985b). Two of 62 young (3.2%) returned to nest in British Columbia (Campbell et al. 1997) and 8 of 428 (1.9%) returned in New York (Murphy and Pyle 2020). A study in New York revealed a natal return rate of 3-4% (Murphy 2007). In Oregon, 22.4% of nestlings

were observed in a subsequent year. Male nestlings tended to return at a higher rate (25.6%) than females (18.7%), but the difference was not significant. Many returning yearlings were prevented from acquiring a territory as a result of competition with adults; these birds were nonterritorial. The high return rate in Oregon was probably because habitat was restricted to areas within 200 m of aquatic habitats, with the remainder of the area being desert (Redmond and Murphy 2012).

Breeding site fidelity by adults is high. At Lake Opinicon, 43% of adults returned to breed in subsequent years, but they were less likely to return the year after banding (36%) than in later years (50%). Males returned to the same territory 33% of the time compared with 11% for females. Average dispersal distances were 0.04 km for returning males and 0.58 km for females. The same territories are frequently used, especially if breeding was successful the previous year. Of territories that fledged at least 1 young the previous year, 75% were reoccupied compared with 51% for unsuccessful territories (Blancher and Robertson 1985b). In New York, males reused their former breeding territories 92.7% of the time compared with 72.5% for females. In Oregon, 65.2% of adult males and 65.5% of adult females returned the year after they were banded. Geolocators were attached to adults in Nebraska and Oklahoma and 8 of 10 (80%) Nebraska birds returned and 2 of 2 (100%) Oklahoma birds returned. There are numerous examples of the same nest site being used year after year, with the old nest occasionally being repaired and reused several times. If a nest is unsuccessful, use of the site may be skipped for a year (Fairfield 2000; Hamas 1983; Mousley 1916a; Murphy and Pyle 2020; Peck and James 1987; Redmond and Murphy 2012).

Limiting Factors

Eggs have been found in Ontario nests from mid-May until the first week of August, with most present in the last 3 weeks of June. At 1 nest at Cape Henrietta Maria, egg laying was not initiated until the second week of July, suggesting that extreme northern nests may be about a month behind those in the south (James and Peck 1995b; Peck and James 1987, 1997). In Algonquin Park, nests are under construction from mid-May to early July, eggs occur from late May to late July, nestlings are present from mid-June to late July, and fledglings have been observed from early July to late August (Tozer 2012). At Lake Opinicon, eggs were laid significantly earlier at lakeshore than upland sites. The water ameliorated ambient temperatures, resulting in warmer spring temperatures near the lake (Blancher and Robertson 1985a)

The female selects the nest site and builds the nest in 7-14 days, with inclement weather increasing nest construction time. Replacement nests may be built more quickly. One Ontario nest was completed 3 weeks before egg laying commenced. In other areas, the time between nest completion and egg laying ranged from 1 to 20 days (average 6 days). Eggs are typically laid at the rate of 1 a day, but occasionally a day is skipped between the penultimate and last eggs. Incubation starts with laying of the penultimate egg. The incubation period of Ontario clutches was 12-18 days, with most eggs hatching in 13-15 days; the 18-day incubation period was considered a delay in initiation of incubation rather than a true incubation period. Elsewhere, the incubation period has been reported as 14-17 days. The incubation period may increase with latitude due to effects of ambient temperatures. Incubation periods determined by the same researcher were significantly shorter in Kansas than in New York. Hatching is asychronous in most 3-egg clutches and all larger clutches. Fledging occurs at age 13-19 days, mostly 16-17 days. The fledging period is strongly

correlated with brood size, with longest fledging periods in broods of 4 or 5 young (Campbell et al. 1997; Davis 1941; Graber et al. 1974; Morehouse and Brewer 1968; Murphy 1983a, 1983b; Murphy and Pyle 2020; Peck and James 1987).

Most authors state that the Eastern Kingbird is single brooded (Davis 1941; Murphy 1983a; Murphy and Pyle 2020). Blancher and Robertson (1982, 1984b) presented compelling evidence for a second brood at Lake Opinicon, although it was not totally conclusive that the same pair was involved (Peck 1984). Renesting occurs, with the likelihood of renesting declining with the season. In Kansas and New York, 88.9% of nests that failed during nest construction were replaced, 30.4% of those that failed during incubation were replaced, and 6.7% of nests with nestlings that failed were replaced (Murphy 1983a). Clutches of 1-6 eggs have been reported in Ontario, with most containing 3 or 4 eggs. Clutch size diminishes with season. At Lake Opinicon, most late-May nests contained 4 eggs; most clutches laid from late May onward contained 3 eggs. Replacement clutches were significantly smaller than those of first nests (3.13 eggs compared with 3.74 eggs; Blancher and Robertson 1985a, 1985b). Murphy (1986a) observed a similar decline in clutch with season in Kansas. Elsewhere, clutches of 2-6 eggs have been reported, with 5- and 6-egg clutches rare. Most clutches contain 3 or 4 eggs. Clutch sizes vary by latitude and longitude, with larger clutch sizes in the west and north (typically 4) compared with 3 eggs in the south and east (Campbell et al. 1997; Graber et al. 1974; Murphy 1983a, 1986a, 2000; Murphy and Pyle 2020; Tyler in Bent 1942).

The age at first breeding is 1 year, but it is uncertain what proportion of yearlings breed. Some may not be able to establish territories and adults that die are readily replaced by floaters. Once breeding has been initiated, it continues every year thereafter. The mating system is monogamous. If both birds of a former pair return, about 85% of them remate. At Long Point, 1 pair mated for 5 years. Extra-pair copulations are common. About 60% of nests contain extra-pair young and 50% of nestlings are extra-pair. Some intraspecific parasitism may occur, but the extent of this is unknown (Fairfield 2000; Hayes and Robertson 1989; Murphy and Pyle 2020).

At Lake Opinicon, aerial hawking was the most common foraging technique, and hover-searching frequently occurred. Rarely, the Eastern Kingbird flew from a perch to the ground to capture prey or sallied and gleaned from leaves (Blancher and Robertson 1985a). Most foraging is by sitting and waiting, then attacking aerial prey. Hover-gleaning and attacking prey on the ground are seldom-used foraging techniques. During rain or emergence of aquatic invertebrates, it may glean caterpillars from underneath leaves and from the surface of water bodies. During major insect emergences, it may hover and make multiple captures during a single flight. Most foraging flights are from a perch 1-4 m tall, for an average distance of 1.3 m (range 0.5-9.0 m). In Kansas, perch height averaged 1.3 m (range 0.3-9.1 m) and the average sally distance was 2.9 m (range 0.9-7.6 m). Commonly used perches are fences and fence posts, power lines, shrubs, trees, and herbaceous plants. Occasionally, it forages on the ground, particularly in plowed fields. Near Guelph, foraging occurred as far as 180 m from the nest. Most (46.0%) foraging occurred 90-150 m from the nest, 16.6% of time was spent foraging within 60 m of the nest, 10.0% beyond 180 m, and the remaining 27.4% of time was spent foraging 150-180 m from the nest. In Oregon, there were no differences in the foraging techniques of the sexes: 88.3% aerial hawking, 8.7% outward strikes, 17% perch-to-ground sallies, and 1.3% hover-gleans. During inclement weather, it moved into the canopy of tall

deciduous trees to capture insects by upward-striking and hover-gleaning (Dyer 1974; Graber et al. 1974; Murphy 1987; Murphy and Pyle 2020).

Both adults feed the young, with the female doing most of the deliveries. Nests in Ontario that lost the male all failed to fledge the entire brood. Only 23% of young fledged from nests without a male compared with 57% of nests with both adults. Young are fed mostly insects, predominantly beetles, grasshoppers, flies, butterflies, moths, bees and wasps, dragonflies and damselflies, and rarely small frogs. Young may also be fed fruits of mulberries, cherries, dewberries, common elderberry, nightshade, juneberries, currants, and raspberries. Adults feed mostly on flying insects, although some fruit is consumed later in the breeding season. These include cherries, sassafras, red-osier dogwood, wild grapes, and fruits that are commonly fed to young. Over 85% of the diet consists of insects: 32% hymenopterans, 25% beetles, 12% orthopterans, and 4% bugs. Typically, this kingbird feeds on large adult insects such as beetles, butterflies and moths, grasshoppers, leafhoppers, and cicadas and other bugs. Beetles consumed ranged in size from 3 to 20 mm, including June and click beetles and weevils. Hymenopterans consumed include wasps, bees, and ants. Other prey items include robber flies and geometer moth caterpillars. In Kansas, the diet at 2 sites included 49% and 58% beetles, 32% and 22% hymenopterans, 10% and 2% flies, and 0% and 11% lepidopterans. In Manitoba, midges comprised most of the food. It also eats spiders and rarely dives into water for aquatic insects and small fish. It has been observed eating treefrogs (Beal 1897a; Campbell et al. 1997; Chandler 1996; Davis 1941; Graber et al. 1974; Hayes and Robertson 1989; Hespenheide 1971b; Holt 1918; MacKenzie and Sealy 1981; McIlwraith 1894; Morehouse and Brewer 1968; Morton 1971; Murphy 1986a; Murphy and Pyle 2020; Tyler in Bent 1942).

The Eastern Kingbird is a rare host of the Brown-headed Cowbird. It is an egg rejecter, so parasitism rates are probably higher than observed. Cowbirds may also eject or damage kingbird eggs. In Ontario, 12 of 1,066 nests (1.1%) were parasitized. Other reported parasitism rates are 1 of 402 nests (0.2%) at Delta Marsh; 0 of 213 nests in British Columbia, although adults were observed feeding a young cowbird; 4% in western New York; 0 of 450 nests in central New York; 2 of 119 nests (1.7%) in the Dakotas, Minnesota, and Montana; and 13% in eastern Kansas. Parasitism usually does not affect the growth rate of kingbird nestlings, and occasionally kingbirds and cowbirds are fledged from the same nest (Campbell et al. 1997; Graber et al. 1974; Igl and Johnson 2007; Murphy 1986b; Murphy and Pyle 2020; Peck and James 1997; Rothstein 1975; Tyler in Bent 1942).

Habitat loss and degradation may limit the amount of suitable breeding areas. There have been large losses of pastures and orchards in southern Ontario and throughout the Eastern Kingbird's range. The decline in numbers of small farms and removal of hedgerows are negative factors. Through natural succession, many old fields have reverted to forest, making them unsuitable habitat. In Illinois, densities in favoured habitats were similar in the 1950s to the early 1900s, although there were less of these habitats. Densities were much lower in the later period in marginal habitats and some formerly used habitats, such as urban areas, were no longer used (Graber and Graber 1963; Graber et al. 1974; Murphy and Pyle 2020; Roy and Choiniere in Gauthier and Aubry 1996).

Nest location and breeding success are strongly correlated. Predation is the greatest cause of nest failure, and the more water there is near the nest, the greater the success rate. At Lake Opinicon, nesting success was greatest on stumps surrounded by water, followed by nests on large islands,

small islands, and the mainland. Breeding success in a given territory is strongly related to breeding success the previous year. Pairs nesting in previously successful territories were twice as likely to be successful as those nesting in previously unsuccessful territories. Previously successful birds that nested at the same site were 81% successful compared with 57% for birds that selected a different site. Previously unsuccessful birds were only 18% successful if they nested at the same site compared with 34% for those selecting a new site (Campbell et al. 1987; Blancher and Robertson 1985a, 1985b). In Oregon, natural and artificial nests were equally likely to fledge young. Differences in nest-site characteristic between failed and successful nests were similar for natural and artificial nests. The angle of the supporting branch was about 2.35 times steeper for successful nests for both types of nests, but the difference was significant only for natural nests (51.2° for successful nests compared with 21.8° for failed nests). Although not significant, successful nests of both types tended to be higher. Successful nests tended to be on more vertical branches and placed higher and closer to the top of the tree and closer to the centre of the tree than failed nests (Cancellieri and Murphy 2014).

In Saskatchewan, fire appeared to have no effect on the Eastern Kingbird. Its abundance was similar in burned and unburned areas (Pylypec 1991).

Weather may greatly affect nesting success. Cool and/or wet springs may delay nest initiation by as long as 2 weeks. Food is scarce under these conditions and adults often cannot find enough food to adequately feed young. Starvation of nestlings is common, particularly in larger broods. Nestlings exposed directly to intense sunlight may also die (Murphy 1983a, 1983b, 1983c, 1986a, 1986c; Murphy and Pyle 2020). Gorzo et al. (2016) used Breeding Bird Survey (BBS) data to analyze the response of the Eastern Kingbird to large-scale weather extremes in South and North Dakota, Montana, and Wyoming. Its abundance was significantly associated with weather. It responded negatively to both within-year precipitation and precipitation in the previous year.

The Eastern Kingbird frequently nests in orchards where pesticide use is common. Pesticides are a potential source of egg and nestling mortality, but this needs further study. Pesticides are also used along roads, railways, and hydro corridors, all habitats that may be used for nesting (Graber and Graber 1963; Murphy and Pyle 2020).

This flycatcher frequently collides with vehicles because it commonly forages and nests adjacent to roads (Murphy and Pyle 2020)

Status

The Eastern Kingbird has always been a common breeding species in Ontario, at least since European settlement. McIlwraith (1894) called it one of the most familiar birds in rural areas. Baillie and Harrington (1937) considered it common in the south and occurring north to James Bay and southern Thunder Bay and Temiskaming districts, and west to Lake of the Woods. In the Kingston area, it was common in the 1850s and 1900-10, and was the most common breeding flycatcher during the first atlas (Weir 2008). The first atlas confirmed that the Eastern Kingbird bred from the southern border of Ontario north through much of the Boreal Forest Region, except in the northwest. There were also scattered records along the Hudson and James bay coasts (Helleiner in

Cadman et al. 1987). James (1991) termed it common to locally abundant in the south, uncommon in the north to Red Lake and Moosonee, and rare north to Winisk and Cape Henrietta Maria.

The second atlas indicated a significant decline in the probability of observation of the Eastern Kingbird province-wide since the first atlas and in all regions except the Hudson Bay Lowland. Although declines south of the Canadian Shield were statistically significant, it was observed in virtually every square south of the Shield during both atlases. The greatest decline occurred in the Great Lakes–St. Lawrence Forest Region in the Shield, particularly in the Algonquin Highlands. This decline may be due in part to forest maturation and conversion of old-field habitats to forest. It was much more abundant south of the Shield than in it. Greatest abundance occurred from Lake Simcoe in a broad band east to the Brockville and Perth area, and in Bruce, Grey, and northern Wellington and Dufferin counties (Blancher in Cadman et al. 2007).

Long-term (1970-2021) population trends determined by the BBS indicate annual decreases in Canada of 0.929% and 1.94% in Ontario. The short-term (2011-2021) trends were an annual increase of 1.73% in Canada and an annual decrease in Ontario of 2.145%. All estimates were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

It is several days after fledging before young can fly strongly. Although young may start to capture their own food the second week after fledging, they remain highly dependent on the parents for 5 weeks after fledging (Murphy and Pyle 2020).

MIGRATION

Migration occurs both diurnally and nocturnally. Most authors concluded that the Eastern Kingbird migrates mostly in flocks during the day, but some nocturnal migration occurs as evidenced by casualties at chimneys and towers. During autumn migration, birds stage during the day along the southern shores of Amherst Island, Wolfe Island, and Prince Edward Point, then cross Lake Ontario at night. Habitat used during migration is similar to breeding habitat (Campbell et al. 1997; Graber et al. 1974; Murphy and Pyle 2020; Tyler in Bent 1942; Weir 2008).

The Eastern Kingbird arrives in the province in the first week of May, rarely in early April. Spring migration may continue until June, with the peak in the second week of May. Males arrive about 5 days earlier than females, and older birds of both sexes arrive about a week before younger birds. Autumn migration may begin in mid-June and continue until mid-September, with rare stragglers to mid-October (Cooper et al. 2009; James 1991; Keast 1990; Murphy and Pyle 2020).

The Eastern Kingbird is common during migration and may be locally abundant in autumn when larger flocks may occur. Taverner and Swales saw hundreds at Point Pelee 24-27 August 1907, with occasionally 15-20 in a single tree. In the latter half of August, flocks of 150-400 may be observed in the Kingston and Presqu'ile areas (James 1991; LaForest 1993; Tyler in Bent 1942; Weir 2008).

Olive-sided Flycatcher

Contopus cooperi

BREEDING SEASON

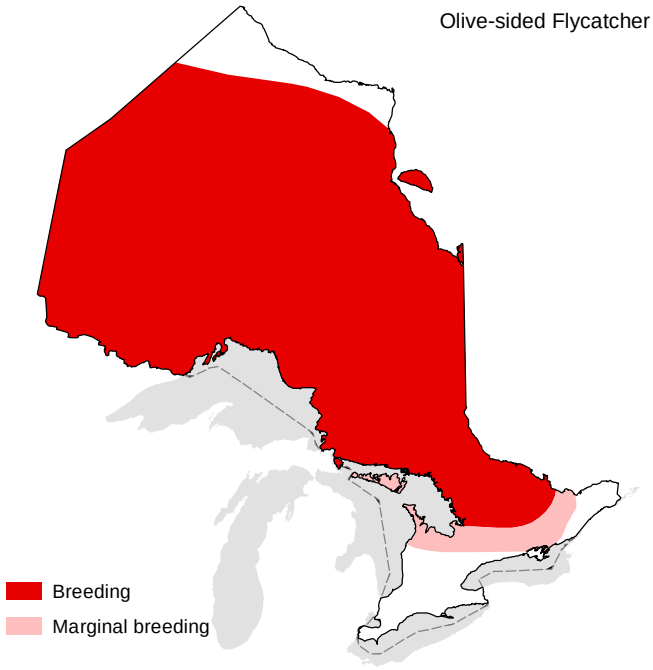
Habitat Requirements

The Olive-sided Flycatcher nests in coniferous and mixed forests, usually in wetlands, but occasionally in upland habitat. Ontario nesting habitats include black spruce bogs and burns, jack pine stands and burns, mixed woods, and treed margins of beaver ponds and cattail marshes (Peck and James 1987).

In the Boreal Forest Region, the Olive-sided Flycatcher is characteristic of burns and clear-cuts as long as there are standing snags and stubs, but it also occurs in swamps and floodplain forests. Near Pickle Lake, it bred in small numbers at edges of bogs, in burned areas, and in clear-cuts (Erskine 1977; James 1980; McLaren and McLaren 1981).

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Olive-sided Flycatcher preferred very open treed swamps and regularly foraged from and nested in jack pines adjacent to

riparian areas (James and Peck 1995a). In Quetico Park, it occurred in low-density coniferous forests with an understorey and in mixed forest and mixed scrub. It was rare in coniferous forests without an understorey and in heath areas. Following forest fires, it was most common the first 3 years after fire. It was absent in intermediate-aged and old-growth stands, and uncommon in mature stands (Apfelbaum and Haney 1985). In Algonquin Park, it occurred commonly in drowned lands with tall dead trees, in spruce and tamarack swamps, in pine forests, and near beaver ponds (MacLulich 1938; Tozer 2012).



In Durham Region in the Great Lakes–St. Lawrence Forest Region south of the Shield, the Olive-sided Flycatcher nested in a spruce bog with some white spruce and tamarack surrounding an open area dominated by leatherleaf. Speirs and Orenstein (1975) considered it a mid-successional species associated with conifers.

Outside Ontario, the Olive-sided Flycatcher has been documented nesting primarily in sparsely treed bogs, burns and clear-cuts with residual trees or on edges of these habitats, at edges of beaver ponds, along forested shorelines with standing dead trees, at ecotones between riparian habitat and coniferous forest, in mixed forests, and in wetland shrubby areas. Although typically associated with coniferous and mixed stands, it rarely occurs in deciduous stands. It usually occurs in very young and young stands, frequently in areas that are nutrient poor, and most often near water. Areas near water may have a greater density of insects. In California, it nested in mature open forests. Tall perches and open habitats for foraging are important habitat components. In Alaska, males perched and sang from the tops of coniferous trees, predominantly white spruce. More than 80% of perch trees had dead tops or were completely dead. Perches were prominent trees averaging 1.4 times taller than the forest canopy. Mean height of perches was 17.8 m (Altman and Sallabanks 2020; Bent 1942; Campbell et al. 1997; Capen 1979; Dawson 1979; Hack et al. 2024; Kirk et al. 1996; Niemi and Pfannmuller 1979; Noon et al. 1979; Séguin in Gauthier and Aubry 1996; Temple et al. 1979; Walkinshaw and Henry 1957a; Wright 1997).

At the landscape level, the Olive-sided Flycatcher is significantly more abundant in areas with clear-cuts than those without clear-cuts, and in fragmented landscapes than extensively forested areas (Altman and Sallabanks 2020). Baker et al. (2016a) reported that highest Canadian densities occur in mature conifer stands within patchy landscapes influenced by natural disturbances such as fires. Wetlands have a positive influence on its abundance at the landscape level, but a negative effect at the local level. In Minnesota, it was associated with lowland conifer communities

embedded within landscapes containing a high proportion of non-forest (Zlonis et al. 2017). In Nova Scotia, its presence was positively correlated with canopy height and valleys and negatively correlated with canopy height heterogeneity, distance to a coniferous stand, and distance to a stand with dead material. Canopy height was the most important factor (Bale et al. 2020).

In 2 study areas in Montana, the Olive-sided Flycatcher selected territories on steeper slopes than were randomly available. Ground slope was 33.8° and 15.5° at territories in the study areas compared with 15.9° and 7.2° at random sites, respectively (Robertson and Hutto 2007).

Ralston et al. (2019) surveyed 20 sites in boreal forest habitat in New York, Vermont, Maine, Nova Scotia, and Newfoundland for the Olive-sided Flycatcher. The Olive-sided Flycatcher occurred at only 3 locations indicating specialized habitat requirements. Its presence was positively correlated with black spruce, tamarack, and mean temperature. It was restricted to lower-elevation sites with higher temperatures, predominantly in black spruce–tamarack swamps.

Westwood et al. (2009) modelled Olive-sided Flycatcher habitat in Nova Scotia and New Brunswick. Its population density was highest in stands dominated by spruce species (excluding white spruce), black spruce, and balsam fir. It was least abundant in stands dominated by pines and deciduous species. For all tree cover types except alder, density increased with the amount of forest that had a depth to water table of 1 m or less, with the proportion of the area within 250 and 1,000 m classified as wet, and with lower mean canopy cover and mean stand height. Population density increased with landscape complexity and connectivity. Density decreased with the presence of roads. Areas within national parks had a slightly higher population density than areas outside parks.

In Alaska, vegetation at perches, nests, and random areas was similar. There was almost complete coverage by vegetation less than 50 cm tall dominated by mosses, lichens, and dwarf shrubs. Dwarf birches and Labrador tea were the most abundant shrubs with spruce saplings and willows also common. Spruce dominated the trees taller than 1.4 m with a diameter at breast height (DBH) of less than 8 cm, with alder and tamarack common. Spruce also dominated the larger trees, although there were few larger than 23 cm DBH (Wright 1997). In Montana, there were no differences in the height of perches selected by flycatchers in burned (16.7 m) or selectively harvested (18.3 m) stands for singing males, or for foraging males (15.2 m compared with 14.7 m) and females (8.7 m compared with 9.5 m). Females selected perches that were an average of 55% shorter than those selected by foraging males, and 115% shorter than those used by singing males. The probability of a bird selecting a live tree for a perch was significantly higher in selectively harvested (64%) than burned (17%) forests. Females preferred perches that were significantly shorter than available trees. Male perch height was similar to that of available trees. Both sexes strongly selected standing dead and dead-topped trees as perches in selectively harvested stands but not in burned stands. Tree species preferred for perching included fir, larch, and white birch (Robertson 2012).

Ontario nests were on horizontal branches of conifers, mostly black and white spruce, but also jack pine and balsam fir. One nest tree in a burned area was dead. Most nests were 0.3-2.5 m from the trunk of the tree; 2 nests were at the end of a branch and 1 was against the trunk. Nests were 4-

15 m from ground, with most 7-10 m up. Most nests were well concealed in foliage, but 1 was conspicuous (Peck and James 1987).

All reported nests were on horizontal limbs (usually the bottom limb), and most were distant from the trunk. In Alaska, nests were an average of 16.7 cm from the trunk atop live branches averaging 50.4 cm long. In Oregon, nests were 91.4-106.7 cm from tree trunks on branches 137.1-167.6 cm long. More than 90% of nests are in conifers, with other coniferous nest trees including red cedar, tamarack, pitch pine, and hemlock. All nests reported in an Alaskan study were in live conifers. Nest trees were significantly shorter than perches and the surrounding canopy. Deciduous trees that have been used for nesting are apple, sycamore, cottonwood, elm, locust, oaks, alder, willow, and trembling aspen. Extremes in nest heights reported are 1.5-60 m, with most 6-12 m from ground. Mean height of 19 Alaska nests was 6.4 m (range 3-12 m); mean nest height in Montana was 12.1 m (Altman and Sallabanks 2020; Bent 1942; Campbell et al. 1997; Robertson and Hutto 2007; Séguin in Gauthier and Aubry 1996; Walkinshaw and Henry 1957a; Wright 1997).

The Olive-sided Flycatcher is fiercely territorial, and may attack other bird species such as hawks, crows, and Scarlet Tanagers (Bent 1942). Limited information on territory size is available. Most estimates are 10-20 ha, but territories as large as 25, 40, and 45 ha have been reported. Average size of 16 territories in Alaska was 18.4 ha (range 10.8-26.4 ha). Territories in Alaska were long and narrow and were often along a watercourse or drainage. The average length of territories was 625 m (range 360-1,120 m). Territories may not be contiguous and are frequently separated by unsuitable habitat. When territories abut, it is usually on 1 side only. The closest nests are 200 m apart (Altman and Sallabanks 2020; Wright 1997).

Although there are few banding recoveries for the Olive-sided Flycatcher, data indicate strong breeding-site fidelity. Birds have been captured 5 and 6 years later in the same location in California, 2 birds in California returned the subsequent 2 breeding seasons, and 5 of 9 Alaska birds returned to the same territory. Reuse of nests has not been reported outside Ontario, but subsequent nests have been found in the same tree as close as 1 m to the old one. In Alaska, nests on regularly used territories were an average of 271 m from the previous year's nest with a range of 45-625 m (Altman and Sallabanks 2020; Wright 1997). A nest found in 1998 in Sudbury District was used again in 1999 (Peck 2000).

Limiting Factors

Eggs have been reported in Ontario nests throughout June (Peck and James 1987). In Algonquin Park, nests are under construction from early to mid-June, eggs are present from mid- to late June, nests contain young from early to mid-July, and recently fledged young have been documented from late July to late August (Tozer 2012). In Alaska, timing of territory establishment was irregular. Some birds apparently on territory in late May and early June were not detected again, and some territories were not established until late June or early July. Of 23 males, 6 (26%) were found only once or twice and did not maintain a territory throughout the season (Wright 1997).

Nests are typically built in 5-7 days, although 1 took 10 days to complete. The egg-laying interval is 1 day and the incubation period is 14-19 days, with most eggs taking 15-17 days to hatch. Young may leave the nest when they are 15-17 days old if disturbed, but the normal fledging period is 19-

23 days (Altman and Sallabanks 2020; Bent 1942; Campbell et al. 1997; Pearce and Kirk 2007; Séguin in Gauthier and Aubry 1996; Walkinshaw and Henry 1957a; Westwood and Stehelin 2018; Wright 1997).

A single brood is raised annually; there is no evidence of second broods. Renesting may occur once or even twice if a clutch is lost. In this event, a new nest is built. In Alaska, all but 1 pair renested within 225 m of the first nest and the other was 600 m distant. The mean distance of replacement nests from the first nest was 144 m and the closest was 25 m. The replacement clutch is laid in 3 weeks or less (10-12 days in Alaska). Ontario clutches contained 2-4 eggs, mostly 3 eggs. The Olive-sided Flycatcher almost always lays 3 eggs with 4-egg clutches scarce and 2-egg clutches rare. In Alaska, 10 first clutches all contained 4 eggs. One Michigan nest contained 6 eggs and 5 young were fledged from this nest. It is unknown if these eggs were produced by 1 or 2 females. Two-egg clutches are usually replacement nests. In Alaska, 2 of 3 replacement clutches contained 3 eggs and the other contained 4 eggs (Altman and Sallabanks 2020; Bent 1942; Séguin in Gauthier and Aubry 1996; Walkinshaw and Henry 1957a; Wright 1997).

The nesting system is monogamous although there is 1 instance of suspected polygyny in Alaska and 1 in Oregon. There are 2 records of the same pair remaining together in consecutive years. The age at first breeding is 1 year, but many birds may not breed or attract a mate (Altman and Sallabanks 2020; Wright 1997).

The Olive-sided Flycatcher hunts from an open perch, usually the top of a tree or snag. It preys exclusively on flying invertebrates. In windy or cool, inclement weather, both sexes forage from lower perches less than 15 m from the ground such as shrubs, saplings, and exposed branches of slash piles and root wads. Most flights under these circumstances are directed downward toward the ground. In Alaska, 2 females foraged from low snags or broken saplings 1-3 m tall, occasionally disappearing for as long as 15 seconds into low (0.5 m or less) flowering vegetation. These females also hovered over or flew directly over the top of low vegetation. These perches were directly adjacent to sunlit patches of flowering shrubs and forbs that supported bumble bees, yellowjackets, and moths. Near-ground foraging had not been previously reported, but was frequent, representing 70% of 27 foraging attempts. Unlike most other flycatchers, it rarely takes invertebrates from foliage and usually does not eat prey that does not fly. It does not eat caterpillars, millipedes, or other non-aerial invertebrates often eaten by other flycatchers, but occasionally eats spiders. Honey bees and flying ants constitute more than 80% of the breeding season diet; almost all birds sampled had eaten these hymenopterans and more than 40% had fed on them exclusively. Other invertebrates eaten, in order of decreasing abundance, were beetles, moths, grasshoppers, true bugs, dragonflies, and flies. Animal food was 99.95% of the diet, with the remainder being fruit pulp and spruce foliage (Altman and Sallabanks 2020; Bent 1942; Hagelin et al. 2015; Séguin in Gauthier and Aubry 1996). In New Brunswick, the Olive-sided Flycatcher exhibited no response to increasing numbers of spruce budworms (Morris et al. 1958).

Brown-headed Cowbirds have not been documented parasitizing the Olive-sided Flycatcher in Ontario, and it is a very rare cowbird host. Campbell et al. (1997) reported 1 incident of parasitism in British Columbia, apparently only the fourth record in North America. Altman and Sallabanks (2020) reported no additional observations of parasitism.

It has been estimated that 17% of this flycatcher's habitat in the Boreal Forest Region of Canada has been disturbed by anthropogenic activities. Depending on how it is done, clear-cutting may be detrimental or beneficial. Clear-cutting that removes snags adjacent to small clearings or in small wetlands may decrease habitat quality. Overall, clear-cutting is usually beneficial because it creates forest edges and openings suitable for foraging. Clear-cuts that leave isolated trees and snags may be beneficial provided they are close to suitable breeding habitat and do not remove existing breeding areas. It has been suggested that the Olive-sided Flycatcher is dependent on fire, and clear-cuts may be ecological traps where birds have limited reproductive success (Altman and Sallabanks 2020; Baker et al. 2016a; Séguin in Gauthier and Aubry 1996). In the Canadian Shield of Ontario, it was significantly less abundant in early successional clear-cuts than in early successional burns, but there was no difference in its abundance in mid-successional clear-cuts and burns. It was significantly more abundant in early successional than mature stands, but equally abundant in mid-successional and mature stands (Zimmerling et al. 2017). In Montana, its reproductive success was lower in harvested forests than in burned forests. This may be due to higher densities of predators in clear-cuts. There may also be increased abundance of aerial insects in clear-cuts, thus attracting Olive-sided Flycatchers into an ecological trap (Robertson and Hutto 2007). Snag retention in clear-cuts is an important habitat consideration (Robertson 2012). In Newfoundland, Whitaker and Montevecchi (1999) studied its distribution in relation to riparian edges and buffer strips retained around watercourses and water bodies where clear-cutting occurred. In unharvested balsam fir stands, it occurred only within a 30-m riparian band and was absent in forest interior. In clear-cut areas, it was present in the riparian buffers but absent in the clear-cuts. These authors categorized it as an open-edge species. Pearce and Kirk (2007) concluded that the continued decline of the Olive-sided Flycatcher throughout its range despite continued addition of early successional habitat through forest harvesting suggests that forest management practices may be a significant factor in population declines.

The Olive-sided Flycatcher may be vulnerable to acid precipitation which has the potential to reduce insect prey and may also release mercury into the environment (Baker et al. 2016a).

Reduced availability of insect prey has been raised as a potential threat. Many insects are declining and have shrinking ranges. There is also the potential for mismatch of timing of flycatcher breeding activities and insect emergence (Baker et al. 2016a).

In California, the presence of the Olive-sided Flycatcher was related to presence of early successional habitats and fire. Meehan and George (2003) found that fire had negative impacts on reproduction, perhaps related to reduced food availability in recently burned areas. Another California study concluded that low- to moderate-severity fires could be beneficial by burning small trees and leaving older trees unscathed, resulting in the open forest dominated by large trees that it preferred (Hack et al. 2024). In most areas, it is more abundant in burned than unburned forest (Altman and Sallabanks 2020). In Oregon, it responded positively to fire and its abundance increased with increasing severity of the burn. It showed a positive response beginning in year 4 after the fire (Stephens et al. 2015). Fire suppression may be a threat in Canada because 97% of fires are suppressed before they reach 200 ha in size (Baker et al. 2016a).

Deforestation of wintering habitat has been identified as a limiting factor to the Olive-sided Flycatcher (Baker et al. 2016a).

Price (2004) predicted that the Olive-sided Flycatcher could disappear as a breeding species in southern Ontario if the average summer temperature increased by 2°C.

Status

McIlwraith (1894) considered the Olive-sided Flycatcher rare in Ontario and not very abundant anywhere; he had only 1 record of a migrant. Most of his observations were made in the Hamilton area and there were few observers within its main breeding range, so his comments may not be representative of its status at that time. Baillie and Harrington (1937) termed it not uncommon from latitude 44° N to James Bay and west to Thunder Bay. Although they had no direct evidence, they assumed it nested to the western boundary of the province. MacLulich (1938) considered it common at Algonquin Park. The first atlas confirmed that it bred throughout the Canadian Shield and Boreal Forest Region north to latitude 56°N along the Severn River. Its distribution in the Hudson Bay Lowland was sporadic and concentrated mostly in the northwest. There were scattered records in the south from the Bruce Peninsula, Manitoulin Island, and in the Frontenac Axis (Shekey in Cadman et al. 1987). James (1991) considered it an uncommon breeder in forested areas of the province south to Lake Simcoe and Brockville.

There was no significant change in the breeding distribution of the Olive-sided Flycatcher between the 2 atlases. It breeds in low density throughout the Canadian Shield and Hudson Bay Lowland, except for the strip of tundra along the Hudson Bay coast. It is rare south of the Shield where habitat is marginal. There was no significant difference in its probability of observation province-wide, but there were significant declines south of the Shield and in the southern Shield (Cheskey in Cadman et al. 2007).

Breeding Bird Survey (BBS) data for 1970-2021 indicated declines of 1.85% per year in Canada and 1.67% in Ontario. During 2011-21, the rate of decline was 2.05% annually in Canada and 0.52% in Ontario. All estimates were highly reliable (A.C. Smith et al. 2023). BBS results are biased toward southern populations of birds because surveys are conducted from roadsides (Westwood and Stehelin 2018); only a small proportion of the Olive-sided Flycatcher's range is sampled. The Committee on the Status of Endangered Wildlife in Canada originally designated the Olive-sided Flycatcher threatened in Canada, but later downgraded its status to special concern based on revised population estimates. It is listed as special concern in Ontario.

The short-term objective of the recovery strategy for the Olive-sided Flycatcher is to halt its national decline by 2025 while ensuring that the population does not decrease by more than 10% over this time. The long-term objective after 2025 is to ensure a positive 10-year population trend for it and to maintain its current distribution (Baker et al. 2016a).

POSTFLEDGING PERIOD

After fledging, young remain close to the nest for several days and depend on the adults for food for their first week. Fledglings remain on the territory for as long as 17 days after fledging, and the family may remain together until autumn migration (Altman and Sallabanks 2020).

MIGRATION

The Olive-sided Flycatcher has the longest migration route of any North American flycatcher, and arrives later in spring and departs earlier in autumn than most other flycatchers. It usually arrives in mid-May or later, with earliest arrivals in very late April. Normally, it lingers in the south until early June, but is often seen as late as mid-June. In autumn, it is an early migrant, appearing in the south in mid-August. Most leave the province by early September, but stragglers may persist until early October (James 1991; Westwood and Stehelin 2018).

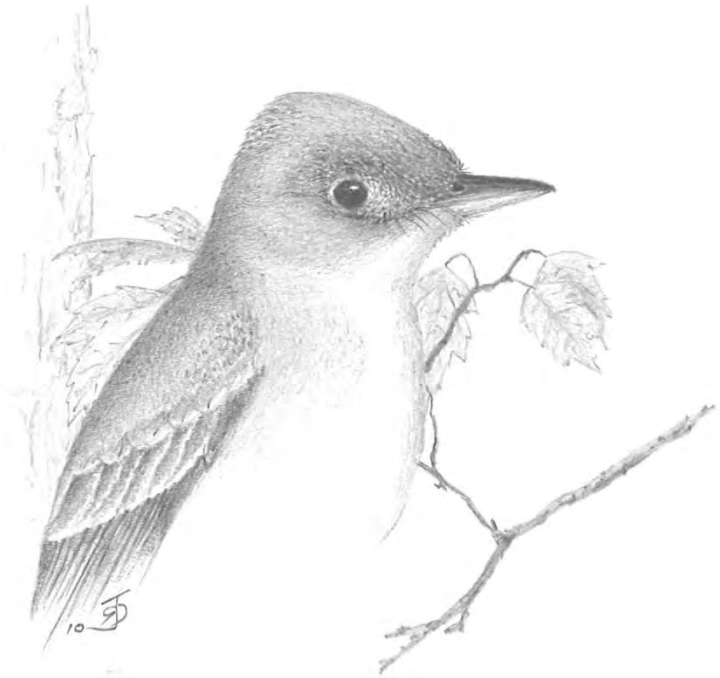
The Olive-sided Flycatcher may occur in a variety of habitats during migration, but it prefers edges and open areas with suitable perches. It is most frequent at edges of mature coniferous and mixed forests, especially if they are adjacent to water, but it also occurs along edges of deciduous woodlands, particularly swamps and floodplains. Edge habitats it may use during migration include ponds, sloughs, lakes, wetlands, blowdowns, rivers, burns, clear-cuts, utility corridors, and highways. Tall trees with dead tops or other open perches are essential (Campbell et al. 1997).

The Olive-sided Flycatcher is at moderate risk for striking buildings during migration (Loss et al. 2014).

During migration, the Olive-sided Flycatcher is rare to uncommon, and tends to be more common in autumn (James 1991; Weir 2008).

Eastern Wood-Pewee

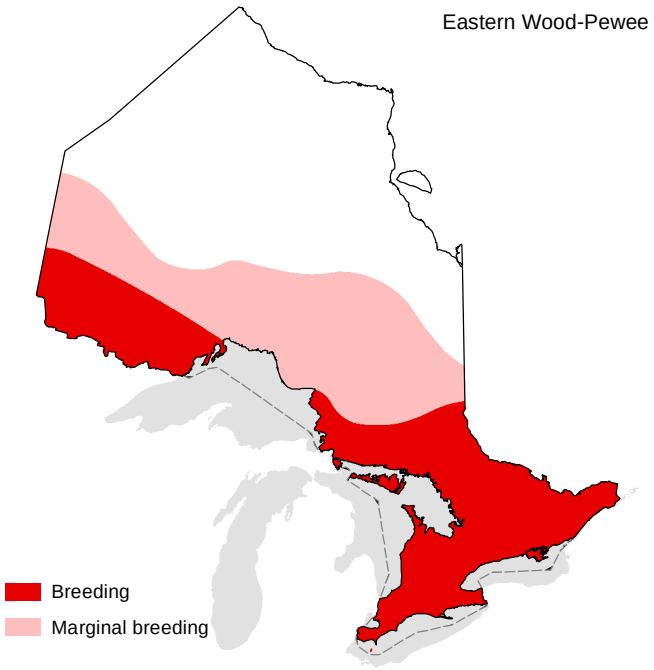
Contopus virens



BREEDING SEASON

Habitat Requirements

In Ontario, the Eastern Wood-Pewee breeds most frequently in deciduous woodlands, occasionally in mixed-wood forests, and rarely in coniferous stands. It may occasionally nest in more open habitats such as orchards, hedgerows, shrublands, residential gardens, parks, and campgrounds. It has a definite preference for open areas near the nest such as forest edges and clearings, roads, and water. Upland sites are greatly preferred over wet areas (Peck and James 1987). In eastern Ontario, it settled in pine plantations and deciduous forests nearly simultaneously and at similar densities, suggesting no preference for either stand type (Falconer and Nol 2020). McIlwraith (1894) stated that it frequently nested in orchards, but this habitat is seldom used now. It continues to nest in urban woodlands (Weir 2008).



Kirk et al. (2012) documented the Eastern Wood-Pewee in mature and old-growth white pine stands in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield of Ontario. It was more common in mature than old-growth stands. In burned forests in Quetico Park, it occurred only in stands that had been burned 1-23 years previously. It was absent in intermediate-aged stands (67-73 years), mature stands (112-176 years), and old stands (367-370 years; Apfelbaum and Haney 1984). In Parry Sound District, it avoided pure jack pine stands. It was present in a jack pine stand with 50% canopy closure, with trembling aspen, white birch, and white pine codominating in the canopy. In an open jack pine stand with 25% canopy closure and several other deciduous and coniferous canopy species, it was present at half the density of the more closed-canopy habitat (James 1979a).

In eastern Ontario in the Great Lakes–St. Lawrence Forest Region south of the Shield, territories had lower basal area, tree species diversity, and fewer pines than unoccupied areas. Wood-pewees selected for fewer trees and more openness in the forest, which would favour aerial foraging (Savignac 2012a). In Durham Region, Speirs and Orenstein (1975) found it on 9 of 11 of their plots. Highest densities occurred in mature beech-maple woodlands, followed by mature maple-oak forest, a relict farm woodlot of mature maple-beech sloping down to a coniferous riparian forest, and an upland mature white cedar–elm forest. It occurred mostly in late-successional stands, but also in subclimax forests.

Although the Eastern Wood-Pewee may occur in almost every forested habitat outside Ontario, it is most common in deciduous woods, less frequent in mixed woods (depending on canopy species composition), and rare to absent in pure conifers. It has nested in maple-beech, cedar-aspen, balsam fir–spruce-poplar, hemlock–yellow birch, poplar-birch, maple, ash-basswood, pitch pine, and mixed pine-spruce stands. In Ohio, dry ridge tops forested with oaks were preferred nesting habitat and it was equally abundant in uncut forest and shelterwood cuts. In Illinois, it was most abundant in savannahs, followed by upland forests, floodplain forests, and developed open space with mature trees. Most studies concluded that it requires intermediate-aged to mature stands. It may be present in immature stands, but in low numbers. In bottomland forests in South Carolina, it occurred only in late-successional stands. In New Hampshire and Maine, it was significantly more abundant in large sawtimber stands (with average tree diameter at breast height [DBH] greater than 60 cm) than in smaller size classes of stands. It was positively correlated with the number of dead trees larger than 10 cm DBH and taller than 5 m, the total foliage volume of coniferous trees larger

than 10 cm, the total foliage volume of deciduous trees 2-10 cm DBH, and the total foliage volume of both coniferous and deciduous trees less than 2 cm DBH. It was negatively correlated with percent ground cover. It was associated with openings such as forest edges and breaks in the canopy. In Minnesota, it inhabited a clear-cut with dead snags and few live residual trees. Although it occurs in swamps and moist habitats, it seems to prefer upland areas. It may be considered an edge species that prefers a tall, broken canopy. Many authors described individual home ranges as being very heterogeneous and difficult to characterize. Its habitat requirements do not overlap significantly with those of the Least and Acadian flycatchers, but there is a macrohabitat overlap with the Great Crested Flycatcher (Adams et al. 1988; Back 1979; Beals 1960; Buffington et al. 1977; Capen 1979; DeGraaf and Chadwick 1987; DeGraaf et al. 1998; DesGranges et al. 1987; Erskine 1977; Fitch 1958; Freemark and Collins 1992; Graber et al. 1974; Hespenheide 1971a; Hoffman 1989a; Johnston 1971; Keller and Yahner 2007; Limoges in Gauthier and Aubry 1996; Lindell et al. 2007; Lynch 1987; Mossman 1988; Mossman and Hoffman 1989; Newell et al. 2013; Niemi and Hanowski 1984a; Niemi and Pfannmuller 1979; Niemi et al. 1995; Samson 1979; Temple et al. 1979; Thompson and Capen 1988; Tyler in Bent 1942; Walk et al. 2011; Watt et al. 2020).

At the landscape level in southern Ontario, abundance of the Eastern Wood-Pewee was negatively correlated with the amount of forest cover 100 m or more from edge, woodlot size, the amount of forest cover within 2 km, and the amount of regional forest cover. All relationships except the last one were significant (Austen et al. 2001). In North Dakota 400-m landscapes with less than 30% tree cover, its probability of occurrence increased linearly as tree cover within 100 m increased from 20% to 70%. In landscapes with more than 30% tree cover, its probability of occurrence increased as tree cover increased from 20% to 50%, then levelled off and declined as tree coverage increased to 90-100%. The probability of occurrence at 70% tree cover was greater in open than in wooded landscapes (Cunningham and Johnson 2016). In North Dakota, it preferred landscapes that were 59-75% forested; no areas had more than 75% forest cover there. In New York, it selected landscapes that were 81-100% forested (Cunningham and Johnson 2019). In Missouri, its density was negatively affected by forest cover within 10 km and by increasing sapling density at the point. Density peaked at high levels of canopy cover and low levels of forest cover in the landscape. It may be best adapted to open wooded habitats at the landscape scale (Watt et al. 2020). Using Breeding Bird Survey (BBS) data for the south-central states, Brennan and Schnell (2007) determined that the Eastern Wood-Pewee appeared to be most abundant in relatively undisturbed areas with high edge-to-interior ratios. Populations tended to be higher in densely wooded areas and lower in more sparsely wooded locations. Grundel and Pavlovic (2007a) reported similar results from Indiana. The Eastern Wood-Pewee was significantly more abundant in forested areas with more than 90% crown closure than any other habitats. There were no significant differences in its abundance in savannahs, woodlands with 50-90% canopy closure, and shrub habitat, where it was significantly more abundant than in open areas with less than 20% canopy closure. Grundel and Pavlovic (2007b) reported highest densities of wood-pewees at tree densities of 375-500 per ha, with numbers declining with lower or higher tree densities.

In Muskosa District and Haliburton County, the Eastern Wood-Pewee was associated with higher tree canopy volume and tree density, characteristic of the periphery of a clearing. It was typically found in forest edges of cottage clearings regardless of the size of the lot (Clarke et al. 1983).

In a Connecticut woodlot over a 59-year period, there was a progressive shift to larger trees, a sparser shrub layer, and a less diverse tree canopy dominated more by oaks and maples with a severe decline in hemlock. There was no change in the abundance of the wood-pewee despite the authors' expectations that it would increase in response to declines in hemlock (Buchanan et al. 2016).

The Eastern Wood-Pewee is not an area-sensitive species; it nests in forest edges and suburban habitats. In Illinois, it nested in forest patches as small as 1.8 ha and in Iowa it nested in riparian corridors as narrow as 20 m (Watt et al. 2020). In the mid-Atlantic states, its probability of detection was similar for forests 0.3-3,200 ha in area, but it preferred woodlands larger than 2-4 ha (Robbins 1979; Robbins et al. 1989). In Pennsylvania, abundance of the wood-pewee was positively associated with forest size. In southern Ontario, it occasionally nests along gravel roads with mature trees on either side that form a canopy over the road (personal observation). In North Dakota, its abundance was positively associated with forest size and the number of trees larger than 23.1 cm DBH. Probability of observation in aspen groves of different sizes was approximately 13% in 1-ha woodlots, 85% in 10-ha woodlots, and 100% in 70-ha and larger forests (Grant and Berkey 1999).

Except for 1 nest in a shrub, all Ontario nests were in trees. Ninety-three percent of nests were in deciduous trees, most of which were alive, although the limbs that nests were on were often dead. Tree species most frequently selected for nesting were elm, oak, maple, birch, and apple, and many nest trees were large and mature. Most nests were well out from the trunk on a horizontal limb, either at natural forks or forks created by the intersection of limbs or saddled on the upper surface of a limb. Diameters of limbs with nests ranged from 3.8 to 5 cm, and the distance of the nest from the trunk ranged from 0.6 to 6 m, with most 1.5-3 m from the trunk. Height from ground ranged from 1.8 to 21 m, with most 4.5-9 m up (Peck and James 1987).

Nest placement is similar in other areas. Other tree species that it has nested in include willow, black walnut, pear, flowering dogwood, and sycamore. In Missouri, nests were 2.5-26.6 m from the ground (mean 18 m). Manitoba nests averaged 7.0 m from the ground. Nests tend to be placed higher than those of the Least Flycatcher. The wood-pewee has been observed robbing materials from Ruby-throated Hummingbird and tanager nests to construct its own nest. Nest materials may be taken from within-season failed or successful nests and used to build a new nest. Nests may be reused for second broods but failed nests are not used for replacement clutches (Graber et al. 1974; Johnston 1971; Kendrick et al. 2013, 2014; Limoges in Gauthier and Aubry 1996; McIlwraith 1894; Trail 1987; Tyler in Bent 1942; Underwood et al. 2004; Watt et al. 2020).

The wood-pewee is a fierce defender of its territory, expelling other wood-pewees as well as Mourning Doves, phoebes, Blue Jays, bluebirds, Field Sparrows, grackles, and gray squirrels. Least Flycatchers and Great Crested Flycatchers are tolerated. Territory sizes of 0.4-7.7 ha have been reported, but larger estimates may have been home ranges rather than territories. In eastern Ontario, territories averaged 1.70 ha in deciduous forests, 1.83 ha in pine plantations, and 1.76 ha overall

(Falconer and Nol 2020). In Quebec, territories were 0.4-1.3 ha and home ranges were 4 ha or larger. Territories averaged 0.71 ha in sugar maple stands and 0.46 ha in hemlock stands. Quebec territory sizes are similar to those reported from Illinois and Kansas (Fitch 1958; Graber et al. 1974; Johnston 1971; Limoges in Gauthier and Aubry 1996; Watt et al. 2020). Near Quebec City territories were randomly distributed through forests with no evidence of clumping or colonialism (Bourque and Desrochers 2006).

No information is available on natal philopatry but no males returned as yearlings in Ohio (Watt et al. 2020). Limited evidence suggests that adults have a moderate to high homing rate to nesting areas. In Illinois, 22.2% of birds were recaptured the next year. In Ohio, 100% of breeding adults returned the following year (Newell et al. 2013). In northern Ohio, 29-57% of males returned over a 3-year period (Watt et al. 2020). Tyler (in Bent 1942) stated that females returned year after year to the same group of trees and often built a nest on the same branch. In 1 instance, there was a nest in the same fork of a tree for 35 years. There are 2 breeding season recoveries of banded adults. One was recaptured at the same banding station in Quebec almost exactly a year after it was banded there, suggesting breeding-site fidelity. The other was banded during the breeding season in Michigan and recovered 2 years later in Quebec, indicating movement between nesting seasons (Brewer et al. 2018).

Limiting Factors

Eggs have been found in Ontario nests throughout June and July until mid-August, with most clutches present in the last half of June and the first week of July (Peck and James 1987). In Algonquin Park, nests are under construction in early June, eggs are present from mid-June to early July, nestlings are present from early to mid-July, and fledglings have been observed from late July until early September (Tozer 2012).

The pair bond is established shortly after the birds arrive. The pair travels around the territory together, checking several sites before starting to build the nest. Nest construction takes about 6 days (range 4-10 days). Eggs are laid on consecutive days. The incubation period appears to be 12-14 days. It may be longer than this because the mean incubation period in Missouri was 14.1 days. Young fledge at age 16-18 days. In Missouri, the mean length of the nesting cycle from the initiation of a clutch until fledging was 35.5 days, including 14.1 days for incubation and 15.4 days for the nestling period; mean nesting period in Ohio was 17.2 days (Kendrick et al. 2014; Limoges in Gauthier and Aubry 1996; Newell et al. 2013; Tyler in Bent 1942; Watt et al. 2020).

Breeding activity extends into August or even September in some areas, so it is likely that more than 1 brood is raised (Watt et al. 2020). In eastern Ontario, 16.9% of pairs were suspected of double-brooding (Falconer and Nol 2020). Newell et al. (2013) confirmed double-brooding in Ohio when a female reshaped a nest in which she had fledged 3 young 10 days previously. A total of 5 young were fledged by this pair in this nest. There was another apparent case of a double brood and 6-12% of pairs may have raised 2 broods. In Missouri, Kendrick et al. (2014) reported that 19 of 92 pairs (20.6%) that successfully raised a first brood attempted a second brood, but only 3 (15.8%) were successful. An average of 9.4 days elapsed between a successful nest and the first egg of the second clutch. Nine pairs reused their nest for a second brood but none were successful. Mean distance between subsequent nests was 42.7 m (range 23.5-72.6 m). Curry (2006) reported a 1961 nest from

Speyside that contained half-grown young on 3 July and 2 young later on 19 August, suggesting that 2 broods were raised in this nest. Newell et al. (2013) confirmed that renesting occurs if a clutch is lost. In Missouri, 53 pairs attempted a second nest after failure and 5 attempted a third nest with an average of 8.15 days between nest failure and the first egg in a replacement clutch. One pair made 3 unsuccessful attempts to raise a second brood, thus making 4 nesting attempts (Kendrick et al. 2014). One to 4 eggs have been reported in Ontario nests, with over 60% of clutches containing 3 eggs (Peck and James 1987). The normal clutch size is 2-4 eggs, with 3 eggs typical. Four-egg clutches are rare and a 5-egg clutch was reported in Illinois. Clutch size declined with time in Missouri (Graber et al. 1974; Kendrick et al. 2013; McIlwraith 1894; Tyler in Bent 1942; Watt et al. 2020).

The age at first breeding is undocumented. It is likely that second-year birds breed because yearlings with brood patches have been captured. The mating system is typically monogamous (Watt et al. 2020) but Newell et al. (2013) confirmed polygyny in Ohio. One male was mated polygynously in 2 consecutive years and 5 other cases of polygyny were observed. The 6 males were each seen with 2 different females that had nests an average of 110 m apart. Over a 2-year period, at least 6.3% and 21.7% of males were polygynous. Polygynous males had nests on xeric ridges in areas of greater basal area of oaks, and this was preferred habitat. Eleven percent of 53 eastern Ontario males were polygynous (Savignac 2012a).

The wood-pewee forages in the lower edge of the forest canopy, or just below it. In 1 study area, foraging height ranged from 8 to 14 m (mean 11 m), higher than the average foraging height of Least Flycatchers and lower than that of Great Crested Flycatchers. While foraging, the wood-pewee perches more in dead trees or on dead limbs and twigs than other flycatchers. Over 90% of food is obtained by sallying from a perch a distance of less than 1 m to more than 30 m (average 5.2 m) to catch flying insects. It may use the same foraging sites and perches for an entire season. The remainder of food is obtained by gleaning insects from foliage or from the ground. During periods of emergence of aquatic insects, these may be captured near the surface of the water (Graber et al. 1974; Johnston 1971; Keast et al. 1995; Limoges in Gauthier and Aubry 1996; Watt et al. 2020). In Illinois in open-canopy habitat, it foraged in tree species according to their availability. In closed-canopy forest, it foraged in black oak and white oak more than expected and less than expected in sugar maple and red elm based on tree availability. It also foraged more than expected in black locust and hackberry. In open-canopy habitat, the shrub layer (0-5 m from the ground) and subcanopy (6-10 m) were the preferred foraging strata, accounting for 68% of foraging activities; 27% of foraging activity occurred at 11-15 m and 5% at heights of 16 m or more. In closed-canopy habitat, the wood-pewee showed an aversion to foraging in the shrub layer, with only 14% of foraging activity there compared with 36% in open-canopy areas. The subcanopy level was preferred for foraging in closed-canopy forests (37% of activity), with 22% of foraging at heights of 11-15 m and 27% higher than 16 m. It obtained prey by flycatching significantly more often in open-canopy habitat and sallying more often in closed-canopy forest (Hartung and Brawn 2005).

Almost all the diet is comprised of flying insects, although approximately 1% of the food is vegetable matter. The wood-pewee preys on insects 5-30 mm in length, with most food items 10-14 mm long, intermediate in size between the Least Flycatcher and Great Crested Flycatcher. Diet overlap with the Least Flycatcher and Great Crested Flycatcher is 46% and 25% respectively. Most

food brought to nestlings is minute, although occasionally larger items may be brought such as cabbage white butterflies, damselflies, and crane flies. Dominant food items include flies, bugs, moths, butterflies, hymenopterans, beetles, grasshoppers, stoneflies, and mayflies. Young nestlings in 1 nest had consumed 52.5% grasshoppers, 32.5% bugs, and 15% spiders. Another brood had eaten 66% orthopterans, 12.5% flies, 17.5% caterpillars, and 4% spiders. Important insects in adults' diet include flies (house, blow, dance, root-maggot, snipe, and flower flies), beetles (leaf, ground, and long-horned beetles), moths, ichneumonid wasps, ants, leaf bugs, and treehoppers. It also eats spiders and millipedes in small numbers. Vegetable matter eaten includes fruits of elderberries, raspberries, dogwoods, pokeweed, blueberries, poison ivy, and panic grasses. There is a report of it capturing trout fry in a pond. Feeding habits and diet are similar during migration (Graber et al. 1974; Johnston 1971; Kendrick et al. 2014; Tyler in Bent 1942; Watt et al. 2020).

The Eastern Wood-Pewee is vulnerable to Brown-headed Cowbird parasitism and frequently only cowbirds are fledged from parasitized nests (Tyler in Bent 1942; Watt et al. 2020). The rate of parasitism is low throughout its range at 5.4% (Underwood et al. 2004). In Ontario, 5.5% of 165 nests were parasitized (Peck and James 1997) and 1 of 202 eastern Ontario nests (0.5%) was parasitized (Falconer and Nol 2020). In Missouri, 4 of 310 nests (1.3%) and 0 of 133 nests were parasitized (Kendrick et al. 2013; Roach et al. 2018). In Manitoba, Underwood et al. (2004) monitored 20 wood-pewee nests and added real or artificial cowbird eggs to 12 nests. None of the nests were parasitized naturally by cowbirds, and all parasitic eggs were accepted. The low frequency of wood-pewee parasitism may be to high placement of nests and breeding season asynchrony. Average wood-pewee nest height was 7.0 m. In the same area, Yellow Warblers were a common host of the cowbird, but nests higher than 5 m from the ground were rarely parasitized. The average date of wood-pewee clutch initiation was 23 June whereas the average last date of egg laying by cowbirds was 25 June. Wood-pewees are highly aggressive toward cowbirds and this may deter parasitism (Watt et al. 2020).

The wood-pewee is not considered vulnerable to forest fragmentation because it breeds in small remnant woodlots. In West Virginia, Farwell et al. (2019) examined its response to shale gas infrastructure, which consisted of well pads, access roads, and pipelines. It increased in abundance near all facilities. The forest gaps created by infrastructure provided additional habitat for it. In fragmented Illinois forests, the ratio of hatching-year to after-hatching-year birds was 0.2 indicating poor reproductive success (Robinson 1992; Watt et al. 2020). In New Jersey, Rich et al. (1994) examined the effects of different widths and types of fragmenting corridors on the wood-pewee. It was significantly more abundant adjacent to unpaved roads creating an opening 8 m wide than adjacent to 23-m wide power-line corridors. In South Dakota, it was significantly more abundant in large contiguous riparian forests than in small, isolated woodlots (Gentry et al. 2006).

The wood-pewee is unaffected by forest harvesting, or increases. A review of 42 studies on the effects of partial harvesting of forests found no significant effects on the wood-pewee (Vanderwel et al. 2007). Holmes and Pitt (2007) examined the effects of selection harvesting near Sault Ste. Marie in northern hardwood stands. It increased after stands were harvested. In Algonquin Park, Jobes et al. (2004) and Tozer et al. (2010) found no difference in abundance of wood-pewees in areas subjected to varying intensities of group-selection forest harvesting (0.5 and 4 gaps per ha). In

Illinois, Robinson and Robinson (1999) created openings of 0.02-0.4 ha within a 2,000-ha forest. The wood-pewee was significantly more abundant in recently cut ravines than in uncut ravines, but was not affected by logging on ridges. In Minnesota, it exhibited a modest increase following timber harvest (Hanowski et al. 2002). Forestry practices that convert woodlands to areas dominated by poplars are detrimental because this habitat is seldom used. Removal of old large trees, dying trees, and snags has a negative effect due to loss of foraging and nesting habitat (Niemi et al. 1995; Pashley and Barrow 1992). In Missouri, daily nest survival rate was negatively correlated with mean canopy cover within 150 m of the nest. A more open canopy may provide an ideal mix of perching sites and open spaces to maximize foraging efficiency (Roach et al. 2018).

Although the wood-pewee nested in similar densities in pine plantations and deciduous forests in eastern Ontario, nesting success was lower in plantations due to higher abundance of predatory red squirrels and Blue Jays. In plantations, nest survival was higher where trees were more dispersed. Nests further from tree trunks had better survival in deciduous stands (Falconer and Nol. 2020).

In forests sprayed for gypsy moth control, the Eastern Wood-Pewee had reduced stores of subcutaneous fat, probably due to reduced populations of insect prey. The diet of those on sprayed and unsprayed plots differed significantly, with flies and bugs being more important in the diet on sprayed plots (Sample et al. 1993).

In North Carolina, abundance of the wood-pewee was negatively correlated with the number of houses and buildings within 200 m of the centre of the habitat patch (Lumpkin and Pearson 2013). In urban forests of Chicago, it had strong negative associations with distance to edge and amount of urban cover. It exhibited a strong positive response to increases in oak trees and a negative association with nonnative honeysuckles (Schneider and Miller 2014). Other studies have observed lower densities of the wood-pewee in sites heavily invaded by honeysuckle than in sites with native shrub understories.

Browsing by white-tailed deer may have contributed to the decline of the Eastern Wood-Pewee. In the northeastern states, it was not found breeding on plots with more than 8 deer per km^2. Heavy browsing results in fewer trees in the subcanopy, the area where it typically forages (Niemi et al. 1995; Watt et al. 2020). Nonetheless, the wood-pewee persisted at Rondeau when deer populations were as high as 55 per km^2 (Savignac 2012a).

In Quebec, declines of sugar maple forests affected wood-pewee breeding densities. In stands affected by die-back, densities were 27% lower than in healthy stands. Die-back of the canopy had adverse effects on birds inhabiting the upper canopy; species preferring the shrub layer increased (DesGranges et al. 1987).

In Pennsylvania, Rohnke and Yahner (2008) examined the same woodland twice 16 years apart. During this time, overstorey and subcanopy tree density decreased as did short shrubs, but tall shrub density increased. The Eastern Wood-Pewee declined by 90% apparently due to changes in forest structure. Habitat quality for it may decline as second-growth forests mature, and large tracts of homogeneous deciduous forest with few canopy gaps are of lesser quality (Ahlering and Faaborg 2006).

In New Jersey and Pennsylvania, hemlock declined from 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The wood-pewee responded favourably to hemlock decline and increased (Toenies et al. 2018).

In Georgia, the Eastern Wood-Pewee increased relative to fire severity. More severe fires suppressed the understorey and created more open-canopy conditions, resulting in higher insect abundance and improved foraging habitat (Klaus et al. 2010). In North Carolina pine-oak forests, it also responded favourably to fire. It occurred more frequently immediately following fire, regardless of its severity and declined with time since fire. Peak occupancy occurred at sites where there had been a severe burn in the past 0-5 years (Rose and Simons 2016). Fire suppression may be a limiting factor for the wood-pewee.

Status

The Eastern Wood-Pewee has always been a common breeding species in Ontario, and it presumably was more abundant before extensive forest clearing took place. McIlwraith (1894) stated that it was distributed throughout the province and Baillie and Harrington (1937) considered it a fairly common breeder north to southern Thunder Bay and southern Sudbury districts. They noted that there were breeding season records further north from Spanish River, Lake of the Woods, and Temagami. During the first atlas, it was common in most of Ontario south of the French and Mattawa rivers (Rising in Cadman et al. 1987). James (1991) considered it common in the south, becoming locally uncommon in the north to Woodland Caribou Provincial Park and Cochrane.

The second atlas indicated that the province-wide probability of observation of the Eastern Wood-Pewee had not changed significantly since the first atlas. Significant declines occurred in the Great Lakes–St. Lawrence Forest Region both in and south of the Canadian Shield, with a significant increase in the Boreal Forest Region. It was most abundant south of the Shield where it occurred in almost every square and its probability of observation was over 80%. Highest densities occurred in a broad band along the southern edge of the Shield, on the Bruce Peninsula, in a band from Toronto to Wellington County and down to Long Point, and in a few smaller areas south of the Shield (McLaren in Cadman et al. 2007).

Although there has been no historical change in the Eastern Wood-Pewee's North American breeding distribution (Watt et al. 2020), BBS data indicate a significant continental decline. An exception is in Illinois where its population has remained stable since the early 1900s despite substantial changes to the structure and composition of forests due to widespread logging in the 1800s and early 1900s, exposure to pesticides, and reductions in wintering habitat (Walk et al. 2011). Over the long-term (1970-2021), trends determined by the BBS were annual decreases of 2.17% in Canada and 1.61% in Ontario. The short-term trends (2011-21) were increases of 0.911% annually in Canada and 0.902% in Ontario. The reliability of all results was high (A.C. Smith et al. 2023).

The Eastern Wood-Pewee has been designated special concern nationally and provincially.

POSTFLEDGING PERIOD

Fledglings can fly when they leave the nest, but those younger than 18 days old often remain lower in shrubs. They follow the adults around begging for food for 3-4 weeks after fledging (Watt et al. 2020).

In Ohio, juvenile and adult Eastern Wood-Pewees moved to densely regenerating clear-cuts during the post-breeding period. Early successional habitats may be important shortly after breeding because they provide dense cover and abundant food resources (Vitz and Rodewald 2006, 2007). In Michigan, Akresh et al. (2009) captured 100% of juvenile wood-pewees in riparian versus upland habitat. Riparian habitat was dominated by trembling aspen with an understorey of alder and honeysuckle. Upland habitat was even-aged trembling and large-toothed aspen. In Minnesota, Streby et al. (2011b) did not capture any wood-pewees in regenerating clear-cuts during the breeding season, but caught 2 fledglings and 10 adults during the postbreeding season. In Missouri, Porneluzi et al. (2014) netted birds during the postfledging period in an oak-pine-hickory forest 2-15 years after it was clear-cut. There was no significant trend over time in abundance of the wood-pewee during the study.

MIGRATION

The Eastern Wood-Pewee is known to migrate at night due to kills at television towers, but it is unknown if migration also occurs during the day. It has been observed in morning flights in New Jersey suggesting that some diurnal migration occurs (Graber et al. 1974; Watt et al. 2020).

First arrivals usually occur in Ontario around mid-May, although the peak of migration is around the end of May. Autumn migration is predominantly in August, but birds may start to move southward in July. Adults migrate first, and it is regularly seen in small numbers until mid-October (James 1991; Watt et al. 2020).

During migration, the wood-pewee may be found in a variety of habitats where there are trees and shrubs. These include forest edges, early successional clearings, deciduous and mixed woodlands (Watt et al. 2020), hedgerows, and rural and suburban lots. During autumn migration in Pennsylvania, mean abundance was not significantly different in forest interior, forest-agricultural edge, or suburban habitat, but mean abundance in these habitats was significantly higher than in pole-stage forest and shrub-sapling-stage forest (Rodewald and Brittingham 2004). During spring migration in Pennsylvania, it was more abundant in larger forests but no relationship between its abundance and forest size was evident in autumn (Keller and Yahner 2007).

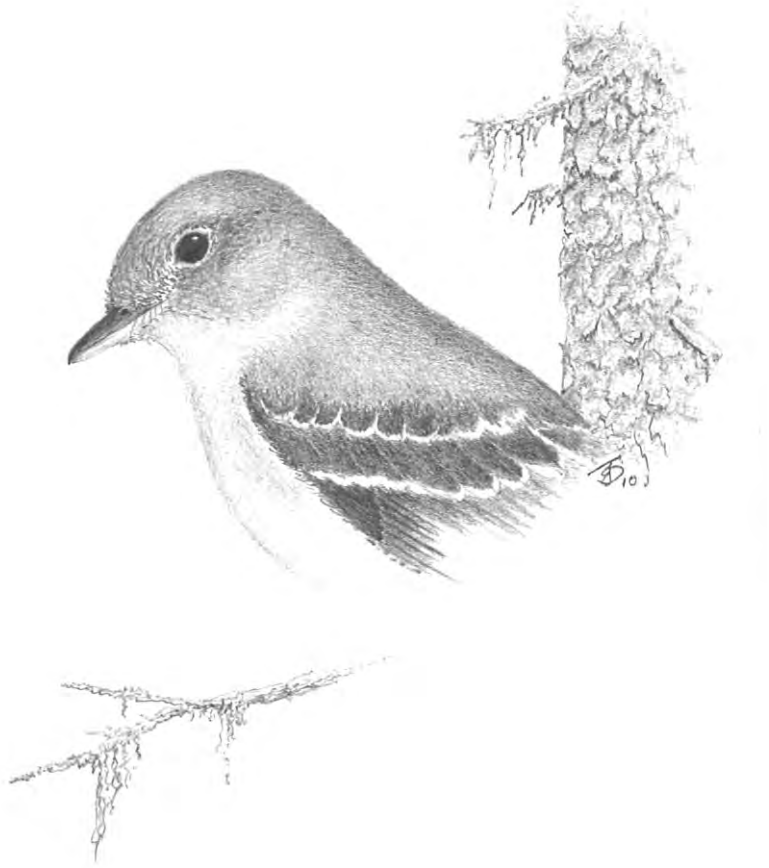
In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season for 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming during the second period. Autumn departure was significantly earlier during the second period for the Eastern Wood-Pewee, but there were no differences in spring arrival dates or length of the breeding season.

Collisions with communication towers and other tall structures are a minor source of mortality during migration (Watt et al. 2020).

The Eastern Wood-Pewee is usually solitary during migration, but is common during both spring and autumn migration (James 1991). Banding results from the Long Point Bird Observatory since 1960 show significant increases in both spring (1.5% per year) and autumn (1.8% per year). It declined in the late 1960s, increased during the 1970s and 1980s, and numbers levelled off in the 1990s (Anonymous 2012a; Badzinski 2000; Hussell et al. 1992).

Yellow-bellied Flycatcher

Empidonax flaviventris



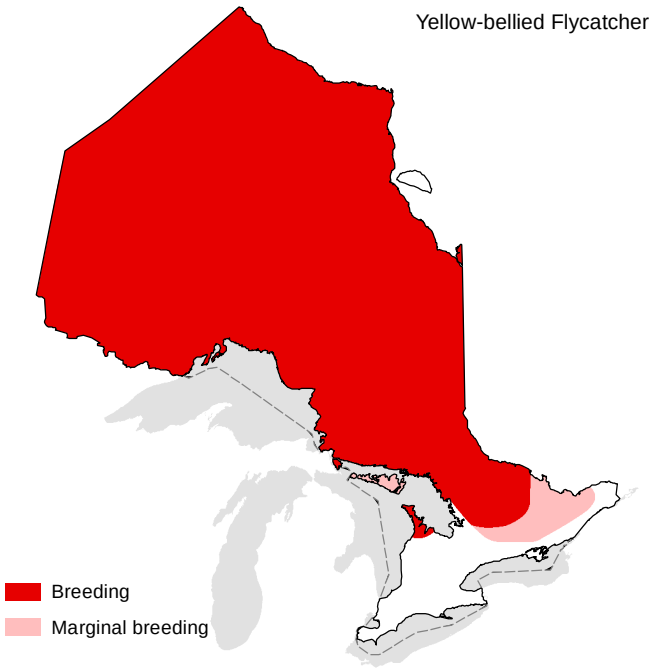
BREEDING SEASON

Habitat Requirements

The Yellow-bellied Flycatcher nests in 2 distinct habitat types: coniferous forests and forested cliffs or steep, rocky slopes. In Ontario, it nests most frequently in bogs and fens dominated by black spruce, and also damp to wet forests of tamarack, white cedar, and balsam fir (Peck and James 1987).

In the Hudson Bay Lowland, the Yellow-bellied Flycatcher occurs wherever there are large forested areas, nesting mostly in spruce-tamarack fens (Wilson and McRae 1993).

In the Boreal Forest Region of Ontario, abundance of the Yellow-bellied Flycatcher was significantly correlated with forest stand age at the local level of 50 ha and the amount of edge and intact mature and old forest at a landscape scale of 5,000 ha. It was associated with older, closed, coniferous forests within a mature forest matrix (Rempel 2007). Near Pickle Lake, it occurred mostly in spruce forests but also in dense jack pine regeneration (James 1980). North of Lake Nipigon, it nested solely within alder swamps (Kendeigh 1947). Near Hearst, it nested in uncut upland mixed



and lowland coniferous stands and in clear-cuts 11-24 years old (Welsh and Fillman 1980). Near White River, it was more abundant in clear-cuts 18-20 years old than in clear-cuts 3-15 and 23-25 years old and in mature forests, but not significantly (Venier and Pearce 2005). In the Clay Belt, it was most abundant in wet stands that were nutrient poor. It was associated with mid-succession forests (Welsh 1993; Welsh and Lougheed 1996).

In the Great Lakes–St. Lawrence Forest Region near Gogama, the Yellow-bellied Flycatcher was characteristic of jack pine stands and was rare to absent when deciduous trees exceeded 10% of cover. The pines in inhabited areas were often only 6-8 m tall, but canopy coverage was always greater than 75% and tree cover was often very dense. In young pine stands, shrubs were almost absent in breeding areas, but shrubs covered as much as 50% of the ground in areas where trees were taller. Sheep laurel and blueberries were the dominant shrubs. Maximum densities occurred in young stands where tree branches were near the ground (James and Peck 1995a). It also occurs in mature and old-growth white pine stands in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield (Kirk et al. 2012). In Algonquin Park, it nests in dense coniferous forests that are a mix of red and white pine, hemlock, white cedar, and balsam fir, as well as in bogs. Dry mixed-wood forests are occasionally used for nesting. The other main breeding habitat includes forested cliffs and talus slopes. These consist of steep, rocky slopes and cliffs as tall as 100 m, and it also nests sparingly in similar habitat along the Niagara Escarpment. In nesting areas, the vegetation is structurally diverse with canopy trees, a sapling and shrub layer (often of wild raisin, grey alder, and mountain holly), and the ground is usually carpeted with mosses or lichens. The understorey is often quite dense (Brunton and Crins 1975; Crins in Cadman et al. 2007; Peck and James 1987; Prescott in Cadman et al. 1987; Tozer 2012).

Throughout its range, the Yellow-bellied Flycatcher occurs predominantly in coniferous forests. In the eastern Boreal Forest Region, it is typical of spruce forests and is more common in young stands (Erskine 1977). In Quebec, it occurs mainly in stands of intolerant hardwoods and jack pine, and is uncommon or even absent in spruce stands and peatlands (Limoges in Gauthier and Aubry 1996). Nonetheless, it nested in young and mature black spruce forests in Quebec and in clear-cuts where saplings were 2-5 m tall. It was absent in younger clear-cuts and recent burns. It was equally abundant in all habitats that it occupied (Imbeau et al. 1999). This flycatcher also prefers cool mountainsides and wet mixed woods with an understorey of mosses strewn with boulders and logs. In subalpine areas of New Hampshire, it occurred midslope where there was no surface water or

some wet depressions present. Average canopy height where it occurred was 9.0 m, canopy closure was 65%, and mean diameter at breast height of trees was 10 cm (Sabo 1980). There are some geographical variations in its habitat preferences. Most authors stated that it is associated with dense, young coniferous or mixed stands, but others found it more often in mature or open stands. It is usually found in mesic sites that are nutrient poor. A study of populations in mixed-wood stands found that it was associated with increasing abundance of spruce or balsam fir. In another area, it occurred only in hemlock–yellow birch forests (Beals 1960; Bent 1942; Campbell et al. 1997; Dawson 1979; DeGraaf and Chadwick 1987; Gross and Lowther 2020; Kirk et al. 1996; McLaren and McLaren 1981; Niemi and Pfannmuller 1979; Smith 1957; Temple et al. 1979; Thompson et al. 1999; Walkinshaw and Henry 1957b).

Ralston et al. (2019) surveyed for the Yellow-bellied Flycatcher in boreal forest habitat at 20 locations in New York, Vermont, Maine, Nova Scotia, and Newfoundland. It was observed at 19 of the 20 sites indicating that it had broad habitat preferences and an ability to use multiple boreal forest habitats.

In Newfoundland balsam fir stands, Whitaker and Montevecchi (1997, 1999) considered the Yellow-bellied Flycatcher a forest-interior specialist. It was significantly more abundant in forest interior than in riparian forest edges, but there was no significant difference in its abundance in forest interior and nonriparian forest edges. There was also no difference in its abundance in riparian areas of extensive forests and in 20-50-m wide riparian strips retained adjacent to clear-cuts. In balsam fir–white cedar forests in eastern Quebec, there was no significant difference in its density in riparian and nonriparian stands (LaRue et al. 1995). In Minnesota, its abundance was positively correlated with lowland conifers, black spruce, and tamarack. Forty-five percent of the variation in its abundance was related to nutrient-poor stands of black spruce, tamarack, and white cedar; 28% with patch richness within 500 m; 14% with increasing stand age; and 11% with stand area. The Yellow-bellied Flycatcher was the most abundant boreal species and was found in most stands and point locations. It appeared to breed in most lowland coniferous forests. It preferentially selected nutrient-poor stands surrounded by a variety of forest types. The models for it were not significant, suggesting that it was a generalist species (Zlonis et al. 2017).

All Ontario nests were on the ground, usually in mosses but occasionally in grasses or leaves. Hummocks in moss and moss-covered logs were frequently selected for nest sites (Brunton and Crins 1975; Peck and James 1987).

Ontario nests are typical of those reported throughout the Yellow-bellied Flycatcher's range. The centre of the nesting territory is usually heavily vegetated with mosses, forbs, sedges, ferns, shrubs, and small trees. The nest site is characteristically cool, moist, and shady. Nests are usually on the ground in mosses, but occasionally in mud or cavities in upturned roots of fallen trees. Some nests were under roots of standing trees or stumps, and on cliffs near watercourses. The nest is usually extremely well hidden and invisible from directly above and embedded in moss or at the base of a fern under dead stems from the previous year (Bent 1942; Gross and Lowther 2020; Walkinshaw and Henry 1957b).

Little information on territory size is available. Limoges (in Gauthier and Aubry 1996) reported that the territory size of a single pair near Black Sturgeon Lake in Ontario was 1.01 ha in an alder swamp. In Pennsylvania, territories were 0.7-1.0 ha (Gross and Lowther 2020). In subalpine areas of New Hampshire, territories averaged 1.8 ha (Sabo 1980). In Alaska, singing males were at least 100 m apart (Gross and Lowther 2020).

No information is available on natal philopatry or breeding site fidelity by adults.

Limiting Factors

Eggs have been found in Ontario nests from the second week of June until the third week of July, but most clutches are present during the last third of June (Peck and James 1987, 1997). In Algonquin Park, clutches usually occur in the last half of June and young hatch in the first half of July (Brunton and Crins 1975). Eggs are laid at 1-day intervals, and incubation presumably begins with the laying of the last egg. The incubation periods of 2 Ontario nests were at least 13 days and 15 days. Elsewhere the incubation period has been determined to be 15 days and young fledge when they are 13-15 days old (Gross and Lowther 2020; Peck and James 1987, 1997; Walkinshaw and Henry 1957b).

Usually only 1 brood is raised annually, but some pairs in the Appalachians are double brooded. Egg dates in Wisconsin suggest that double-brooding may occur there. The male tends to the first brood while the female builds another nest for the second brood in a new location within the territory. The original nest may be used for the second brood. It is unknown if renesting occurs after a clutch is lost. Clutches of 4 and 5 eggs have been reported in Ontario, with most containing 4 eggs. Elsewhere, most clutches contain 4 eggs, with 3-and 5-egg clutches uncommon to rare respectively. In second clutches in Pennsylvania, 5 contained 3 eggs and 2 contained 4 eggs (Bent 1942; Brunton and Crins 1975; Campbell et al. 1997; Gross and Lowther 2020; McIlwraith 1894; Walkinshaw and Henry 1957b).

The age at first breeding is 1 year, and the mating system is seasonally monogamous. In Pennsylvania, unmated males defended territories adjacent to mated males, providing the potential for extra-pair mating (Gross and Lowther 2020).

The Yellow-bellied Flycatcher obtains most food by sallying from a perch to catch flying insects, but also gleans invertebrates from vegetation. It forages predominantly in the understorey, particularly in low, dense conifers and shrubs. In Ontario, 72% of foraging occurred in deciduous trees and 28% in conifers (Greenberg et al. 1999). In New Hampshire, 42% of foraging was on coniferous foliage and 56.8% was on deciduous foliage. Foraging heights were 1.1% at 0.1-2 m, 47.5% at 2-5 m, 42.4% at 5-8 m, and 8.9% above 8 m (Sabo 1980).

Kendeigh (1947) analyzed the stomach contents of 2 birds north of Lake Nipigon. By frequency, the diet consisted of 25.8% spiders, 24.7% beetles (including click and leaf beetles), 23.7% lepidopterans, 12.1% dance flies, 6.3% stink bugs, 6.3% ants, and 1.1% lepidopterans. An examination of 103 stomachs revealed that 97% of the diet consisted of animal material and the remainder was vegetable matter. The diet consisted of 46.3% hymenopterans (including 13.4% ants), 16.5% beetles, 14.9% flies (house, crane, and horse flies), 8.5% spiders, and adult and larval moths. Vegetation that the Yellow-bellied Flycatcher ate included mountain-ash berries, poison ivy berries, cedar foliage,

and general vegetation rubbish. In the breeding season, it eats midges, stoneflies, crane flies, beetles, small caterpillars, spruce budworm larvae, and mosquitoes (Bent 1942; Crawford and Jennings 1989; Graber et al. 1974; Gross and Lowther 2020). Near Manitouwadge, abundance of the Yellow-bellied Flycatcher was not correlated with spruce budworm abundance (Venier et al. 2009). Similar results were found in New Brunswick (Morris et al. 1958). Mitchell (1952) analyzed the contents of 10 stomachs in 2 years during a spruce budworm outbreak in Maine. By volume, they contained 0% and 10% budworm larvae and pupae.

The Yellow-bellied Flycatcher is not very vulnerable to cowbird parasitism and few parasitized nests have been reported. Of 18 Ontario nests and 6 Michigan nests, none were parasitized (Peck and James 1997; Walkinshaw 1961). Campbell et al. (1997) reported that 2 British Columbia nests were not parasitized and that only 3 parasitized nests had been documented in North America. The habitat and range of the Yellow-bellied Flycatcher and Brown-headed Cowbird do not overlap much.

Conversion of coniferous forests to intolerant hardwoods may reduce habitat quality for the Yellow-bellied Flycatcher. Its primary habitats, coniferous swamps and talus slopes, are typically protected from forestry and development activities. Forest fragmentation may result in drying and loss of mosses that nests are associated with (Gross and Lowther 2020). Vanderwel et al. (2009) reviewed studies on the effects of partial harvesting of forest. There was no evidence of change in its abundance when 30%, 50%, or 70% of trees were removed. In the Canadian Shield of Ontario, there was no difference in its abundance in early successional clear-cuts and burns, but it was significantly more abundant in mid-successional clear-cuts than in mid-successional burns. It was equally abundant in early successional, mid-successional, and mature stands (Zimmerling et al. 2017). In Newfoundland, it occurred in 49% of cut forests and 38% of natural forests. Its presence was unaffected by the amount of forest cover in the landscape (Taylor and Krawchuk 2005). Whitaker et al. (2008) netted 59% of birds in cut forests and 41% in natural forests. In Minnesota, where it was the most abundant species, Zlonis et al. (2017) did not find it in clear-cuts and concluded that it would be negatively affected by extensive logging.

On Anticosti Island, the Yellow-bellied Flycatcher was able to use the ground layer of vegetation in a recently harvested clear-cut despite high densities of white-tailed deer. Browsing by deer reduced the amount of deciduous cover, especially white birch, but spruce was unaffected. It preferred coniferous cover (Cardinal et al. 2012).

In Alberta, there were no significant differences in the abundance of the Yellow-bellied Flycatcher at seismic lines, pipelines, or well pads than in forest interior adjacent to these features (Bayne et al. 2016).

Burris and Haney (2005) studied the impact of blowdown of spruce-fir forests in Minnesota. Blowdown resulted in a significant decline in canopy cover and an increase in the shrub layer. Significantly more Yellow-bellied Flycatchers occurred in the blowdown than in control plots. Its presence was correlated with shrub cover, and possibly coarse woody debris.

Price (2004) predicted that the Yellow-bellied Flycatcher would disappear as a breeding species in southern Ontario if the average summer temperature increased by 2°C. In the Boreal Forest Region

of Quebec and Labrador, its abundance was associated with cooler breeding season temperatures and relatively lower amounts of breeding season precipitation. Warming trends might adversely affect it (DesGranges and LeBlanc 2012).

Status

McIlwraith (1894) had records of the Yellow-bellied Flycatcher only during migration, but correctly presumed that it bred in the province. He considered it scarce everywhere. Baillie and Harrington (1937) stated that it was a summer resident from northern Wellington County north to the trans-Canada railway and west to Lake of the Woods. The southeastern breeding limit was Mer Bleue and there was 1 historical breeding record from Amherst Island. At that time, breeding had been confirmed from Wellington and Bruce counties and Parry Sound and Muskoka districts. Smith (1957) found it well distributed in the Clay Belt, and Brunton and Crins (1975) stated that it was more common in Algonquin Park than previously thought. Near Pickle Lake, it was second highest in breeding density to the Ruby-crowned Kinglet (James 1980). During the first atlas, it was fairly common within its breeding range, and more abundant in the north. It ranged sparingly throughout the Canadian Shield to the northern extent of the province, with scattered records from the Bruce Peninsula and Manitoulin Island (Prescott in Cadman et al. 1987). No evidence of breeding was found in Wellington and there was only 1 record from Grey during the first atlas. Peck and James (1997) reported a nest from Grey, which was the most southerly recent record. James (1991) termed the Yellow-bellied Flycatcher uncommon in the north and rare in the south to southern Georgian Bay and Brockville.

The second atlas indicated that the Yellow-bellied Flycatcher was somewhat more widespread than documented during the first atlas, and its probability of observation more than doubled province-wide. Significant increases in its probability of observation occurred in the Canadian Shield and Hudson Bay Lowland. Greatest abundance was in the northern Shield, particularly in a wide band north of Sault Ste. Marie and New Liskeard and south of a line from Moosonee to Red Lake (Crins in Cadman et al. 2007).

Long-term (1970-2021) population trends determined by Breeding Bird Survey (BBS) results indicated annual increases of 2.23% in Canada and 2.38% in Ontario. Short-term (2011-21) trends were annual increases of 7.67% in Canada and 0.855% in Ontario. Reliability of the data was medium for long-term trends and low for short-term trends (A.C. Smith et al. 2023). Gross and Lowther (2020) stated that the Yellow-bellied Flycatcher was notoriously overlooked on the BBS and concluded that its abundance was underestimated.

POSTFLEDGING PERIOD

In Minnesota, Streby et al. (2011b) captured 4 Yellow-bellied Flycatchers during the breeding season in regenerating clear-cuts. They caught 6 fledglings and 25 adults during the postbreeding period. Major and Desrochers (2012) also captured Yellow-bellied Flycatchers in clear-cuts during the postfledging period in Quebec.

MIGRATION

The Yellow-bellied Flycatcher is a late spring migrant. At Long Point, few are observed before 24 May. Usually migration is over there by 10 June, but stragglers have occurred until 15 June. Ninety

percent of birds occurred in the 19-day period of 22 May to 9 June. Males migrated earlier in spring than females, and second-year birds probably migrated later than older birds. Twenty-two percent of males occurred prior to 21 May, the earliest date for a female. It is an early autumn migrant that probably spends no more than 66 days on the breeding grounds. At Long Point, the earliest adult arrived on 18 July and the latest was 31 August. Most adults occurred in a 33-day period from 25 July to 26 August, with 8 August the median date. Juveniles arrived in the second or third week of August. Most juveniles passed through in the 28-day period of 18 August to 15 September. There was no apparent differential timing by sexes (Hussell 1982a). In eastern North America, peak numbers of autumn migrating adults occur in mid-August. Juveniles migrate approximately 24 days later, with peaks in late August and early September (Hussell 1982b). Bent (1942) stated that it left the breeding grounds in the last half of August. He reported that migration at Point Pelee started in mid-August and continued well into September.

During migration, the Yellow-bellied Flycatcher occurs in swamp thickets along streams, on borders of swamps and ponds, in flooded willow swamps, in birch stands near beaver ponds, at edges of open trembling aspen stands, and in second-growth deciduous stands. It may also frequent edges of black spruce muskegs, mature spruce–trembling aspen–white birch stands, young to intermediate-aged trembling aspen stands, and hedgerows (Bent 1942; Campbell et al. 1997; Gross and Lowther 2020).

Because it is a nocturnal migrant, the Yellow-bellied Flycatcher is prone to being killed at television towers and other tall obstructions (Graber et al. 1974; Weir 2008).

In Pennsylvania, an infestation of the viburnum leaf beetle resulted in an almost complete loss of southern arrowwood, which previously was the third most abundant shrub species. The number of spring migrating Yellow-bellied Flycatchers decreased significantly after the loss of the arrowwood (Smith and Hatch 2017).

The Yellow-bellied Flycatcher is an uncommon migrant that is more frequent in autumn (Hussell 1982a; James 1991).

Early migration monitoring data at Long Point suggested a significant decline in the 1960s, a major increase in the 1970s, and a small decline in the 1980s. Based on these data, the population would be 22% of when banding was initiated (Hussell 1991a; Hussell et al. 1992). Badzinski (2000) analyzed trends at Long Point during migration and stated that spring numbers have been stable since 1960 but autumn numbers have declined significantly by 2% per annum. She concluded that Long Point might be sampling 2 separate populations that followed different spring and autumn routes.

Acadian Flycatcher

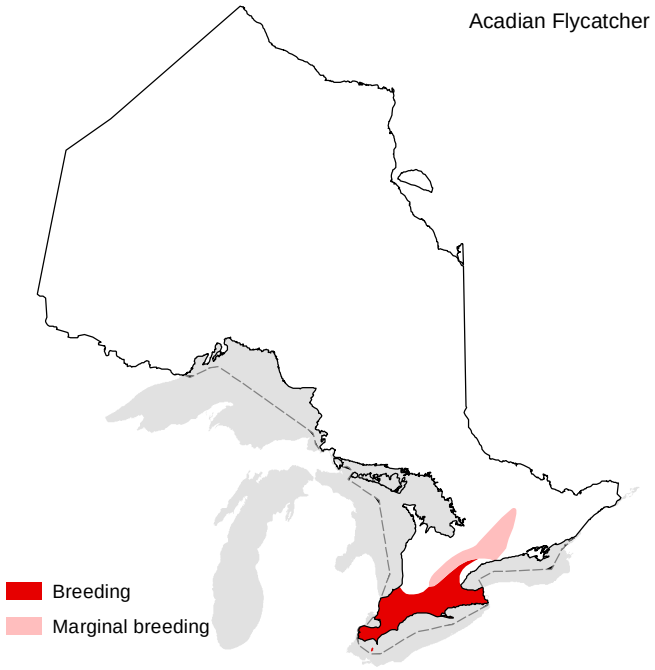
Empidonax virescens

BREEDING SEASON

Habitat Requirements

The Acadian Flycatcher breeds in mature deciduous forests, predominantly in maple-beech woodlands. One Ontario nest was in a wooded sand dune and another was in a heronry (Peck and James 1987). In Ontario, its primary habitat requirements are large, mature, deciduous forests with a closed canopy, limited woody growth in the understorey, and a watercourse or pools of water. In Elgin County, it breeds in heavily wooded ravines near Lake Erie and in larger upland forests. Ravines appear to be preferred in Ontario, possibly because they are less likely to be logged and have undisturbed older-growth features (Heagy 2010; Lancaster et al. 2004).

Forest composition and structure are very important habitat components in Ontario. The first Ontario nest was found in a mature, extensive black ash forest. The Acadian Flycatcher also nests in



mature red and silver maple swamps, but appears to prefer sugar maple–beech forests and black maple forests if water is present. Wooded ravines are favoured habitat. Almost invariably, canopy trees are tall and the canopy is completely or almost closed. Uneven-aged stands may be preferred. The understorey is very open with very few saplings, few if any shrubs, and the ground is virtually devoid of vegetation in prime habitat (Bisson et al. 2000; Martin et al. 1999; McCracken 1999a; Page and Cadman 1994a; Snyder 1953; Wormington 1977).

Elsewhere, the Acadian Flycatcher has been considered associated with old-growth and mature forests, and typically occurs in pure deciduous stands or deciduous stands with limited numbers of conifers. Preferred habitats in Illinois were floodplain forests and steep ravines in upland forests (Walk et al. 2011). In New Jersey, it was significantly more abundant in hardwood swamps than in oak-pine forests (Rich et al. 1994). In South Carolina, it was found only in mature bottomland deciduous forests and was absent in mid- and early succession bottomland forests. In Wisconsin, it breeds in many old coniferous plantations. Plantations used were mature, had closed gaps in pre-existing oak forests, had undergone 1 or more commercial thinnings, and had developed deciduous understories. Most authors state that it is found where there are limited numbers of saplings or shrubs, but in the mid-Atlantic states and Ohio, it was positively associated with foliage density 0.3-1 m tall. In Ohio, territories contained 50% greater arthropod biomass and 250% lower understorey vegetation density than unoccupied areas, but distribution within stands did not appear to be related to any other vegetation features. Forest types it has nested in elsewhere include hemlock, sugar maple–beech, mixed pine-maple, black gum swamps, pine stands heavily undergrown with hardwoods, upland oak with mixed hardwoods, oak-maple-poplar, beech-maple-hemlock, riparian cottonwood–sugar maple–Manitoba maple, beech–yellow birch–oak-maple, maple-ash-basswood, and oak-hickory (Allen et al. 2009; Bakermans and Rodewald 2006; Bielefeldt and Rosenfield 1994; Buffington et al. 1997; Bushman and Therres 1988; Christy in Bent 1942; Gates and Giffen 1991; Haney 1999; Hespenheide 1971a; Mossman 1988; Mossman and Hoffman 1989; Mumford 1964; Newman 1958; Noon et al. 1979; Robbins et al. 1989; Temple et al. 1979; Walkinshaw 1966a).

Benzinger (1994) concluded that the Acadian Flycatcher was associated with hemlock in New Jersey. In Pennsylvania and New Jersey, it was closely associated with hemlock. Ninety percent of all nests were in hemlock and this tree species was used for nesting more than expected. Use of hemlock for nesting ranged from 66.7 to 100% (Allen et al. 2009). In New Jersey and Pennsylvania

over a 15-year period, hemlock declined from constituting 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased due to creation of gaps in the canopy. The Acadian Flycatcher was adversely affected by the hemlock decline and its population decreased more than any other species (Toenies et al. 2018).

Presence of water appears to be an essential habitat component, and most nests are over pools of water or streams. Forested streams of almost any size may be used including small spring branches well up into wooded hills. Territories are often linear along watercourses. Preferred watercourses usually have steep ravines with closed-canopy forest. Complete breeding failure in Haldimand County in 1998 was attributed to drought that resulted in woodland pools drying up. Territorial males failed to attract mates, presumably because the habitat lacked the necessary open pools of standing water. This suggests that water is critical habitat. In Ohio and Illinois, however, successful nesting was reported in woodlands without water (Chapa-Vargas and Robinson 2007; Christy in Bent 1942; Graber et al. 1974; Martin et al. 1999; McCracken 1999a; Mossman 1988; Mumford 1964; Page and Cadman 1994a; Robinson 1992).

In Ohio, the Acadian Flycatcher occurred only in forests that were at least 85 m wide (Bakermans and Rodewald 2006). In Illinois, it nested in riparian forests 80-3,170 m wide (no narrower woodlands were studied). Distribution of 359 nests indicated that it rarely nested near anthropogenic edges. A larger number of nests than expected occurred within the first 5 m and 50 m from forest-creek edges but frequencies of nests near a beaver pond and backwater swamps were somewhat less than expected. Narrow floodplain corridors did not create an ecological trap because birds experienced higher than normal nesting success (Chapa-Vargas and Robinson 2007). In Ontario, it often nests in forested ravines and riparian corridors that may be as narrow 200 m in width (Heagy 2010). In Georgia, the Acadian Flycatcher was equally abundant in narrow, medium, and wide corridors, but the narrow corridors in that area were fairly wide, ranging from 36 m to 330 m. It was less likely to be found in wider corridors (480-2,088 m), but the differences were not significant (Hodges and Krementz 1996). Lindell et al. (2007) reviewed studies that determined presence and abundance of the Acadian Flycatcher in relation to edge and concluded that it avoided forest edges. In Tennessee, Kroodsma (1984) examined its distribution in relation to an edge created by a hydro corridor. It appeared to be negatively affected by the presence of edge, with populations significantly denser in forest interior. Birds were detected as close as 40 m to edge. Rich et al. (1994) found that it was more abundant on forest-interior point counts than on edge counts in New Jersey, but had insufficient data to test this statistically. Successful nests in Ohio were significantly further from forest edge (90.1 m) than unsuccessful nests (64.0 m; Bakermans and Rodewald 2006).

The Acadian Flycatcher is area sensitive and requires woodlands much larger than its territory size. Although it may occasionally occur in smaller woodlots (1-5 ha), forests 30-36 ha appear to be the minimum size to support a population. In other regions, it has been estimated that 30-50 ha and 38-120 ha are required for a viable population. In Ontario, 92% of forests supporting this species are larger than 25 ha and 56% of patches are larger than 100%. Of the 14 most productive breeding sites in Ontario, 11 are in areas with more than 30% forest cover within 1 km (Austen et al. 1994; Bushman and Therres 1988; Friesen et al. 2012; Page and Cadman 1994a; Robbins 1979). The abundance of the Acadian Flycatcher was correlated with larger forests in Pennsylvania (Keller and Yahner 2007).

Nests are in live deciduous trees or shrubs, almost always in the terminal fork of a horizontal or down-sloping limb. Nests frequently hang over a stream or pool. An open space below the nest is important because adults require space to fly, hover, and manoeuvre close to the nest. Ontario nests were in beech (a favoured species), sugar maple, hemlock, yellow birch, flowering dogwood, and hawthorn. Elsewhere, it has nested in hophornbeam, blue beech, red elm, willow, hemlock, shagbark hickory, white oak, white elm, basswood, elderberry, hazelnut, witch-hazel, flowering dogwood, black oak, and red maple. In many areas, hemlock is the preferred nest tree. In each woodlot, 1 species of tree or shrub appears to be favoured for nesting, although the structure of the vegetation may be more important than the species (Allen et al. 2009; Bisson et al. 2000; Bushman and Therres 1988; Christy in Bent 1942; Graber et al. 1974; Martin in Cadman et al. 2007; Martin et al. 1999; McLaren 1974; Mumford 1964; Newman 1958; Peck and James 1987; Schumacher 1995; Snyder 1953; Walkinshaw 1966a). Ontario nests were 0.5-3.5 m from a trunk and 2-9 m from the ground, with most 3-6 m up (Bisson et al. 2000; Peck and James 1987). Overall, nest heights of 1-16.7 m have been reported, with an average height of approximately 4 m. In Pennsylvania and New Jersey, average height of nests, which were mostly in hemlock, was 5.8 m and 6.2 m with an overall average of 6.0 m (Allen et al. 2009; Christy in Bent 1942; Graber et al. 1974; Mumford 1964; Walkinshaw 1966a; Wilson and Cooper 1998a). Often nest material is scavenged from old nests, and occasionally old nests are repaired and used again (Christy in Bent 1942; Peck and James 1987). There is a record of it using an old vireo nest (Allen et al. 2020).

In addition to Acadian Flycatchers, other species may be expelled from the territory including Downy Woodpecker, Eastern Wood-Pewee, Least Flycatcher, Ovenbird, Cerulean Warbler, Scarlet Tanager, vireos, chipmunks, and squirrels. Territories seldom border each other, and the female defends a small area (approximately 120 m^2) around the nest. Males defend a larger territory. In southern Ontario, mean distance between territories was 500 m. Over 2 years, territories averaged 2.7 ha (range 0.76-4.09 ha) and 1.94 ha (range 0.94-3.09 ha). In Illinois, 4 territories were 0.7-1.7 ha (average 1.1 ha). In Pennsylvania, males had territories that averaged 1.0 ha. One Michigan study reported that 13 territories averaged 1.0 ha (range 0.5-1.6 ha). Another Michigan study documented the size of 80 territories. The average size was 1.2 ha (range 0.7-1.7 ha). Fifteen Indiana territories averaged 1.6 ha (range 0.8-2.8 ha). This study was undertaken during a drought year and territories are larger in dry years or in dry sites due to a lower density of insects on leaves (Allen et al. 2020; Christy in Bent 1942; Evans et al. 2009; Graber et al. 1974; Heagy 2010; Mumford 1964; Walkinshaw 1966a).

Natal philopatry rates appear to be very low. In Michigan, 103 nestlings were banded and 0 returned to nest (Walkinshaw 1966a). In Indiana, 1 of 218 (0.5%) hatch-year birds returned (Allen et al. 2020).

Adult site fidelity is high. Almost all adults returned to the same or adjacent territory in Michigan. Males apparently maintain the same territory for their lifetime. Territories usually remain the same but expand if a previous neighbour does not return. Of 31 males that returned in Indiana, 28 returned to the same territory and the other 3 settled within 750 m of the original territory. The average return rate in Ohio was 46% for males and 32% for females. Only 1 male and 1 female changed territories between seasons and no birds shifted territories within seasons. In Ontario,

occupancy of breeding areas is often intermittent, possibly due to the low population (Allen et al. 2020; Heagy 2010; Mumford 1964; Shustack and Rodewald 2010; Walkinshaw 1966a).

Limiting Factors

Males establish territories as soon as they arrive. The shortest interval recorded between males' arrival and completion of nest construction is 11 days. Females begin building the nest 3-11 days after they arrive. Nest building typically takes 1-7 days, but occasionally as long as 2 weeks. Egg laying begins within 1-2 days of nest completion, and eggs are laid daily. Eggs have been found in Ontario from 10 June until the end of July, with most present from mid-June until the end of the first week of July. Incubation may start with laying of the penultimate egg. The incubation period is 13-15 days, with most eggs taking 14 days to hatch; clutches usually hatch within a single day. The nestling period is 12-18 days, but young may leave the nest at age 8-11 days if disturbed. In Michigan, the mean nestling period was 13.9 days (range 13-15 days). In Ontario, fledging may occur as late as mid-August. In Indiana, young did not fledge from 1 nest until the first week of September (Allen et al. 2020; Christy in Bent 1942; Fields 1990; Graber et al. 1974; McLaren 1974; Mumford 1964; Newman 1958; Page and Cadman 1994a; Peck and James 1997; Walkinshaw 1961, 1966a; Wilson and Cooper 1998b).

Two broods may occasionally be raised, particularly in the south, but double-brooding also occurs commonly in Michigan. Evans et al. (2009) confirmed 2 cases of double broods in Ontario. Double broods were common in Pennsylvania with 21.8% and 42% of females attempting 2 broods in 2 years. The potential for 2 broods may be related to habitat. In large forests, second broods may be attempted (13.6% in Indiana), but in edge forests adjacent to agricultural lands, only 2.5% attempted second broods. The time required to fledge 2 broods was 76 days in Michigan, with the length of time between fledging the first brood to laying of the first egg in the second clutch ranging from 4 to 10 days. A new nest is built for a second brood, usually within 40 m of the previous nest. One female had 7 nests over 3 years within an area of 0.14 ha; 1 had 10 nests in 3 years within 0.13 ha; 1 had 3 nests 1 year within 0.04 ha; and another had 3 nests 1 year within 0.07 ha. Renesting is common if a clutch is lost, and as many as 4 renesting attempts may be made. Clutches of 1-4 eggs have been reported in Ontario, with 3 eggs most common. Throughout the Acadian Flycatcher's range, clutches of 1-5 eggs have been documented, with 1-egg and 5-egg clutches very rare. The most frequent clutch size is 3 eggs. Early nests may have larger clutches, and clutch sizes tend to increase northward (Allen et al. 2020; Baillie and Harrington 1937; Christy in Bent 1942; Graber et al. 1974; McLaren 1974; Mumford 1964; Page and Cadman 1994a; Peck and James 1997; Walkinshaw 1961; 1966a; Wilson and Cooper 1998b).

The age at first breeding is 1 year, but 10% or more of territorial males may not attract a mate. The mating system is typically monogamous. The same pair stays together for renesting attempts and second broods. Two cases of bigamy were documented in Michigan. One male had 2 mates and fed young in both nests. Another had 2 mates in territories 578 m apart with 1 or 2 other Acadian Flycatcher territories in between. Polygyny has also been confirmed in Ontario, Indiana, and Pennsylvania. Ontario polygyny rates of 18.8% and 24.1% have been reported (Allen et al. 2020; Heagy 2010; Mumford 1964; Page and Cadman 1994a; Walkinshaw 1966a). Polygyny may be more prevalent than realized due to the difficulty of confirming the presence of more than 1 mate. Many

birds mate for life, but some occasionally select a different mate in subsequent years. Four of 29 southern Ontario nestlings (14%) were the result of extra-pair fertilizations and 3 of 12 pairs (25%) had extra-pair young. No extra-pair young occurred in forest fragments that supported a single pair. Males that sired extra-pair young held territories in the same forest (Evans et al. 2009). In contiguous forest in Pennsylvania, 40% of young were extra-pair. In another Pennsylvania study, 11 of 14 nestlings (78.6%) were extra-pair and 6 of 7 nests (86%) contained extra-pair young. Of 14 nests, 64% contained at least 1 extra-pair young and 57% of young were extra-pair. Two extra-pair sires held territories 1.0 and 1.2 km away from the females that they had mated with (Hung et al. 2008).

Foraging occurs in the lower canopy 0.3-22 m from ground, but mostly at heights of 1.3-4 m. Limited evidence suggests that males may forage higher than females. The Acadian Flycatcher catches prey by hovering and gleaning from vertical tree trunks, undersides of leaves, or clusters of dead leaves, after sitting on an exposed perch searching for prey. It tends to flycatch more in forests with open subcanopies and preferentially fed in beeches in West Virginia. On cool days, it may glean insects from leaves and branches without flycatching; occasionally it forages on the ground. Sallies from perches are mostly directed at prey on leaves. Most sallies are directed upward reflecting its tendency to take prey from the bottom of leaves. In Illinois, it was selective in the trees that it used for foraging. Of species that occur in Ontario, in order of preference, red maple, silver maple, white elm, Manitoba maple, blue beech, shellbark hickory, and sycamore were used more than their availability. From most to least avoided, pumpkin ash, pin oak, green ash, Shumard oak, and bitternut hickory were used less than their availability. Two of the preferred trees, silver maple and shellbark hickory, were uncommon and ranked 18th and 11th in abundance, respectively. The pumpkin ash was strongly avoided, yet was the second-most abundant tree species. A sample of 100 stomachs contained 97% animal matter, predominantly insects. Food consisted of 40.0% wasps, bees, and ants; 18.9% adult and larval moths; 13.8% beetles (weevils and ground, lady, and tiger beetles); 8.2% flies (house and crane flies); 6.4% crickets; 6.0% bugs (leafhoppers, treehoppers, stink bugs, and assassin bugs); 1.0% miscellaneous insects (dragonflies and scorpionflies); and 2.9% spiders, harvestmen, and millipedes. Raspberries were found in 5 stomachs. In West Virginia, 78 food items from 9 stomachs included 22% spiders, 20% caterpillars, 20% beetles, 15% hymenopterans, 13% flies, and 10% bugs. Other invertebrates the Acadian Flycatcher has eaten include damselflies, aphids, cockroaches, termites, isopods, deer flies, and mosquitoes. Food selected ranges from 2 to 12 mm in length. It eats fruits of common elderberry and rough-leaved dogwood (Allen et al. 2020; Christy in Bent 1942; Gabbe et al. 2002; Graber et al. 1974; Hespenheide 1971b; Maurer and Whitmore 1981; Mumford 1964; Schumacher 1995).

The Acadian Flycatcher is subject to parasitism by the Brown-headed Cowbird. Eighteen of 133 Ontario nests (13.5%) were parasitized. Parasitism rates vary geographically: 50% in Illinois and in Missouri in fragmented habitat, 14.5% in contiguous forest in Illinois, 12-17% in Wisconsin, 24% in Michigan, 21% in Arkansas, 5% in Pennsylvania, 7.5% in forested areas of Indiana, 3% in Missouri forested landscapes, and 0% in Georgia and South Carolina (but low sample sizes in these areas). In Missouri, 34 of 264 nests (12.9%) were parasitized. Parasitized nests rarely fledge Acadian Flycatchers; only about 2% of parasitized nests fledge both flycatchers and cowbirds. Cowbirds may remove host eggs and the flycatcher may abandon the nest and start another clutch, remove the cowbird egg,

or build a second floor in the nest over the cowbird egg. Early nests have the highest rate of parasitism. Nests initiated in July usually are not parasitized. In Arkansas, unparasitized nests were significantly higher (6.2 m) than parasitized nests (4.5 m). In Wisconsin, the rate of cowbird parasitism was unrelated to distance from edge, with similar parasitism rates near the edge as 300 m into forest interior. In the Midwestern states, the rate of parasitism was negatively correlated with percent forest cover, percentage of forest interior, and mean patch size. In central Indiana, 5.6% of nests further than 5 km from a field were parasitized compared with 13.5% of nests in forests adjacent to clear-cuts. In Illinois, the probability of parasitism decreased with increasing percentages of anthropogenic habitats within 500 m of nests. Parasitism decreased with percent water within 500 m and as the breeding season progressed, but the magnitude of these trends was negligible. Another southern Illinois study found that nests within 550 m of forest edge experienced higher rates of parasitism and predation (Allen et al. 2020; Bielefeldt and Rosenfield 1997; Brittingham and Temple 1996; Chapa-Vargas and Robinson 2007, 2013; Christy in Bent 1942; Graber et al. 1974; Heagy 2010; Jenkins et al. 2016; Kilgo and Moorman 2003; Mumford 1964; Page and Cadman 1994a; Peck and James 1997; Walk et al. 2011; Walkinshaw 1961, 1966a; Wilson and Cooper 1998a, 1998b). In Ohio, Rodewald (2009) examined factors that affected parasitism rates of Acadian Flycatchers. Density of woody stems in the nest patch was positively related to brood parasitism, with parasitized nests surrounded by 1.6 times more stems than unparasitized nests. Parasitized nests were in landscapes with more than twice the amount of urbanization within 1 km as unparasitized nests. There was a significant relationship between urbanization and habitat around the nest. The primary habitat characteristic associated with increasing urbanization was an increase in woody stems. The dominant species was an invasive exotic shrub that may have provided increased perches for cowbirds or increased visibility of nests. Cowbird abundance was not associated with increasing urbanization. In Wisconsin, canopy cover within 10 m of the nest was more open (89.0%) at parasitized than unparasitized (96.3%) nests. No other variables that were measured differed between parasitized and unparasitized nests (Brittingham and Temple 1996).

The amount of suitable habitat for the Acadian Flycatcher has declined in Ontario. By 1920, only 11% of southern Ontario was forested. This increased to 19% by 1986, but most of it is second-growth forest that is regularly harvested. Some of its preferred nest-tree species are at risk due to pests or diseases. These include hemlock (affected by the hemlock woolly adelgid), beech (beech bark canker fungus), and flowering dogwood (dogwood anthracnose fungus). Heagy (2010) stated that the hemlock woolly adelgid had not yet reached Ontario, but it is now present and steadily spreading northward.

Forest fragmentation is one of the greatest limiting factors to the Acadian Flycatcher in Ontario. Many of the remaining woodlands in Ontario and other areas are too small to support viable populations. Sixty-seven percent of woodlots in southern Ontario are smaller than 5 ha and only 431 patches are larger than 100 ha (Heagy 2010; Mossman 1988; Page and Cadman 1994a). Farwell et al. (2019) examined the response of the Acadian Flycatcher to forest fragmentation by shale gas infrastructure (well pads, access roads, and pipelines) in contiguous forest in West Virginia. It exhibited no significant response, possibly because it was present in low numbers. In the eastern

United States, approximately 42% of its detections on Breeding Bird Survey (BBS) routes were in fragmented landscapes (Donovan and Flather 2002).

Forest management and other activities that open up the forest canopy are detrimental to the Acadian Flycatcher. Several Ontario populations apparently disappeared as a result of intensive logging. It will tolerate light selection cutting and thinning of understorey trees. Any thinning that opens up the canopy results in an increase in shrub and sapling growth and is detrimental. Diameter-limit harvesting is widely practised in southern Ontario woodlots and is incompatible with the habitat requirements of the Acadian Flycatcher. At Rondeau, alteration of the forest canopy by high water levels and severe winds probably contributed to its decline in this area (Bushman and Therres 1988; Friesen et al. 2012; McCracken 1999a; Page and Cadman 1994). In Illinois, Robinson and Robinson (1999) created openings of 0.02-0.4 ha within a 2,000-ha forest. There were no significant differences in the abundance of Acadian Flycatchers in cut forests compared with controls, or in different age classes of cuts.

In Indiana, the Acadian Flycatcher exhibited a significant response to fire, rarely occurring in burned areas and least likely to occur in burns of the 31 species studied (Grundel and Pavlovic 2007b). In pine-oak forests in North Carolina, Rose and Simons (2016) determined that the Acadian Flycatcher was adversely affected by severe- and moderate-intensity fires, with negative effects persisting for as long as 25 years.

The amount of urban habitat in the landscape matrix is important in determining if woodlands will be used for breeding by the Acadian Flycatcher. In Ohio, it was more than 3 times abundant in riparian stands with 1% or less urban development. Nest success was greatest in areas with limited urban development within 1 km, and in wider forests (Bakermans and Rodewald 2006). Shustack and Rodewald (2010) studied the effects of urbanization on the breeding season of the Acadian Flycatcher in Ohio. They examined the timing of breeding of birds in 35 woodlands along a rural to urban gradient. The dates of the first singing male and initiation of the first clutch was later in urban woodlands. Urbanization reduced the length of the breeding season with the result that birds initiated fewer nests and fledged fewer young than rural birds. This may be because urban forests are less desirable and are selected later by smaller females that initiate clutches later than larger females. Kearns and Rodewald (2017) considered the Acadian Flycatcher an urban avoider in Ohio. It settled more densely in rural than urban areas and its condition and overall reproductive productivity declined with increasing urbanization. In North Carolina, abundance of the Acadian Flycatcher was negatively correlated with the density of houses and other buildings within 200 m (Lumpkin and Pearson 2013).

Kearns and Rodewald (2017) studied nest locations of the Acadian Flycatcher relative to predator abundance. Nest location was unrelated to any type of predator activity, including mammalian and avian predators, and specifically Blue Jays. Variation in daily nest survival was best explained by mammalian predator activity. Nest survival was low when avian predator activity was high and mammalian predator activity was low. In all other situations, nest survival was greatest in areas with high predator activity. There was no evidence that it used predator density information to select nest sites.

Invasive plant species may make habitat unsuitable for the Acadian Flycatcher. It is absent in some otherwise apparently suitable ravines along Lake Erie where there is a profusion of garlic mustard or multiflora rose. In some woodlands in Middlesex County, common buckthorn dominates the understorey and renders the habitat unsuitable (Friesen et al. 2012).

Excessive browsing by deer may be a significant limiting factor. The decline at Rondeau Provincial Park was attributed in part to heavy browsing by deer, and deer have been implicated in declines in other areas. Deer may consume vegetation within 2 m of the ground and therefore eliminate suitable nesting sites (Gates and Giffen 1991; Mumford 1964; Page and Cadman 1994). In Delaware, the Acadian Flycatcher was significantly more abundant in areas that supported low (10 or fewer per km^2) and moderate (11-19 per km^2) deer densities than in areas that supported 20 or more deer per km^2 (Tymkiew et al. 2013).

Drought may be a significant limiting factor. If woodland pools or watercourses dry up, habitat becomes unsuitable and breeding may not occur (McCracken 1999a).

Price (2004) suggested that the range of the Acadian Flycatcher could expand within southern Ontario if the average summer temperature increased by 2°C. In North Carolina, its abundance was correlated with temperature, suggesting that climate change may be beneficial to it in this area. The study area was in the Appalachian Mountains where it is colder than other areas at this latitude (Lumpkin and Pearson 2013).

Status

Page and Cadman (1994a) presumed that the Acadian Flycatcher was widely distributed in the Carolinian Forest Region prior to settlement and clearing, but there were no ornithologists present at that time to verify this. By the mid-1800s, much of the Carolinian Forest had been cleared, and it was rare in the remnant forests south of Ontario. McIlwraith (1894) knew of no Ontario records, but correctly predicted that it would be found along the north shore of Lake Erie. The first Ontario record was a specimen collected in Middlesex County in 1882, and 2 years later the first nest was found near Dunnville. Several birds were taken in Chatham-Kent in 1909, including a breeding female. In the early 1900s, there were 2 breeding reports from Middlesex County. Breeding was confirmed at Rondeau in 1931 and 1933 and, by 1937, this was the only known nesting location. By 1994, there were 8 locations where repeat nesting had occurred (Rondeau Provincial Park, Wheatley Provincial Park, Springwater Forest Conservation Area, the Wilson Tract, Mistele-Baker Bush, Dundas Valley, Westover, and Point Abino Marcy Woods). At this time, numbers were greatly reduced at Rondeau with no recent records from Wheatley or Point Abino. A 1973 breeding record in Pickering Township was the most northerly and easterly in the province. The Haldimand-Norfolk Natural Areas Inventory documented breeding at 5 locations (South Walsingham Sand Ridges, Vanessa Swamp, Delhi–Big Creek Valley, Deer Creek Valley, and northeast of Sweets Corners). During the first atlas, the breeding population was estimated at 40-75 pairs. In 1992, only 38 birds were reported, 10 of which were migrants. In 1997, 34 singing males were found at 13 sites, including 3 new areas. Some of these were thought to be late migrants, and the Ontario breeding population was estimated at 20-100 pairs, but probably fewer than 50. The population appeared to remain stable during the 1990s, and the 1998 breeding population was estimated at 35-50 pairs. As of 2011, the population appeared to be stable at 35-50 pairs. Since 1997, 5-10 nests have been found annually in Elgin County suggesting

that this area supports a viable population (Austen et al. 1994; Baillie and Harrington 1937; Friesen and Stabb 2001; Heagy 1997; Lancaster et al. 2004; McCracken 1999a; McLaren 1974; Page and Cadman 1994a). Heagy (2010) estimated the Ontario and Canadian population at 112 adults, including 64 territorial males and 48 pairs. She concluded that the population had been stable for the past 10 years, but that it was not self-sustaining and required continuous immigration from other populations.

The probability of observation of the Acadian Flycatcher increased significantly between atlases by 86%. Martin (in Cadman et al. 2007) attributed the apparent increase to directed searches for the species by the recovery team rather than an actual increase. He concluded that its distribution was well documented in the Carolinian Forest Region but that it may have been missed in larger woodlands in the Great Lakes–St. Lawrence Forest Region south of the Canadian Shield. The population estimate at that time was 27-35 pairs in any given year, with concentrations occurring in larger forest blocks in southwest Middlesex, southeast Elgin, and Norfolk counties. Sites generally support flycatchers for a few to several years followed by a period of abandonment and then recolonization (Martin in Cadman et al. 2007).

The Acadian Flycatcher is designated endangered nationally and provincially. The initial recovery plan target was establishment of 250 pairs at 10 discrete sites. Since then, research has indicated that recruitment of only a single immigrating breeding pair every 2 years may be sufficient to prevent its extirpation in Ontario. The current target is to maintain the existing population of 35-50 pairs (Friesen et al. 2012).

POSTFLEGING PERIOD

Young cannot fly well until they are 14 or 15 days old, and may continue to be fed by adults until they are 25 days old. In Missouri, fledglings attained independence a mean of 19.5 days after fledging (Jenkins et al. 2016).

In Ohio, adult and juvenile Acadian Flycatchers were common during the postbreeding period in densely regenerating clear-cuts. These and other early successional habitats may be important late in the breeding season as a source of dense cover and abundant food (Vitz and Rodewald 2006, 2007). In Missouri, Porneluzi et al. (2014) netted birds during the postfledging period in an oak-pine-hickory forest for 2-15 years after it was clear-cut. The Acadian Flycatcher was one of the more common species captured. Its abundance showed a curvilinear trend that approached significance. It increased gradually to a peak around 6-9 years after harvesting and declined thereafter.

Ausprey and Rodewald (2011) studied the survivorship of fledgling Acadian Flycatchers in mature Ohio hardwood forests in a gradient from rural to urban environments. Survivorship was associated with the number of small trees and negatively associated with the number of large trees. Microhabitats selected were not significantly different from those in random areas. Fledglings selected areas with 3 times more nonnative honeysuckle cover and 2.4 times more native shrub cover than occurred at nest sites. Survivorship was not related to the degree of urbanization despite higher densities of predators in urban areas. The authors concluded that urban forests may provide suitable habitat for juvenile Acadian Flycatchers.

In mature deciduous forests in Ohio, mean home range of fledglings while still on the natal territory was 2.33 ha (range 0.74-3.67 ha). Home range sizes on natal territories were associated with increasing coverage by nonnative honeysuckles, suggesting that honeysuckles provided inferior habitat (Ausprey and Rodewald 2013).

Jenkins et al. (2016) radiotracked fledgling Acadian Flycatchers in Missouri. Nests and locations of juveniles differed significantly in mean canopy cover, total tree density, and total basal area, with all parameters higher for fledgling locations. Mean characteristics for nests and fledgling locations, respectively, were: canopy cover, 94.97% and 95.87%; total tree density per ha, 975 and 1,278; and basal area, 54.26 and 59.59 m^2 per ha. Fledgling survival was negatively correlated with tree stem density, but positively correlated with more big trees and high litter depths. Family groups used both mid- and high-canopy areas for foraging. Fledglings also used areas with high tree densities such as forest edges or patches of cedar. Distance to edge did not affect fledgling survival rates.

MIGRATION

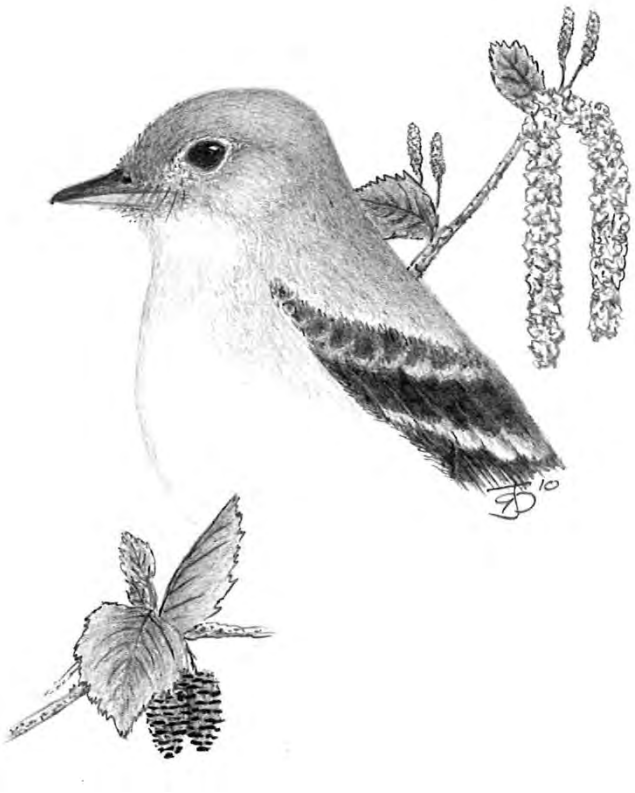
Limited information is available on migration timing. At Point Pelee, the Acadian Flycatcher is most often present in late May and the first week of June. Typical arrival in Ontario is in mid-May, but it has been documented in late April (Burrell et al. 2015; James 1991; Page and Cadman 1994a). Males arrive on the breeding grounds about a week before females (Allen et al. 2020). Most leave the province by the end of August, but it has been recorded in late September (James 1991). In Indiana, adults appeared to leave well before juveniles (Allen et al. 2020).

During migration, the Acadian Flycatcher inhabits a broad range of forest types, all ages of forests, forest edges, and urban woodlots (Heagy 2010). In Pennsylvania, Keller and Yahner (2007) found that it was most abundant in larger woodlands in unfragmented landscapes during spring migration, but had insufficient information to determine any relationships during autumn migration.

The Acadian Flycatcher is a rare migrant in the south. During spring migration, it occurs in very low numbers along the northern shore of Lake Erie. Usually only 2 or 3 are banded at Long Point in spring, with a range of 0-8 (James 1991; Page and Cadman 1994a).

Alder Flycatcher

Empidonax alnorum



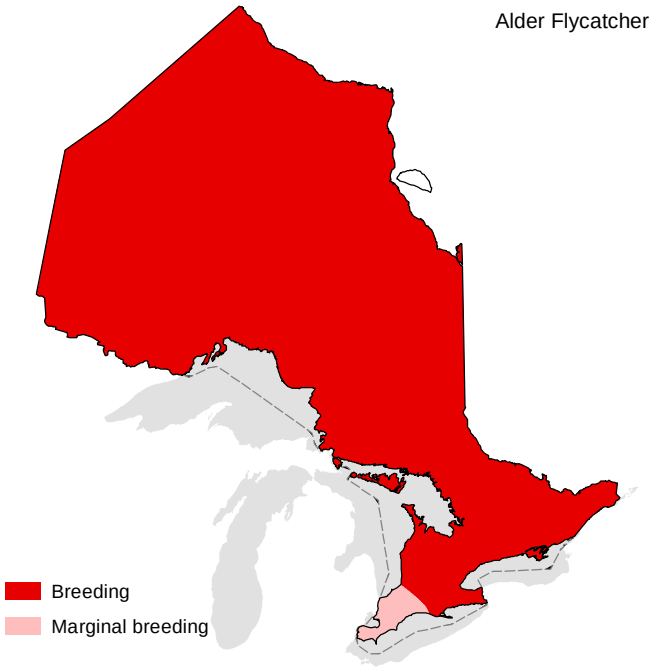
BREEDING SEASON

Habitat Requirements

The Alder Flycatcher prefers shrubby moist to wet areas, but occasionally nests in dry sites (Peck and James 1987).

In the Hudson Bay Lowland, the Alder Flycatcher bred in virtually all willow thickets along the Ontario James Bay coast (Manning 1952).

In the Boreal Forest Region, Rempel (2007) characterized the Alder Flycatcher as a species of young mixed-wood forests with open canopy and an interspersion of young and old forest. It occurred in areas of high edge among vegetation communities, where there was a low proportion of mature and old forest, in young stands, and in areas dominated by softwoods. In general, it occurred in softwood stands with openings. Rempel et al. (2007) concluded that it was associated



with younger, more open hardwood forests, with high disturbance and edge levels. It preferred moist, dense growths of alder and willows along the northeastern shore of Lake Superior (Baillie and Hope 1943). Near Pickle Lake, it occurred primarily along rivers and disturbed upland areas where alders were common (James 1980). Near Hearst, it nested in uncut lowland coniferous stands and clear-cuts 3-24 years old. It was most abundant in 9-11-year-old clear-cuts in lowland forests (Welsh and Fillman 1980). Near White River, it was significantly more frequent in clear-cuts that were 8-10 years old than in younger or older clear-cuts or mature stands (Venier and Pearce 2005). In the Clay Belt, it was common in alder wetlands (Smith 1957) and did not occur in stands older than 14 years old (Welsh 1993).

In the Great Lakes–St. Lawrence Forest Region near Gogama, the Alder Flycatcher appeared in jack pine stands 6 or 7 years after cutting or a burn once there was ample shrubby growth. It disappeared when the stand was 20-25 years old when trees matured and shaded the ground (James and Peck 1995a). Near Kingston, it preferred alder and willow thickets, especially those along edges of woodlands (Weir 2008). Snyder (1953) reported it breeding in Ontario in alder, willow, and grape along creeks, and occasionally in regenerating aspens 1.3-3 m tall. Unlike the Willow Flycatcher, the Alder Flycatcher did not appear to breed in urban shade trees, cemeteries, orchards, or other dry habitats.

In boreal Canada, it occurs in burns and clear-cuts in the early shrubby stages of succession, wet areas dominated by sedges and low shrubs such as sweet gale and willows, abandoned farmland, bogs and fens dominated by low shrubs, and young deciduous and mixed stands (Erskine 1977; Kirk et al. 1996; McLaren and McLaren 1981).

Similar habitat preferences have been reported from British Columbia, Quebec, and the United States. In addition, it may nest in damp to wet buckthorn, dogwood, elderberry, or viburnum thickets, and young plantations. The Alder Flycatcher may use edges created by roads, airstrips, hedgerows, and clear-cuts. Where it occurs with Willow Flycatcher, the Alder Flycatcher tends to nest in denser and taller shrubs with a wet substrate. In Michigan Great Lakes coastal wetlands, it was positively associated with increasing shrub density, shrub foliage diversity, and frequency of willow, open water, floating vegetation, and deciduous trees. It preferred meadows with abundant grass cover and scattered coniferous snags as well as willow thickets. In Quebec, it occurred on burns and clear-cuts with saplings shorter than 2 m and 2-5 m tall. It was not observed in young or mature forest. It was significantly more abundant in clear-cuts than burns. Clear-cuts supported more

deciduous saplings but fewer snags than burns (Campbell et al. 1997; Dawson 1979; Imbeau et al. 1999; Lowther 2020a; Mossman et al. 1991; Niemi and Pfannmuller 1979; Noon et al. 1979; Riffell et al. 2001; Seutin in Gauthier and Aubry 1996; Temple et al. 1979; Zink and Fall 1981).

Most Ontario nests were in deciduous shrubs, trees, and vines; occasionally they were in coniferous trees, and rarely among grasses and herbs. Plant species most frequently selected for a nest site were willows, dogwoods, beaked hazel, and hawthorns. Most nests were in crotches, occasionally attached to upright stalks, and were 0.3-1.8 m from the ground, with most 0.6-0.9 m up (Peck and James 1987).

Ontario nests were typical of those reported throughout its range. Other species that nests have been found in are gray dogwood, red-osier dogwood, red raspberry, black raspberry, meadowsweet, beaked willow, crack willow, nannyberry, wild raisin, juneberry, honeysuckle, and cow parsnip (Campbell et al. 1997; Lowther 2020a; Seutin in Gauthier and Aubry 1996; Snyder 1953; Walkinshaw 1966b).

An exclusive territory is defended, but there is limited information on territory size. Territory sizes averaged 1.3, 1.5, and 3.0 ha for 3 populations in New York, and 0.2 ha in Connecticut (Lowther 2020a; Seutin in Gauthier and Aubry 1996).

No information is available on natal philopatry and limited information is available on adult site fidelity. In Connecticut, 3 of 3 females and 1 of 9 males returned the next year (Lowther 2020a).

Limiting Factors

Eggs have been reported in Ontario nests from mid-June until the end of July, with most clutches present in the last third of June and the first week of July (Peck and James 1997). In Algonquin Park, eggs are present from mid-June to mid-July, a nest with young was found in late July, and recently fledged young have been seen from mid-July until mid-August (Tozer 2012).

It takes approximately 36 hours for the female to build the nest, and eggs are laid at the rate of one a day. The incubation period has been reported as 12-14 days, but 3 Ontario nests had incubation periods of approximately 11 days. If disturbed, nestlings may leave the nest when they are as young as 11 days, but fledging normally occurs at age 13-16 days (Lowther 2020a; Peck and James 1987; Seutin in Gauthier and Aubry 1996).

A single brood is raised in a season, but renesting in the same territory occurs if a clutch is lost. The normal clutch size is 2-4 eggs, with most clutches containing 3 or 4 eggs, but 1 Ontario clutch contained 5 eggs (Campbell et al. 1997; Lowther 2020a; Peck and James 1987, 1997).

The age at first breeding is presumed to be 1 year, and the Alder Flycatcher breeds every year thereafter. The mating system is monogamous (Lowther 2020a).

The Alder Flycatcher feeds almost exclusively on insects hawked from the air, but occasionally it gleans from foliage, sometimes by hovering. Although it captures most food while it is in flight, it may snap and capture food while it is perched. It usually forages from perches 2.5-4.4 m high in deciduous trees or shrubs. In the Northwest Territories, 82% of foraging occurred in deciduous species and 18% in conifers. Near Stouffville and Ottawa, it consistently foraged more in trees and less in the open than the Willow Flycatcher. The 2 species used similar foraging strategies, with the

greatest difference being in habitat selection, although there was considerable overlap at Stouffville. It is uncertain if the 2 species compete for food (Barlow and McGillivray 1983; Greenberg et al. 1999; Lowther 2020a).

Little is known about the diet of the Alder Flycatcher, and the most definitive work pooled results for the Traill's Flycatcher. That study determined that it ate 96% animal matter including 41% hymenopterans, 18% beetles, 14% flies, 8% moths and butterflies, and 4% grasshoppers. Adults feed young spread-winged damselflies, long-horned grasshoppers, and robber, snipe, march, and crane flies (Lowther 2020a). North of Lake Nipigon, Kendeigh (1947) analyzed the contents of 4 stomachs. By frequency, the diet consisted of 42.1% beetles (mostly click beetles but also soldier beetles), 19.0% lepidopterans, 10.3% house flies, 8.6% true bugs (including stink bugs), 7.7% hymenopterans (including ichneumonid wasps), 7.2% spiders, 4.1% short-horned grasshoppers, 1.0% soft-winged bugs, and isopods. Nancekivell and Nocera (2025) completed a DNA analysis of the adult diet in New Brunswick and compared the diet of the Alder Flycatcher with those of the Least Flycatcher and Bank, Tree, Barn, and Cliff swallows. All species differed in their dietary breadth and prey preferences. The 2 flycatcher species and the Barn Swallow ate a greater diversity of terrestrial flies whereas the other species ate more aquatic taxa. The 2 flycatcher species and the Barn and Tree swallows had broader, more generalized diets than the Bank and Cliff Swallows. The approximate frequencies of occurrence of invertebrate groups in the diet of the Alder Flycatcher were 60% aquatic flies, 45% terrestrial flies, 40% lepidopterans, 30% bugs 20% terrestrial beetles, and 5% each for aquatic flies, hymenopterans, neuropterans, and caddisflies. Mosquitoes were the most frequently ingested family of invertebrates, followed by long-legged flies, flower flies, bristle beetles, leafroller moths, and midges. Near Manitouwadge, abundance of the Alder Flycatcher was not correlated with spruce budworm abundance (Venier et al. 2009).

The Brown-headed Cowbird parasitizes the Alder Flycatcher, but at a fairly low rate. In Ontario, 14.6% of 55 nests were parasitized. Parasitism rates elsewhere include 5% in Quebec, 10% in British Columbia, 7.5% in 1 area of Michigan, and 5.3% in another Michigan area. In response to parasitism, the Alder Flycatcher may destroy cowbird eggs or incorporate them into the bottom of the nest (Campbell et al. 1997; Lowther 2020a; Peck and James 1997; Walkinshaw 1961).

Habitat for the Alder Flycatcher may have increased initially after European settlement. Forest clearing in the south and forest management in the north would have created more suitable habitat. After clearing in the south, habitat increased again as some farms were abandoned, but now some of these areas are being converted to urban areas or are succeeding into forest habitat. Many wetlands have been lost in the south resulting in decreases in shrub thickets.

The Willow Flycatcher may be the greatest limiting factor to the Alder Flycatcher. The Willow Flycatcher has expanded its range northward. The 2 species attempt to expel each other from their territories. The Willow Flycatcher is more aggressive and may take over Alder Flycatcher territories. When this occurred near Guelph, the displaced Alder Flycatchers did not remain in the area to breed. Initially, the Willow Flycatcher was found only in extreme southwestern Ontario, but it has since spread northward to Ottawa and Sudbury. To date, there is no evidence of a decline in Alder Flycatchers due to expansion of the Willow Flycatcher's range (Barlow and McGillivray 1983; Lowther 2020a; Prescott 1987; Seutin in Gauthier and Aubry 1996; Snyder 1953).

In the Canadian Shield of Ontario, there was no difference in the abundance of the Alder Flycatcher in early successional clear-cuts and burns, but it was significantly more abundant in mid-successional clear-cuts than mid-successional burns. It was significantly more abundant in early successional than mature stands and equally abundant in mid-successional and mature stands (Zimmerling et al. 2017). In Nova Scotia, it was absent in uncut and thinned hardwood stands, but was common in clear-cuts (Freedman et al. 1981). In the Boreal Forest Region of Ontario, Rempel et al. (2007) predicted that it would be more abundant in harvested forests when current management guidelines were applied than it would be under uncut conditions or simulated natural disturbances.

On Anticosti Island, the Alder Flycatcher was present only when deer density was 7.5 per km^2 or less. White birch had diminished regeneration at higher deer densities, and the flycatcher's abundance increased with birch abundance (Cardinal et al. 2012). Many areas of southern Ontario have deer densities in excess of 7.5 per km^2.

In Alberta, the Alder Flycatcher was equally abundant near noisy compressor stations and quiet well pads. It showed no apparent response to chronic noise (Bayne et al. 2008).

In Alberta, the Alder Flycatcher was more abundant at pipelines and well pads than in forest interior adjacent to these features. There was no difference in its abundance at seismic lines and adjacent forest interior; the openings created by seismic lines were probably too narrow to attract it (Bayne et al. 2016; Kalukapuge et al. 2024).

In Minnesota, blowdown of spruce-fir forest resulted in an 80% loss of canopy and a 100% increase in shrubs. The Alder Flycatcher was common in blowdown, but absent in control plots (Burris and Haney 2005).

Price (2004) predicted that the Alder Flycatcher could become extirpated as a breeding species in southern Ontario if the average summer temperature increased by 2°C.

Status

Early estimates of abundance were confounded by the Alder and Willow flycatchers being collectively termed Traill's Flycatcher. Along the northeast shore of Lake Superior, where the Willow Flycatcher did not occur, Baillie and Hope (1943) considered it very common. It is common throughout the province except in the extreme southwest and extreme north, where it is local and uncommon (James 1991; Prescott in Cadman et al. 1987).

The second atlas indicated that the probability of observation of the Alder Flycatcher had increased significantly province-wide since the first atlas. Significant increases were observed in all atlas regions except the Carolinian Forest Region, where there was a nonsignificant decline. Highest densities occurred in the Boreal Forest Region and southern portion of the Hudson Bay Lowland where it may be most abundant in regenerating cutovers. It occurs in low density south of the Canadian Shield, with slightly higher concentrations in eastern Ontario, the central and eastern portions of the Oak Ridges Moraine, and Dufferin and eastern Grey counties. These are all areas with higher than average wetland density (McLaren in Cadman et al. 2007).

The long-term (1978-2021) trends determined by the Breeding Bird Survey were annual decreases of 0.018% in Canada and 0.18% in Ontario. The short-term (2011-21) trends were annual

decreases of 0.962% in Canada and 0.461% in Ontario. All results were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Major and Desrochers (2012) captured Alder Flycatchers during the postfledging period in clear-cuts in Quebec. It was equally common in control plots and in those where the fruit had been removed. During the postfledging period in Pennsylvania, Stoleson (2013) captured 11 adults and 4 fledglings in clear-cuts and none in forested habitat.

MIGRATION

The Alder Flycatcher is a nocturnal migrant. It is late spring migrant. Although it has been recorded in the province in late April, the peak of migration is in late May. At Long Point, it seldom arrives prior to 25 May, slightly later than the Willow Flycatcher, and 90% are recorded between 30 May and 10 June. Males arrive prior to females, and most birds after 5 June are probably females (Hussell 1991b; James 1991). Timing of autumn migration is more difficult to determine because birds are not as vocal, and it is difficult to distinguish between Alder and Willow flycatchers even when they are in hand. In autumn, juveniles migrate approximately 2 weeks later than adults. At Long Point, the Alder Flycatcher occurs from mid-July to mid-September, with the peak of migration occurring in the last half of August. Ninety percent of adults occurred in the 35-day period of 20 July until 23 August. Juveniles appeared in the first 10 days of August with the peak 27-31 August. Stragglers may occur in the province until early October (Hussell 1991c; James 1991).

Little information is available on the Alder Flycatcher's migration habitat preferences. Presumably, it prefers areas of low shrubs and also graminoid wetlands with some shrub coverage. In Pennsylvania, it was significantly more abundant in shrub than forest habitat during spring migration (Smith and Hatch 2008).

The Alder Flycatcher is common during migration (James 1991).

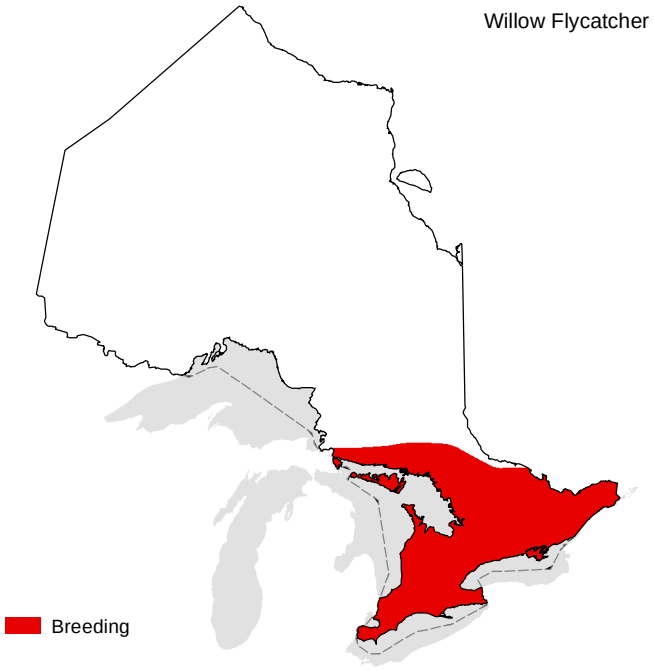
Willow Flycatcher

Empidonax traillii

BREEDING SEASON

Habitat Requirements

In Ontario, the Willow Flycatcher nests in much drier habitats than the Alder Flycatcher. The most commonly used breeding habitats are shrubby fields and pastures dominated by hawthorns, often with other woody species present such as apple, dogwood, willow, and a variety of other species. Less frequently, it nests in willow or willow-dogwood thickets, borders of marshes, and young coniferous plantations with some deciduous trees or shrubs. Miscellaneous habitats where nests were reported include a dogwood ridge in a marsh, small islands in rivers, and in an alder thicket (Peck and James 1987). On Pelee Island, it nested on pastured limestone outcroppings with scattered hawthorns, fragrant sumac, and red cedar (Snyder 1953). Near Stouffville and Ottawa, it appears to have moved into mesic habitat more similar to habitat selected by Alder Flycatchers than



the drier habitats chosen by Willow Flycatchers in Chatham-Kent. This adaptation to wetter habitat may have been essential to its expansion into central Ontario (Barlow and McGillivray 1983; Speirs and Orenstein 1975).

Habitats used in Ontario are similar to those reported throughout the Willow Flycatcher's range, except in the southwestern states. The subspecies that inhabits this area is dependent almost entirely on riparian willows, actively selects willow as the nest-site species, always nests near or over water, and is mildly area sensitive. Habitat selected by other subspecies includes damp and wet shrubby areas as well as upland meadows dominated by shrubs. Upland shrub stands of gray dogwood, beaked willow, pussy willow, common elderberry, hazelnut, roses, northern prickly-ash, juneberry, chokecherry, ninebark, swamp birch, apple, and sweet crabapple are frequently used. Alder thickets tend to be avoided as do wet willow thickets. Shrub thickets appear to be preferred to areas with scattered shrubs. In many areas, it formerly nested in cities and orchards, but is essentially absent from these habitats now (Bent 1942; B.T. Brown 1988; Campbell et al. 1997; DeSmet and Conrad 1988; Finch and Stoleson 2000; Graber et al. 1974; Harris et al. 1987; King 1955; McCabe 1991; Mossman 1988; Sedgwick 2020; Sedgwick and Knopf 1989, 1992; Seutin in Gauthier and Aubry 1996; Taylor and Littlefield 1986; Walkinshaw 1966b). In Iowa wetlands, presence of the Willow Flycatcher was positively correlated with the edge-to-interior ratio, being more likely to occur in irregularly shaped wetlands (Fairbairn and Dinsmore 2001a). In Utah, it was associated with high shrub density with little canopy cover and a moderate amount of ground cover. It was considered a habitat specialist, having the lowest habitat use value of all species studied. It was confined to areas with shrub density of 70-100%, and trees of any size seldom occurred in its territories (Whitmore 1977). In Colorado, it occurred in tall vegetation with more foliage volume above 3 m and fewer trees than average. Its nesting habitat was most similar to that of the Yellow Warbler, and the 2 species often nested within 4 m of each other (Brown and Trosset 1989).

At the landscape scale, the Willow Flycatcher preferred areas that were 8-16% forested in North Dakota (Cunningham and Johnson 2019).

In Ontario, the Willow Flycatcher exhibits no evidence of area sensitivity, occurring regularly in small habitat patches.

Most Ontario nests were in deciduous trees and shrubs, although one was in a conifer. Species selected, in order of preference, were hawthorn, apple, dogwood, and willow. Nests were usually in crotches in horizontal branches, but occasionally in upright crotches, 0.2-1.8 m from the centre of

the nest tree or shrub. Nests were 0.5-3.7 m from the ground, with most 1.1-1.5 m up (Peck and James 1987, 1997).

There are some disparities between Ontario nest sites and those reported elsewhere. Sedgwick (2020) stated that nests were built most frequently in willow, and that the Willow Flycatcher actively selects willow. This is biased due to the intensive research that has been undertaken on the Southwestern Willow Flycatcher. Other subspecies appear to actively select against willow, and use it when it is the only species available. Its aversion to willow has particularly been noted in British Columbia and Wisconsin. In Wisconsin, the preferred nesting species was common elderberry, which appeared to offer the best concealment. In 1 area almost totally dominated by willows, the single nest present was in an elderberry, 1 of the 2 shrubs that were not willow. Other species it has nested in include swamp birch, red-osier dogwood, white elm, basswood, grape, hazelnut, honey locust, tartarian honeysuckle, plum, stinging nettle, blackberry, sycamore, rose, Manitoba maple, buttonbush, pear, bracken fern, cow parsnip, chokecherry, lilac, ninebark, cottonwood, juneberry, aspen, pine, and red elderberry. Unlike in Ontario, most nests were in upright crotches, and those on horizontal branches were fastened to an upright stem. In Wisconsin, the mean diameter of the main stem supporting the nest was 1.3 cm, rarely as large as 1.9 cm. Nests have been reported 0.5-18 m from the ground, but nests higher than 2.5 m are rare. The average nest height is similar to that reported from Ontario. Nests are rarely built in trees or shrubs taller than 3 m (B.T. Brown 1988; Campbell et al. 1997; Finch and Stoleson 2000; Flett and Sanders 1987; Graber et al. 1974; King 1955; McCabe 1991; Sedgwick 2020; Taylor and Littlefield 1986; Walkinshaw 1966b).

The Willow Flycatcher is territorial, and may expel other species from the defended area. In Ontario, it may be aggressive toward the Alder Flycatcher and usurp its territories. There appear to be 2 territories, a small one around the nest that is aggressively defended by the female, and a larger one defended by the male. Territories are usually larger than required to raise a brood, possibly to compensate for lost clutches and the potential need to renest. Adults occasionally leave the territory, so the home range is larger, but its size has not been quantified. Ontario territories were 0.11-0.47 ha (average 0.29 ha). Territory size averaged 0.22 ha during territory establishment, 0.26 ha through nest building and incubation, and 0.41 ha during the nestling and fledging periods. Territory sizes reported elsewhere are 0.08-0.7 ha and 0.06-2.3 ha in 2 study areas in California, 0.32-1.17 ha (average 0.69 ha) for 73 territories in Michigan, 1.72 ha in Colorado, 1.1-1.8 ha in New York, and 0.31 ha in Wisconsin. In Wisconsin, most birds remained within an area of 45 m^2, and territories dissolved 5-7 days after the young fledged. In Wisconsin, the mean distance between nests was 54 m: 37.5 m in thickets and 77 m in scattered shrubs (Finch and Stoleson 2000; Flett and Sanders 1987; McCabe 1991; Prescott 1986, 1987; Prescott and Middleton 1988; Sedgwick 2020; Walkinshaw 1966b).

Natal philopatry appears low and has been reported as 1.4%, 7.5%, 7.8%, 23%, and 25.9%. An exception occurs in populations nesting in montane meadows in California, where natal meadow fidelity was 34.3% and the mean distance of the first nest from the natal nest was 5.65 km. For those individuals that dispersed from their natal meadow, the mean natal dispersal distance was 8.36 km. One female dispersed 134 km. Higher return rates may have been reported in the California study area because the researchers searched over a much wider area than is done in most studies. Another

California study also documented high rates of natal philopatry. Seventeen to 36% of fledglings returned to breed annually. Returning birds entered the breeding population the year after fledging except for 2 that returned 2 years later and 1 that returned 3 years later (Finch and Stoleson 2000; Kus et al. 2017; Matthewson et al. 2013; Sedgwick 2004, 2020; Sedgwick and Knopf 1989; Walkinshaw 1966b). Natal philopatry rates are similar for males and females. Those returning may nest 20-1,600 m from the natal site.

Adult site fidelity is strong, particularly in adult birds that bred successfully the previous year. Breeding site fidelity has been reported at 40-62%, which would account for a high proportion of individuals when mortality is factored in. Higher return rates have been reported in California, with 73.7% of breeding adults returning and 89.3% of those returning to the previous year's breeding site. In Michigan, 40% of males returned the following year, 22.7% the third year, 13.6% the fourth year, and 4.5% the fifth year. Females had a lower return rate of 22.6% the second year and only 3.2% the following 4 years. In Arizona, site fidelity of adult males (52.0%) and females (51.3%) was similar as were median dispersal distances between breeding seasons (16 and 19 m). Breeding success affected female return rates, with 64.4% of females rearing young returning compared with 40.0% for unsuccessful females. Of those that returned, successful females dispersed 15 m compared with 33 m for unsuccessful females. New residents were more site faithful than former residents. Probability of female site fidelity was highest for previously successful birds, those with greater fecundity, novice residents, and unparasitized females. Territorial fidelity by females was related predominantly to breeding performance. Male territorial fidelity was unrelated to residency, site quality, or breeding performance (Finch and Stoleson 2000; Matthewson et al. 2013; Sedgwick 2004, 2020; Sedgwick and Knopf 1989; Walkinshaw 1966b).

Limiting Factors

Eggs have been found in Ontario nests from mid-June until the third week of July, with most present in the last week of June and first week of July (Peck and James 1997). Nest construction usually starts about 4 days after the female arrives, and it may take 36 hours to 10 days to build, with 4 or 5 days typical. Eggs are laid at the rate of 1 a day, except in 4-egg clutches where a day may be skipped. An Ontario 4-egg clutch took 6 days to complete. Some incubation occurs before the clutch is complete, so eggs may hatch over a 1-3-day interval. Incubation periods reported in Ontario are at least 11 days to 14 days. Elsewhere, incubation periods of 11-20 days have been reported. Mean incubation periods of 13.2-13.6 days were reported in California. Cowbird parasitism may prolong incubation. In British Columbia, unparasitized nests had incubation periods of 12-17 days (median 14 days); parasitized nests had incubation periods of 14-20 days (median 16 days). The age at first flight is 11-16 days, typically 14 or 15 days, rarely as long as 19 days. The mean nestling periods were 14.3-14.7 days in California (Campbell et al. 1997; Ettinger and King 1980; Finch and Stoleson 2000; Graber et al. 1974; King 1955; Matthewson et al. 2013; McCabe 1991; Peck and James 1987, 1997; Prescott 1986; Sedgwick 2020; Seutin in Gauthier and Aubry 1996; Walkinshaw 1966b).

Typically 1 brood is raised annually. Double broods are very rare in the north with 1 recorded out of 882 pairs (0.1%), but are more frequent in the south where 5-10% of pairs may raise 2 broods. Renesting is common if a clutch is lost. Usually 1 or 2 replacement nests are attempted if necessary, but 1 female attempted 6 nests in a season. Replacement nests are in the same territory within a

short distance of the previous nest, occasionally in the same tree or shrub. Clutches of 2-4 eggs have been documented in Ontario, with most containing 4 eggs. Clutches of 1-5 eggs have been reported elsewhere, with 3- and 4-egg clutches typical. One-egg clutches are likely a result of egg loss due to predation or disturbance. One clutch of 7 eggs was probably laid by more than 1 female. Replacement clutches tend to be smaller than first clutches and clutch size decreases as the season progresses (Campbell et al. 1997; Finch and Stoleson 2000; Graber et al. 1974; King 1955; Matthewson et al. 2013; McCabe 1991; Prescott and Middleton 1988; Sedgwick 2020; Sedgwick and Knopf 1989; Walkinshaw 1966b).

First breeding occurs at age 1 year, and the Willow Flycatcher breeds every year thereafter. An Arizona population included nonbreeding floaters that were 85.0% males. Most (76%) were yearling males and only 1 bird (0.8%) floated in more than 1 year. In the year following floating, 23.9% settled in the habitat patch where they were first detected and the remainder established a territory in a different patch. Thirteen percent became established at the other side of a lake approximately 30 km distant. An additional 4.3% settled about 100 km distant. The number of territorial birds of both sexes was lowest and the percentage of floaters was highest in a year of severe drought (Theimer et al. 2018).

Most birds are monogamous, but Prescott (1986) documented the first apparent North American incidence of polygyny near Guelph. Two females mated to a single male nested 80 m apart and 6 young were fledged from the territory. In southern populations, it has since been determined that the rate of polygyny is occasionally as high as 15-50%. Factors that may favour polygyny are different chronology of the nests of the 2 females, the ability of females to raise young with limited assistance from the male, shortage of males in combination with high female site fidelity, and female tolerance of other females. In a California population, annual sex ratio explained 68% of the variability in the number of males that were polygynous. Of 43 polygynous males, 65% mated with 2 females simultaneously, 23% mated with 3 females, 5% mated with 4 females, and 7% mated with 5 females. Eighteen males bred polygynously in more than 1 year. Twelve of these (66.7%) switched mating types between years: 8 switched between monogamous and polygynous; 2 switched between monogamous, polygynous, and single (unmated); and 2 switched between polygynous and single. Mate fidelity is strong, and some pairs have remained together for as long as 5 years. Mate switching does occur and birds readily remate if one is lost (Finch and Stoleson 2000; Kus et al. 2017; Pearson et al. 2006; Prescott 1986; Prescott and Middleton 1988; Sedgwick 2020; Sedgwick and Knopf 1989).

The Willow Flycatcher is predominantly an aerial forager, sitting on a perch and then hawking or hover-gleaning insects. It typically perches, often on dead branches at heights of 0.3-3 m, and flies horizontally to capture prey within 3-5 m. it does not use large trees for perching. It may also land on the ground to capture invertebrates. Females sitting on nests may pluck insects crawling nearby. When it is raining, insects tend to move under leaves, and it then flutters to glean. A Wisconsin study found that 30% of invertebrates in the diet were terrestrial, suggesting that these were gleaned from foliage or the ground. There was little relationship between what was eaten and the insects that were available. At Stouffville, there was considerable overlap in the foraging niches of Willow and Alder flycatchers. Willow Flycatchers selected prey more in the open whereas Alder

Flycatchers captured invertebrates more in the interior of trees and shrubs (Barlow and McGillivray 1983; Finch and Stoleson 2000; McCabe 1991; Sedgwick 2020).

At nests near Guelph, nestlings were fed 56.4% adult flies, 16.8% bugs, 6.0% adult moths and butterflies, 5.7% spiders, 4.5% orthopterans, 2.2% adult hymenopterans, 2.1% adult beetles, 1.2% molluscs, 1.2% isopods, and 0.3% larval hymenopterans. In Wisconsin, food items consumed by nestlings were, in order of frequency, deer flies, flower flies, skippers, spiders, spittlebugs, snails, small beetles, lady beetles, dragonflies, ichneumonid wasps, bugs, and a millipede. Captive young in Michigan ate spiders, moths, grasshoppers, flies, mosquitoes, and crickets. Adults have been documented eating flying ants, dragonflies, hymenopterans, flies, and bugs. An earlier study of Traill's Flycatcher diet determined that 96% of the diet was animal matter: 41.4% hymenopterans, 17.9% beetles, 14.2% flies (crane, robber, house, and flesh flies), 7.7% moths and butterflies, 7.2% bugs, 3.9% grasshoppers, and a few dragonflies, mayflies, cattle ticks, spiders, and millipedes. Fruit consumed included elderberries, blackberries, dogwood berries, juniper berries, and chokecherries (Bent 1942; Finch and Stoleson 2000; McCabe 1991; Prescott and Middleton 1988; Sedgwick 2020; Walkinshaw 1966b).

Wiesenborn and Heydon (2007) examined food remains in 56 fecal samples from Southwestern Willow Flycatchers collected from 3 locations in Nevada. Eight orders of invertebrates were represented in the diet including spiders, odonates, cockroaches, beetles, hymenopterans, lepidopterans, bugs, and flies. Leafhoppers were the most abundant arthropod in the samples. Size of prey ranged from 2 to 40 mm and included aquatic water boatmen, terrestrial spiders, arboreal leafhoppers, and ground-dwelling cockroaches. It adapted its diet to consume the insects that were most readily available. Spiders comprised 7.4% of the diet at all sampling locations suggesting that their consumption rate may have been independent of availability. Diets of males and females were similar. It fed more on arthropods captured on plants than insects in flight. Durst et al. (2008) completed a similar 5-year study in Arizona. Approximately 70% of the diet was from 5 prey categories: hymenopterans, flies, leafhoppers, beetles, and ants. The relative abundance of these and other taxa differed significantly among years. Diets of adult males and females were similar but differed from that of nestlings. Adults ate a higher proportion of hymenopterans and nestlings ate more flies.

Parasitism rates by the cowbird vary considerably regionally. Most reported rates are probably underestimates because parasitized nests may be abandoned or the cowbird egg may be woven into the bottom of the nest where it is difficult to detect. In Ontario, 22 of 91 nests were parasitized (24.2%). Generally, parasitism rates are lower in the east, with an average of 11% for 6 studies that reported on 859 nests. In some eastern areas, parasitism rates are quite low: 5.3% in Michigan, 9% in Wisconsin, 4.4% in Ohio, and only 1 known case in Illinois. In the west, parasitism rates of 40.7% have been reported in Colorado, and it is the most heavily parasitized species in California at 63% of nests. In 3 montane meadows in California, lower parasitism rates of 8.4%, 11%, and 18.4% occurred. In New Mexico, 20.2% of 491 nests were parasitized. In British Columbia, 36% of nests were parasitized. Due to the chronology of cowbird egg laying, late nests and replacement clutches of flycatchers are seldom parasitized. Flycatchers rarely fledge any of their own young from parasitized nests, and success rates for cowbirds from Willow Flycatcher nests is also low (Brodhead et al. 2007; B.T. Brown

1988; Campbell et al. 1997; Finch and Stoleson 2000; Graber et al. 1974; Mathewson et al. 2013; McCabe 1991; Peck and James 1997; Sedgwick 2020; Sedgwick and Knopf 1988; Walkinshaw 1966b).

Habitat destruction and degradation may affect local populations. Drainage of thicket swamps is still occurring, and this may eliminate suitable nesting habitat. Old-field habitat continues to decline due to conversion to agricultural or urban lands, or to forested areas as a result of natural succession. Cattle grazing may affect the quality of breeding habitat. Often shrubs are denuded to a height where they are no longer suitable for nesting. Cattle also compact soils, inhibiting regeneration of shrubs and trees (Finch and Stoleson 2000; Harris et al. 1987, 1988; Sedgwick 2020; Taylor and Littlefield 1986).

Birds are very sensitive to disturbance early in the nesting season. During the nest-construction period until the first egg is laid, even slight disturbances may result in nest desertion (McCabe 1991).

Cool spring weather may delay the onset of the breeding season. Late springs retard shrub blooming which may affect insect availability. In Washington, the total span of the nesting season was 67 days in 1 year and 46 days in a year with a cool spring (King 1955). In California, late-spring storms and low temperatures delayed the start of the breeding season and influenced reproductive success by reducing the likelihood of renesting (Matthewson et al. 2013).

Price (2004) predicted that the range of the Willow Flycatcher would contract in southern Ontario if the average summer temperature increased by 2°C.

Status

Snyder (1953) stated that the Willow Flycatcher occurred only in the extreme southern portion of Ontario at that time, north to approximately latitude 43°N. Peck and James (1987) questioned this and thought that it was more widespread then. Nonetheless, it has experienced a recent and significant range expansion in Ontario. Barlow and McGillivray (1983) reported that it first arrived at Stouffville in 1953, and that the range at that time extended to Sudbury and Ottawa. The first nest in the Kingston area was found in 1979, and a substantial increase in the number of pairs occurred in 1981. South of the Canadian Shield, it was more numerous than the Alder Flycatcher, while the Alder Flycatcher dominated on the Shield. The population is probably increasing as a result of range expansion, but breeding densities at given locations are not changing substantially (Barlow and McGillivray 1983; Sedgwick 2020; Weir 2008). During the first atlas, the Willow Flycatcher occurred in most squares south of the Canadian Shield and there was a sizable population in the Sudbury area (Prescott in Cadman et al. 1987). James (1991) considered the Willow Flycatcher locally common in southern agricultural areas, becoming rare north to Sudbury.

The second atlas indicated that there was no significant change in the probability of observation of the Willow Flycatcher between atlases for the entire province. There was a significant increase in the southern Shield consistent with a modest range expansion into this area. Highest densities occurred in Prince Edward County, the Kingston area south of the Shield, from Long Point north to Hamilton and throughout Niagara Region, and in Lambton and Middlesex counties (Sandilands in Cadman et al. 2007).

Range expansions have also occurred in Quebec and British Columbia. The Willow Flycatcher was first recorded in Quebec in 1971, and started to increase significantly in the early 1980s. It was still expanding its range in southern Quebec in the mid-1990s; except for the House Finch, no other species in Quebec had spread as far or rapidly. In British Columbia, it started to become more common around 1975 and increased its range eastward (Campbell et al. 1997; Sedgwick 2020; Seutin in Gauthier and Aubry 1996).

Long-term (1978-2021) population trends on the Breeding Bird Survey were annual decreases of 1.12% in Canada and 1.44% in Ontario. During 2011-21, there were annual decreases of 0.395% in Canada and 3.87% in Ontario. The short-term trends for Ontario were of medium reliability; the long-term trends were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young remain near the nest for 3 or 4 days then follow the adults through the territory for the next 2 or 3 weeks begging for food (Sedgwick 2020).

Vormvald et al. (2011) studied the Willow Flycatcher during the postbreeding period in the Sierra Nevada, California. In shrubby meadows, family groups moved an average of 48 m from the nest in 1 year and 23 m the following year. Ninety-four percent of sightings of families in both years were in riparian willow shrubs within a meadow. The remaining observations were in edges of upland forest surrounding the meadow. The mean 95% home range size for families was 1.8 ha and the mean 50% core area was 0.3 ha. Movement patterns were most often characterized by clustering activity around the central natal area with occasional trips away from the central area. Fledglings gradually moved away from the nest during the dependence period. Distance from the nest increased with age but movements back to the nest also occurred. The authors reported the results of another study in Arizona that found that the mean postbreeding season home range of adults was 143.2 ha, compared with 9.9 ha in the prenesting season and 0.38 ha during breeding.

MIGRATION

Migration is nocturnal and males tend to migrate earlier in spring than females by as much as 1 or 2 weeks. Both sexes compress spring arrival into a 10-14-day period. At Long Point, 90% of birds passed through between 21 May and 9 June, with migration essentially complete by 10 June (Hussell 1991b; Sedgwick 2020). Timing of autumn migration appears to be stimulated by declining abundance of aerial insects. Adults migrate prior to juveniles. At Long Point, the middle 90% of adults passed through between 17 July and 23 August compared with 11 August to 9 September for juveniles. This pattern has been confirmed throughout the Willow Flycatcher's range. It has been documented in the province in late September and early October (Hussell 1991c; James 1991; Sedgwick 2020).

Habitat used during migration is similar to the breeding season. The Willow Flycatcher is most likely to occur in shrubby areas and areas with scattered, small trees. Pastures and dry meadows with scattered shrubs are less likely to be used during migration than in the breeding season. During autumn migration in California, individuals remained at a site an average of 6 days, with a range of 2-19 days (Finch and Stoleson 2000; McCabe 1991; Otahal 1998; Sedgwick 2020).

The highest annual mortality rate occurs during migration. Paxton et al. (2017) studied survival rates of Southwestern Willow Flycatcher populations that wintered in Costa Rica. Although migration constituted only 25% of the annual cycle, it accounted for 62% of the annual mortality.

James (1991) termed the Willow Flycatcher an uncommon migrant, with spring vagrants wandering as far north as Rainy River and Manitouwadge.

Least Flycatcher

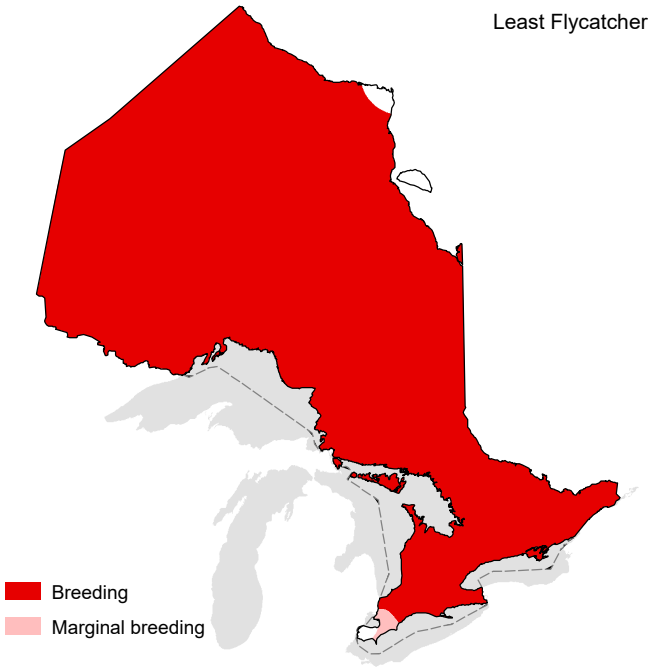
Empidonax minimus

BREEDING SEASON

Habitat Requirements

In Ontario, the Least Flycatcher has nested in semi-open immature deciduous and mixed forests and occasionally in groves of conifers, burns, edges of swamps and bogs, orchards, and shrubby fields. Nesting occurred once in a deciduous grove on a sand dune. Nests are usually near openings such as forest clearings and edges, water, roads, and cottages (Peck and James 1987).

In the Boreal Forest Region of Ontario, the Least Flycatcher was associated with immature to younger hardwoods with fairly open conditions. It was also associated with a high amount of edge which was a measure of forest cover configuration and age-class interspersion (Rempel 2007). Baillie and Hope (1943) found it in a variety of habitats along the northeastern shore of Lake Superior, but it was most abundant in shrubby growth in recent burns. Near Hearst, it inhabited uncut upland mixed and lowland coniferous stands and clear-cuts 11-24 years old (Welsh and Fillman 1980). In the Clay Belt, it was most abundant in stands dominated by poplars or black spruce, but was absent in jack pine stands (Welsh and Lougheed 1996). In boreal Ontario and the Clay Belt, it is most



abundant in deciduous forests, predominantly poplar or birch, but also in sugar maple–beech stands. Less frequently, it occurs in mixed forests, coniferous forests (usually a mix of balsam fir and spruce, rarely hemlock or tamarack), and in deciduous, mixed, and coniferous shrubs. It avoids white, red, and pitch pine stands (Erskine 1977; McLaren and McLaren 1981).

In the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, the Least Flycatcher nests in mature and old-growth white pine stands. Its abundance was significantly correlated with the basal area of deciduous species and stand age, although there was no significant difference in its abundance in mature and old-growth stands (Kirk et al. 2012). Near Quetico Park, it was equally abundant in young (1-23 years) stands and old-growth forests over 350 years old, twice as abundant in intermediate-aged stands (67-73 years), and half as abundant in mature stands (112-176 years; Apfelbaum and Haney 1985). Near Gogama, it was absent in pure jack pine stands, but occurred in mixed jack pine–deciduous forests with open canopies of 25% or less. It was locally common only when trees exceeded 10 m in height and was always associated with trembling aspen and/or white birch (James and Peck 1995a). Similar habitat was selected at Pickle Lake (James 1980). In Algonquin Park, the Least Flycatcher was common in white birch–poplar forests, and it also nested in and at edges of sugar maple–yellow birch forests. It was absent in bogs, black spruce, black spruce–white cedar, fir-spruce, immature white pine, pure white cedar, and fir-spruce-hardwood stands (Martin 1960). In Muskoka District and Haliburton County, its nest locations were associated with very high tree density and canopy volume, and less than average shrub density. It inhabited areas that had been cleared and allowed to proceed to an early successional forest stage (Clark et al. 1983).

In the Great Lakes–St. Lawrence Forest Region south of the Shield, the Least Flycatcher preferred forest edges or openings in wooded wilderness areas. It also occurred in alder thickets along streams or in damp depressions, birch stands, mature aspen-poplar forests, second-growth hardwoods, orchards, and shade trees around houses (Snyder 1953). In Durham Region, it occurred in a mature maple-oak stand with an open canopy (Speirs and Orenstein 1975). McIlwraith (1894) stated that it nested at forest edges and in orchards in the Carolinian Forest Region. In the north, the Least Flycatcher is associated mostly with poplars and birch; in the south it may also nest in hardwood stands. Its usage of orchards appears to have declined significantly since earlier reports. It nested in red pine plantations south of Peterborough. The plantations were 25-70 years old and were managed by row thinning and selective thinning every 10-15 years. Thinning promoted the growth

of red oak and black cherry saplings as well as a ground cover of poison ivy. Occupied areas had more (34%) deciduous trees at least 8 cm diameter at breast height (DBH); unoccupied sites had only 4% deciduous trees. Canopy cover at occupied sites (84.2%) was significantly greater than at unoccupied sites (71.3%). This was the first reported use of pine plantations by nesting Least Flycatchers (Geboers and Nol 2009). The deciduous regeneration that appears after thinning is likely the greatest attractant, along with the well-developed canopy layer and relatively open understorey.

Elsewhere, the habitat requirements of the Least Flycatcher are similar to those in Ontario, but there is considerable disparity in reported preferences. In some areas, it is considered an edge species, nesting on forest edges, adjacent to clearings, and in shrubby areas. Other studies indicate that it prefers dense forests. Information on preferred age of forest is also conflicting. Most studies found that it was associated with young stands and a long-term study associated its decline with forest maturation. In other areas, particularly in the west, it appears to be restricted to mature hardwood stands. In Alberta aspen stands, it was significantly more abundant in old-growth stands than in mature or young stands. In Minnesota, it nested in low density in clear-cuts in forests dominated mostly by trembling aspen and white birch mixed with pine, spruce, and balsam fir. Most early authors stated that it was most common in orchards, scattered trees around houses, and in urban woodlots, and that it tended to avoid forests. The most recent of these studies is over 30 years old, and nesting in these habitats now appears to be rare. The 1 common theme is that it is common in aspen and birch stands as well as those dominated by sugar maple, often with associates of beech or yellow birch, less frequently with oaks. Coniferous forests are usually avoided and, in mixed forests, it selects pockets of deciduous cover, usually poplar or birch. In some areas, it prefers hemlock–yellow birch stands. In eastern Quebec, it nested in riparian stands of balsam fir and white cedar. Other habitats it has nested in included stands dominated by Hill's oak, oak and maple, juneberry, Manitoba maple–willow, and lowland ash-basswood. Many territories are bounded by open areas on 1 side, such as lakes, roads, and forest clearings (Back 1979; Bent 1942; Beals 1960; Bielefeldt and Rosenfield 1994; Campbell et al. 1997; Darveau in Gauthier and Aubry 1996; Erskine 1977; Faanes and Andrew 1983; Flack 1976; Graber et al. 1974; Haney 1999; Holmes and Sherry 2001; Holmes and Sturges 1975; Johnston 1971; Kirk et al. 1996; LaRue et al. 1995; MacQueen 1950; Mossman 1988; Mossman and Hoffman 1989; Mousley 1916a; Niemi and Hanowski 1984a; Niemi and Pfannmuller 1979; Niemi et al. 1995; Noon et al. 1979; Schieck et al. 1995; Tarof and Briskie 2020; Taylor and Taylor 1979; Temple et al. 1979).

In North Dakota at the landscape level, the Least Flycatcher preferred areas that were 51-75% forested; no areas were more than 75% forested (Cunningham and Johnson 2019). In North Dakota 400-m-radius landscapes, its probability of occurrence increased with the amount of tree cover within 100 m. Results were similar in landscapes with more than and less than 30% tree cover (Cunningham and Johnson 2016).

Several studies determined microhabitat preferences of the Least Flycatcher. In Quebec, it occurred where the canopy was tall, well developed, and contained a higher proportion of sugar maple than unused areas. In order, the most important habitat predictors were the height of the first leaved branch, total crown height, proportion of sugar maple, and percent coverage in medium and tall tree strata. It was negatively associated with herbaceous coverage (Darveau et al. 1992). It

prefers drier woodlands than other eastern *Empidonax* flycatchers. Usually it is found in more densely vegetated habitats than the Eastern Wood-Pewee, but in less densely vegetated forests than the Acadian Flycatcher (Hespenheide 1971a; Tarof and Briskie 2020). Unlike Quebec results, which appear to be more typical of Ontario conditions, some studies found it correlated with openness of the canopy and presence of ground cover rather than with closed canopy with little shrub or herbaceous cover. It is positively associated with forest size and negatively associated with woodlot isolation. It is not particularly area sensitive and may occur in woodlands as small as 0.2 ha. In burns and clear-cuts, breeding density may be highly dependent on the number of residual snags (Back 1979; Breckenridge 1956; Campbell et al. 1997; Faanes and Andrew 1983; Hespenheide 1971a; Johnston 1971; Kasumovic et al. 2009; Kirk et al. 1996; MacKenzie et al. 1982; MacQueen 1950; Niemi and Pfannmuller 1979; Samson 1979; Tarof and Briskie 2020; Tarof and Ratcliffe 2004; Temple et al. 1979). In New Hampshire and Maine, it occurred in all ages of stands. It was most abundant in white birch and northern hardwood stands and occurred much less frequently in spruce-fir stands. It was absent in stands dominated by aspens, swamp hardwoods, balsam fir, white pine, or hemlock. Its abundance was positively correlated with canopy closure, total foliage volume of coniferous trees larger than 10 cm DBH, and total foliage volume of deciduous trees 2-10 cm DBH and less than 2 cm DBH. It was negatively correlated with percent ground cover, coniferous trees 2-10 cm DBH, and number of woody stems per ha (DeGraaf et al. 1998). In Alberta, nest habitat parameters were 12.5 m canopy height, 95% canopy cover, 8% shrub coverage, 95% ground cover, and basal area of 29.22 m^2 per ha. Within a 5-m radius around the nest, there were 21.8 trees, 14.9 saplings, and 9.5 snags (Van Brempt et al. 2023).

Near Ottawa, presence of the Least Flycatcher in landscapes was negatively correlated with the total amount of forest edge. Probability of detecting it in a 2.5-by-2.5-km square was 80% when there was less than 10 km of forest edge, 50% at approximately 15 km of edge, and 10% at 25 or more km of edge (Villard et al. 1999). Villard et al. (2007) considered the Least Flycatcher a habitat generalist that was not particularly attracted to either forest edge or interior. They mapped its distribution prior to and after creation of edges by clear-cutting in Saskatchewan. It did not exhibit an avoidance reaction to edge and showed a significant attraction to edge in 1 of 2 experimental plots. Lindell et al. (2007) reported on 2 studies: 1 demonstrated that the Least Flycatcher showed no response to forest edge, the other found that it was more abundant in edge habitat. Near Kingston, breeding density and reproductive success were similar in fragmented and contiguous forest (Tarof and Briskie 2020; Tarof and Ratcliffe 2004).

All Ontario nests were in trees, with 88.8% in deciduous trees, and most were in live trees. Saplings and small trees were selected over large trees. In order of preference, nest tree species were birch, maple, poplar, and pine. Most nests were in crotches or forks, with some on horizontal branches where they were supported by small lateral branches. Some nests were 0.6-2.0 m from the tree trunk. Nests were 0.6-15 m from the ground, with most 3-8 m up. Occasionally nests were built of material from old nests (Peck and James 1987; Tarof and Briskie 2020). Kendeigh (1947) reported a nest north of Lake Nipigon that was 18.3 m from the ground in a 21-m-tall white birch.

Elsewhere, nests have been reported in apple, willows (sandbar and peach-leaved), sugar maple, beech, yellow birch, red maple, Manitoba maple, green ash, cottonwood, common elderberry, black

cherry, oaks (white, red, and black), trembling aspen, hemlock, white birch, pines (white and jack), witch-hazel, balsam poplar, red-osier dogwood, mountain ash, pear, sycamore, locust, sumac, spruce, tamarack, and alder. In Quebec, sugar maple, beech, yellow birch, and red maple were used according to their availability, with no apparent preference for tree species. In Manitoba, green ash, Manitoba maple, and sandbar willow were selected. Other species were used less frequently than expected, particularly peach-leaved willow. Most nests are in upright crotches of small trees, usually where there are 3 or 4 branches in the fork. They may also be on horizontal branches or in vertical crotches of small branches away from the trunk. Nest heights range from 0.6 to 20 m (average 3.5-8.5 m). In Alberta, mean height of nests was 3.63 m, mean height of the nest tree was 10.1 m, mean DBH of the nest tree was 9.85 cm, and the mean amount of cover over the nest was 7%. Seventy-five percent of nests were in trembling aspen and 25% were in balsam poplar. Nests are usually in the lower to middle portions of the canopy. Material from active or old nests of Least Flycatcher and other species may be taken to construct the nest. There is 1 reported instance of it nesting in an abandoned Yellow Warbler nest that contained 1 warbler egg; no attempt was made to repair the nest. Rarely, nests may be reused, with 1 British Columbia nest being used in 3 successive years (Baillie and Hope 1943; Bent 1942; Breckenridge 1956; Briskie and Sealy 1988; Briskie et al. 1990; Campbell et al. 1997; Darveau et al. 1993; Davis 1959; Goossen 1977; Graber et al. 1974; Johnston 1971; Nice and Collias 1961; Tarof and Briskie 2020; Van Brempt et al. 2023).

The Least Flycatcher appears to be colonial, nesting in groups in small portions of suitable breeding habitat. In northern Ontario, it usually occurred in jack pine stands only where there were large enough patches of deciduous trees to support several pairs; it rarely nested singly. Colonial behaviour has been documented elsewhere in Ontario, Quebec, Virginia, Minnesota, and Michigan. Nests have been found as close together as 20 m (Breckenridge 1956; Darveau et al. 1992; Davis 1959; James and Peck 1995a; Peck and James 1997; Perry et al. 2008; Tarof and Briskie 2020). Near Kingston, territories averaged 0.1 ha with contiguous boundaries in dense clusters, but large areas of apparently suitable habitat were unoccupied. Clusters contained 2-30 territories with a density in excess of 11 territories per ha. Distances between clusters averaged 1,245 m (range 346-2,402 m). Clustered breeding may promote extra-pair copulations. The locations of clusters varies annually (Tarof and Ratcliffe 2004). Not all Least Flycatcher populations are colonial. In eastern Ontario, approximately 10% of males settled solitarily. Territory size of solitary males averaged 0.29 ha (range 0.11-0.84 ha). Solitary males may establish territories as far as 2.1 km from other Least Flycatchers (Tarof and Briskie 2020). In Minnesota, clusters of breeding Least Flycatchers contained 5-84 territorial males. Locations of 157 nests ranged 0-170 m from the edge of the cluster. Nests 45 m or more from the edge of a cluster had 34-38% lower predation rates, probably due to the dramatic vocal responses of flycatchers to predators (Perry et al. 2008).

The Least Flycatcher is territorial and actively excludes other Least Flycatchers and particularly the American Redstart, a direct competitor, from the territory. Territories may overlap extensively with other flycatcher species such as Eastern Wood-Pewee, Eastern Phoebe, and Great Crested Flycatcher. The female defends a radius of about 6 m (0.01 ha) around the nest; the male defends a larger area. Because of its colonial habit, territory sizes are small. North of Lake Nipigon, territories averaged 0.52 ha (range 0.40-0.65 ha). In Algonquin Park, territories averaged 0.13 ha (range 0.03-

0.38 ha). In Quebec, territories averaged 0.13 ha in healthy sugar maple stands and 0.23 in declining stands. In New Hampshire, territories averaged 0.18 ha; the average in Michigan was 0.07 ha (range 0.01-0.20 ha). In Virginia, territories ranged from 0.05 to 1.1 ha, but most were smaller than 0.22 ha. The male with the largest territory had a neighbour on 1 side only. During the nestling-feeding phase, his territory shrunk to 0.12 ha. Territories are largest during laying and incubation. Home ranges are larger than the territory. Nearby openings may be shared by pairs as feeding areas (Breckenridge 1956; Davis 1959; DesGranges et al. 1987; Johnston 1971; Kendeigh 1947; MacQueen 1950; Martin 1960; Sherry 1979; Sherry and Holmes 1988; Tarof and Briskie 2020).

The Least Flycatcher exhibits low natal philopatry. In Manitoba, 4.2% of 410 nestlings returned to nest the following year; in Michigan 0 of 46 nestlings returned. In eastern Ontario, 1 of 20 nestlings (5%) returned to breed the following year and it bred in a different cluster more than 1 km from its natal site (Tarof and Briskie 2020).

Adult site fidelity is variable. In eastern Ontario, only 4 of 98 adults (4.1%) returned to breed in the subsequent year. One female occupied the same solitary territory, 1 male occupied the same territory in the same cluster, and 2 males occupied territories in clusters more than 10 km from where they were banded. In Michigan, the adults of 4 pairs were banded. All 4 males and 2 females returned the next year, but none returned the following year (Tarof and Briskie 2020).

Limiting Factors

Eggs have been found in Ontario nests from mid-May until late July, with most present from the second week of June until late June (Peck and James 1987). In eastern Ontario, the earliest egg date was 16 May and the latest was 14 June (Tarof and Briskie 2020). In Algonquin Park, nests are under construction from mid-May to late June, eggs are present from late May until mid-July, nestlings are present from mid-June to late July, and recently fledged young occur from late June to late July (Tozer 2012).

The Least Flycatcher has a compressed nesting season in Ontario. Based on banding results at Long Point, Hussell (1981) determined that it spent an average of no more than 64 days on the breeding grounds. In Manitoba, Sealy and Biermann (1983) reported a nesting season that totalled 58 days. The pre-egg stage was approximately 13 days, 3 days for egg laying, about 13 days for incubation, 15 days for fledging, and postfledging parental care for at least 14 days. In eastern Ontario, males established territories on 11 May, about 6 days before females arrived. Nests are built 1 or 2 weeks after arrival over a period of 5-7 days, usually starting about 2 days after the female's arrival. Three Ontario nests took 6, 6, and 9 days to complete. Usually 1 egg is laid a day, but occasionally a day is skipped between the third and fourth egg. In Manitoba, the mean egg-laying interval was 1.14 days. Incubation begins full-time with the laying of the last egg, although some time may be spent on the nest before the clutch is complete. Eggs hatch slightly asynchronously (1.1 day for 3-egg clutches, 1.5 day for 4-egg clutches, and 1.9 day for 5-egg clutches). The incubation period of 2 Ontario nests was at least 13 days and 14 days at another. Overall, incubation periods of 12-15 days have been reported. Young fledge when they are 12-17 days old, usually at 13-15 days. The mean age at fledging in eastern Ontario was 13.6 days (Bent 1942; Briskie and Sealy 1987a, 1989a, 1989b; Campbell et al. 1997; Darveau in Gauthier and Aubry 1996; Davis 1959; Holmes et al.

1979; MacQueen 1950; Nice and Collias 1961; Peck and James 1987; Tarof and Briskie 2020; Walkinshaw 1961).

One brood is typically raised in a year. Two instances of double brooding were documented in Manitoba. Double brooding is likely to be detected only in intensive studies but detailed research in eastern Ontario found no evidence of second broods. In Manitoba, females laid their first egg in the second clutch 7-8 days after the first brood fledged. New nests were built in both cases; 1 was 3.5 m from the original nest. A pair must remain on the breeding grounds approximately 40 days longer if a second brood is raised. Renesting is common if a clutch is lost. Usually a new nest is built for the replacement clutch; the same nest is rarely used again. Second-attempt clutches are often smaller and have low survival rates. Ontario clutches contained 2-5 eggs, with most (61.4%) containing 4 eggs; 3-egg clutches comprised 26.1% of nests. Near Kingston, the average clutch size was 3.9 eggs (range 3-4 eggs). Overall, the most frequent clutch size is 4 eggs, followed by 3. Two- and 5-egg clutches are rare; 2-egg clutches are frequently replacement clutches. Clutches of 6 and 7 eggs are very rare and may be due to intraspecific egg dumping. A brood of 6 young in British Columbia was attended by 3 adults and the only 7-egg clutch reported was known to be produced by 2 females (Bent 1942; Briskie and Sealy 1987a, 1988, 1989a; Campbell et al. 1997; Darveau et al. 1993; Davis 1959; Graber et al. 1974; Keast 1990; Mousley 1916a; Sealy and Biermann 1983; Tarof and Briskie 2020).

The age at first breeding is 1 year for both sexes, and breeding occurs every year. The normal mating system is monogamy, but polygyny was documented once in Manitoba. Nests of the 2 females were 21 m apart, and both were successful. The male delivered about 55% of the food to 1 nest, but less than 9% to the other (Briskie 1994; Briskie and Sealy 1987a). In Michigan, both members of 2 pairs returned the following year and both pairs remained mated (Tarof and Briskie 2020). Near Kingston, extra-pair paternity was common in colonial nesters (Tarof and Ratcliffe 2004) and in large, contiguous forest (50% of nests) but was less prevalent (11%) in fragmented forest (Kasumovic et al. 2009). Females prefer males holding territories within clusters; solitary territorial males are often unpaired (Tarof and Briskie 2020).

Most (81%) foraging is done by making short sallies (about 1.2 m, seldom more than 2-2.5 m) from perches to hawk insects; 19% of prey is captured by gleaning, including hover-gleaning. The Least Flycatcher forages at heights of 1-20 m (mostly 3-15 m), usually in the space from the top of the shrub and sapling stratum to the lower canopy. It forages at lower heights than the Eastern Wood-Pewee and Great Crested Flycatcher, but there is some overlap with the wood-pewee. About 75% of its perches are dead branches and almost 20% are live branches, with a small proportion of perches being inanimate objects. The Least Flycatcher forages in deciduous species 90-93% of the time with the remainder of time spent in conifers. In Wisconsin, it foraged on trees according to their availability, except for pines which were seldom used. In New Hampshire, it foraged mostly on yellow birch; used beech, sugar maple, and white ash considerably less than their availability; and avoided conifers. Yellow birch appeared to support a higher density of lepidopteran larvae than other tree species (Breckenridge 1956; Greenberg et al. 1999; Holmes and Schultz 1986; Johnston 1971; Robinson and Holmes 1982; Rogers 1985; Sherry 1979; Tarof and Briskie 2020). In New

Hampshire, there was no difference in the sexes' foraging heights (mean of 10.5 m for males and 10.4 m for females), their foraging techniques, or tree species usage (Holmes 1986).

Ninety-eight percent of the diet consists of invertebrates. Over 40% of food consists of hymenopterans, especially ants and parasitic wasps. The remainder of invertebrates eaten are approximately 20% beetles (weevils and long-horned beetles), 10% bugs (leaf and leaf-footed bugs, treehoppers, leafhoppers, and spittlebugs), 10% flies (crane, dance, blow, snipe, and anthomyiid flies), 7% lepidopterans, and 2% orthopterans. Kendeigh (1947) examined the stomach contents of 4 Least Flycatchers from north of Lake Nipigon. The diet consisted of 40.4% stink bugs, 21.8% lepidopterans, 13.1% beetles (including scarab and soldier beetles), 8.4% spiders, 6.5% flies (mostly house flies), 5.5% hymenopterans (including ichneumonid wasps and ants), and 4.4% brown lacewings. At Delta Marsh, midges were the most frequently consumed prey. In Quebec, nestlings were fed mostly beetles (especially the brown leaf beetle), and caterpillars. In New Hampshire, the diet consisted of 49.8% beetles, 21.4% flies, 15% hymenopterans, 8.0% bugs, 4.8% caterpillars, 0.5% spiders, and 0.5% others. Other items that have been fed to nestlings include bugs, dobsonflies, damselflies, and snails. In addition to these foods, adults occasionally eat mayflies, fruit (raspberries, pokeweed, and elderberries), and timothy seeds. Insects consumed ranged in length from 2 to 14 mm, but most were 2-8 mm long. In Virginia, the Least Flycatcher's diet overlapped 46% with the Eastern Wood-Pewee and 28% with the Great Crested Flycatcher. The other 2 flycatchers selected slightly larger invertebrates (Bent 1942; Briskie 1988; Darveau et al. 1993; Graber et al. 1974; Hespenheide 1971b; Johnston 1971; Robinson and Holmes 1982; Tarof and Briskie 2020). Nancekivell and Nocera (2025) used DNA to analyze the adult diet in New Brunswick and compared the diet of the Least Flycatcher to those of the Alder Flycatcher and the Bank, Tree, Barn, and Cliff swallows. All species differed in their dietary breadth and prey preferences. The Least and Alder flycatchers and the Barn Swallow ate a greater diversity of terrestrial flies than the other species, which ate more aquatic taxa. The 2 flycatcher species and the Barn and Tree swallows had broader generalist diets compared with the Bank and Cliff swallows. The approximate frequencies of occurrence of invertebrate groups in the diet of the Least Flycatcher were 80% aquatic flies, 60% terrestrial flies, 60% lepidopterans, 40% aquatic beetles, 40% terrestrial beetles, and 10% neuropterans. The approximate frequencies of invertebrate families in the diet of the Least Flycatcher were 50% mosquitoes, 50% leafroller moths, 40% snipe flies, 40% limoniid crane flies, 40% long-legged flies, 40% marsh beetles, 40% weevils, and 20% bristle flies. Near Manitouwadge, Venier et al. (2009) observed no relationship between the abundance of the Least Flycatcher and the spruce budworm. Morris et al. (1958) reported similar findings in New Brunswick.

The Least Flycatcher is infrequently parasitized by the Brown-headed Cowbird. Of 143 Ontario nests, 3.5% were parasitized. Parasitism rates reported elsewhere are 0% and 13.3% in Quebec, 9.3% and 11.9% in Michigan, 2.8% in Manitoba, and 19% in British Columbia. It usually accepts cowbird eggs, but may occasionally abandon the nest. Hatching of a cowbird egg typically results in no flycatchers fledging. In Manitoba, Yellow Warbler nests were parasitized 6 times more frequently, although the 2 species nested in the same habitat. Lower incidence of flycatcher parasitism was thought to be due to later clutch initiation and nests being better concealed and higher than the warbler's. Flycatcher nests below 2 m had a parasitism rate of 6.1% compared with 1.9% for higher

nests (Briskie and Sealy 1987b; Briskie et al. 1990; Brittingham and Temple 1996; Campbell et al. 1997; Darveau et al. 1993; Peck and James 1997; Tarof and Briskie 2020; Walkinshaw 1961).

Forest management may affect the Least Flycatcher depending upon the treatment used. Vanderwel et al. (2007, 2009) reviewed studies on the effects of partial harvest of forests in the Boreal Forest Region of Ontario. They concluded that its abundance was unchanged when 30% of trees were removed, but that it declined when 50% or 70% of trees were removed. It experienced a 25% decrease when 40% of trees were removed, a 50% decrease when 60% of trees were removed, and a 75% decrease when 75% of trees were removed. In the Boreal Forest Region of Ontario, Rempel et al. (2007) modelled the effects of timber harvesting on the Least Flycatcher. They predicted no change in habitat availability over 100 years if no spatial guidelines were applied, if all guidelines for featured values were adhered to, or if natural disturbance patterns were emulated. In Algonquin Park, it increased 1-2 years after intensive group selection of trees. This involved cutting 0.05-ha circular plots resulting in almost 4 gaps per ha or about 20% of the area. Typical group selection cutting, which affected about 5% of the stand area, had no effect on its abundance (Tozer et al. 2010). Single-tree selection in Algonquin Park also had no effect on the abundance of the Least Flycatcher (Jobes et al. 2004). Near Sault Ste. Marie, it responded positively to single-tree selection thinning in northern hardwoods, increasing in abundance 1-2 years after harvesting. Its abundance was closely associated with sedge and grass cover and tall shrub density (Holmes and Pitt 2007). In the Canadian Shield of Ontario, there was no difference in its abundance in early successional clear-cuts and burns, but it was significantly less abundant in mid-successional clear-cuts than in mid-successional burns. There was no difference in its abundance in early successional and mature stands, but it was significantly more abundant in mid-successional than mature stands (Zimmerling et al. 2017). In Minnesota, it increased in riparian buffer strips that were partially harvested (Hanowski et al. 2002). In large forest tracts, it responds to logging by shifting into forest interior away from disturbance. In New York, the Least Flycatcher was adversely affected by logging and considered a true species of undisturbed forest, contrary to results observed in Ontario. In uncut forests, it constituted 5.1% of the birds present and was seventh in abundance, and this dropped to 2.2% and fourteenth in forests where 25% of trees were cut. Further declines occurred as logging intensity increased. In Vermont, it tended to avoid logged areas, particularly centres of small clear-cuts. It declined in Quebec forests managed for sugar maple production. Beech and yellow birch are eliminated in these forests, and these species are preferred for foraging above sugar maple. In Nova Scotia, the Least Flycatcher occurred both in uncut and strip clear-cut areas. It was one of the dominant species in uncut forest and was absent in clear-cuts, but present in thinned and strip-cut plots at approximately half the density. In areas of Nova Scotia where clear-cutting occurred, it first returned as a regularly breeding species when regenerating forest was 20 years old (Darveau in Gauthier and Aubry 1996; Freedman et al. 1981; Lent and Capen 1995; Morgan and Freedman 1986; Noon et al. 1979; Tarof and Briskie 2020; Webb et al. 1977). In Minnesota, blowdown of spruce-fir forest resulted in an 80% loss of canopy cover and a 100% increase in shrub cover. The Least Flycatcher was more common in the blowdown area, but not significantly (Burris and Haney 2005). In Muskoka District and Haliburton County, Clark et al. (1983) predicted the impact of cottage-lot development on the Least Flycatcher. They concluded that selective tree removal that opened the

canopy would provide good habitat, but that extensive tree removal or reductions in the shrub or sapling layer would be detrimental.

Declines in health of sugar maple stands in Quebec affected the Least Flycatcher. It declined with the amount of die-back in maples, and numbers tended to fluctuate more in declining areas. The mean number of pairs per 0.5 ha was 2.3 in healthy stands compared with 1.0 in die-back stands, a decrease of 57%. There appeared to be no significant differences in breeding success in healthy and declining stands (Darveau et al. 1992, 1993; DesGranges et al. 1987).

The Least Flycatcher appears to decline during drought years. Large reductions in breeding numbers occurred in western aspen forests during drought years. Similar declines were documented in dry years in Michigan and Wisconsin (Blake et al. 1992; Flack 1976). Insects may be less abundant in dry years.

In Pennsylvania, densities were lower in areas highly browsed by deer (Niemi et al. 1995). Deer browsing may be a limiting factor in some areas of southern Ontario and similar problems have been identified in the northeastern United States. It has been suggested that deer populations should not exceed 4-8 animals per km^2 to avoid habitat damage. Southern Ontario populations are generally much higher than that (Tarof and Briskie 2020).

In Edmonton, abundance of the Least Flycatcher was negatively correlated with noise (Proppe et al. 2013). Anthropogenic noise, particularly from roads, was a factor in its local decline. Traffic noise masks the lower note of the song. Females that do not hear this note may not adequately perceive and assess the singing male, or may deem him to be an ill-suited mate. It was more abundant near quiet well pads than noisy compressor stations, suggesting that it was affected by chronic noise (Bayne et al. 2008).

Bayne et al. (2016) assessed the impact of forest fragmentation by energy sector facilities in Alberta. The Least Flycatcher was more abundant in adjacent forest interior than along seismic lines, was similar in abundance along pipelines and in adjacent forest, and was more abundant near well pads than in adjacent forest interior.

The American Redstart has evolved to become very flycatcher-like, and it and the Least Flycatcher appear to be in direct competition. Their habitat niches are so strongly correlated that their abundance changes are synchronous. Both occupy the same forest types, inhabit the stratum between the top of the shrub and sapling layer to the lower canopy, forage by flycatching and hovering for insects, and have very similar bill structures. The flycatcher is usually dominant and successful in excluding the redstart from nesting in its territory. Diet of the 2 species is also similar, being dominated by flies, hymenopterans, and beetles (79% of the redstart's diet, 92% of the flycatcher's diet), but the Least Flycatcher eats considerably more caterpillars (Sherry 1979; Sherry and Holmes 1988).

In Illinois, all 5 Least Flycatchers that were examined were contaminated with DDE, dieldrin, and heptachlor. Concentrations in flycatchers were high compared with species that eat fruit or seeds (Tarof and Briskie 2020).

Price (2004) concluded that the range of the Least Flycatcher would contract in southern Ontario if average summer temperatures increased by 2°C.

Status

It is likely that the Least Flycatcher was more abundant prior to extensive forest clearing in the south. It has always been a common breeder in the province. McIlwraith (1894) considered it very common, Baillie and Hope (1943) reported it very common along the northeast shore of Lake Superior, Baillie and Harrington (1937) considered it a common breeder north to southern Kenora District and the southern portion of James Bay, and Smith (1957) termed it common in the Clay Belt. During the first atlas, breeding evidence was obtained throughout the province except in the northeastern portion of the Hudson Bay Lowland; it bred sporadically in the remainder of this geographic area. It was most abundant in forested areas south of the Canadian Shield (Fraser in Cadman et al. 1987). James (1991) considered it common to locally abundant north to Big Trout Lake and Fort Albany, and rare and local to Fort Severn in the west.

The second atlas demonstrated that there had been no change in the distribution of the Least Flycatcher since the first atlas, except that it apparently disappeared from many squares in the highly agricultural areas of Lambton County. There was no significant change in its probability of observation throughout the province, but there were changes in some regions. A significant increase was noted in the Hudson Bay Lowland that may have been a reflection of better coverage. A statistically significant decline in the area south of the Shield occurred, although it was observed in almost the exactly same number of squares during both atlases. It was most abundant in the Shield in both the Boreal and Great Lakes–St. Lawrence forest regions. Lowest abundance occurred south of the Shield, in all but the eastern portion of the Hudson Bay Lowland, and in the extreme northern portion of the Shield (Mills in Cadman et al. 2007).

Long-term (1970-2021) Breeding Bird Survey data indicate annual decreases of 1.12% in Canada and 1.44% in Ontario. Short-term (2011-21) trends were annual decreases of 0.395% in Canada and 1.65% in Ontario. All results were highly reliable except that the short-term Ontario trend was of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young may remain in the vicinity of the nest and be attended by the parents for 10-15 days after fledging, occasionally for as long as a month (Tarof and Briskie 2020).

Akresh et al. (2009) studied habitat use of postbreeding adults and independent juveniles in Michigan. Although sample sizes were small (3 adults and 9 juveniles), all birds were captured in riparian forest and none were captured in upland forest. In Minnesota regenerating clear-cuts, Streby et al. (2011b) captured 4 Least Flycatchers during the breeding period, but caught 73 adults and 153 fledglings during the postbreeding season. Of the 28 species in the study area that nested in mature forest, the Least Flycatcher constituted 12.9% of those that were captured in regenerating clear-cuts during the postfledging period. Shrubby areas and areas with dense sapling growth appear to be important to it during the postfledging period.

Major and Desrochers (2012) captured Least Flycatchers in clear-cuts in Quebec. Similar numbers were captured in control plots and in those where the fruit had been removed. In

Pennsylvania during the postfledging period, Stoleson (2013) captured 3 adults and 24 juveniles in clear-cuts and none in nearby mature forests with a dense understorey.

MIGRATION

Migration appears to be predominantly nocturnal. The median arrival date in southern Ontario is 18 May. At Long Point, the Least Flycatcher may occur in very early May, but the first large influx always occurs after mid-May, with migrants occurring almost as late as mid-June. Males arrived an average of 8.2 days earlier than females, and older females arrived slightly before yearling females. In other areas, it has also been verified that males precede females (Brewer et al. 2018; Hussell 1981; Mills 2005a). In autumn, adults migrate about a month earlier than juveniles. At Long Point, adults occur as early as the first week of July, with the first migrants probably being failed breeders. Migration of adults continues until the end of August. Over a 3-year period in the 1960s, the mid-90% of adults occurred in a 34-day period between 11 July and 13 August, with an overall median date of 22 July. Juveniles appeared in the first 10 days of August, with their migration peaking in the last week of August and first week of September, with stragglers until mid-October. The mid-90% of juveniles occurred in the 28-day period between 17 August and 13 September, with a median date of 29 August, 38 days later than adults. There was no apparent differential timing in migration by sexes (Hussell 1980, 1981; Hussell et al. 1967; Keast 1990; Tarof and Briskie 2020). During autumn migration in Alberta, adults migrated an average of 13 days earlier than juveniles when the sexes were combined and females migrated 5 days before males when the age classes were combined. Adult females migrated 4 days earlier than adult males and 14 days earlier than juvenile females. Adult males migrated 8 days before juvenile males. There was no difference in the timing of migration of juvenile males and females. Over a 32-year period, the median date of autumn migration advanced by 14 days (4.5 days per decade) for adults but only 2 days (0.65 day per decade) for juveniles (Van Brempt et al. 2025).

During migration, the Least Flycatcher occurs in a variety of habitats: aspen groves, alder and willow thickets, birches, forest edges, and shrubby areas along watercourses and water bodies. It is particularly common near ponds and small lakes and other sources of water bordered by thick growths of aspen, willow, or birch. It may also occur in forest understorey among shrubs and small trees (Campbell et al. 1997). In Kansas, migrating Least Flycatchers occur predominantly in wooded habitats along watercourses, gullies, and windbreaks, but occasionally in tall weedy growth and isolated trees (Tarof and Briskie 2020). During spring migration in Pennsylvania, it was most abundant in mature forests and especially edge-dominated mature forests (forest-agricultural edges and suburban forests). Highest abundance was in suburban forests followed by shrub-sapling forest, forest-agricultural edge, forest interior, and pole-stage forest (Rodewald and Brittingham 2007). During spring migration in Ohio, it was significantly more abundant in mature upland forest stands than in similar riparian forests (Rodewald and Matthews 2005). During autumn migration, juveniles are significantly more abundant in lower-quality planted woodlots and agricultural habitat than the more forested habitats used by adults (Tarof and Briskie 2020).

Mills (2005b) examined first arrival dates of Least Flycatchers during spring migration at Long Point during 1975-2000 to determine if there had been a response to global warming. Examining the results by quartiles revealed that the trend toward earlier arrival was significant. Both sexes

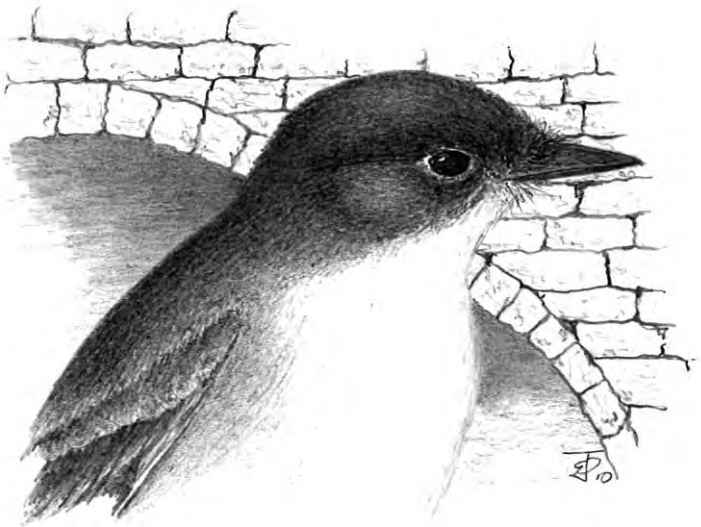
migrated progressively earlier in spring at a rate of 2.7 days per decade. The date of autumn departure was progressively later. The delay in the first quartile during autumn migration was significant suggesting that adults, which migrate in advance of juveniles, contributed to the trend toward delay of autumn migration.

In Pennsylvania, an infestation of the viburnum leaf beetle resulted in almost complete mortality of the southern arrowwood, which was formerly the third-most abundant shrub species. Spring migrating Least Flycatchers declined significantly after the infestation (Smith and Hatch 2017).

The Least Flycatcher is common during migration (James 1991). At Long Point, Badzinski (2000) reported that the number of spring migrant Least Flycatchers had increased by 1% per year since the early 1960s, but that autumn numbers had decreased slightly. There was a decline in the 1960s, an increase in the 1970s, and a smaller decline in the 1980s. Between 1961 and 1988 there was a significant decline of 2.3% per year. Populations fluctuated in concert with budworm-dependent warblers suggesting that it may benefit from budworm outbreaks (Hussell 1980; Hussell et al. 1992).

Eastern Phoebe

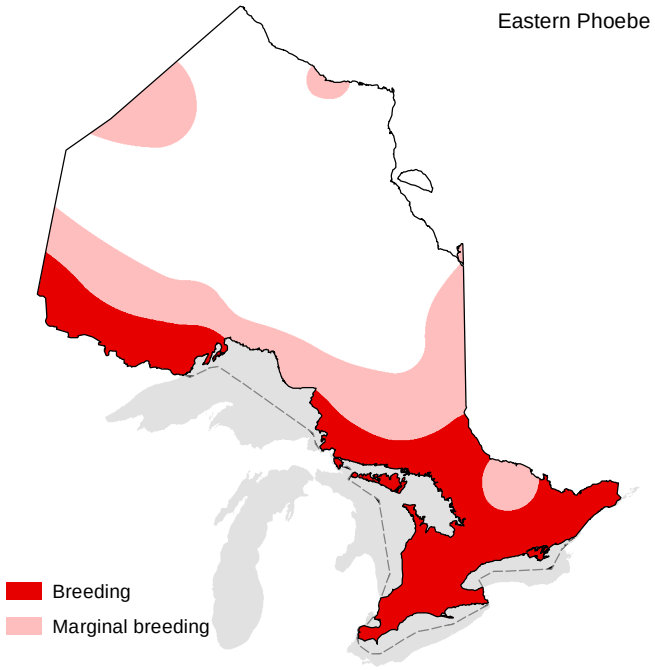
Sayornis phoebe



BREEDING SEASON

Habitat Requirements

The Eastern Phoebe nests in a variety of habitats in Ontario, but usually in open or semi-open areas where there are suitable nest sites. It nests in upland and lowland forests, primarily in mixed and deciduous stands, but occasionally in coniferous forest, with about a third of Ontario nests in forested habitat. Forested areas it selected for nesting were usually open, or the nest was near forest edge. Many birds breed in anthropogenic habitat such as around farms, rural residences, cottages, parks, gardens, gravel pits, and golf courses. Less frequently it nests at shorelines of lakes and rivers, along road and railway rights-of-way, and on dams. It occasionally nests on rock cliffs and rocky outcrops, in marshes, and at dunes and beaches. Key habitat components for nesting are open areas for foraging and a rock outcrop or human-made structure suitable for nest placement (Peck and James 1987). In Algonquin Park, many nests were low on rocky cliffs (Tozer 2012). In Elgin County, the phoebe nests in wooded ravines (Lancaster et al. 2004). In Muskoka and Parry Sound districts, it



was associated with slightly higher than average canopy volume and tree density, features indicative of the edge of a clearing. It requires an open area for flycatching and some canopy for perching. Its preference for low shrub cover and its ability to find nest locations on buildings makes it compatible with cottage lots (Clark et al. 1983).

Similar nesting habitat has been reported elsewhere. Typically associated with woodland and edge habitat near water, the phoebe occasionally nests on rock outcrops in forests several hundred metres from water and openings. It requires some wooded habitat that is more extensive than a hedgerow, but this may include scattered trees around dwellings. In Kansas, nests under bridges were more frequent where there was continuous tree cover along the watercourse, occasional where woodland cover was discontinuous or patchy, and rare where the stream was open. In boreal Canada, it may occur in early stages of succession after a burn or clear-cut if suitable nest sites are present. Woodland types it has nested in include northern hardwoods, lowland hardwoods, birch-maple, aspen-birch, upland and swamp mixed woods, floodplain forests, pine and oak barrens, and spruce-aspen. One study characterized it as a species of upland openings (Back 1979; Campbell et al. 1997; Erskine 1977; Graber et al. 1974; Hill and Gates 1988; Hoffman 1989a; Johnston 1971; Lemieux and Rail in Gauthier and Aubry 1996; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991; Noon et al. 1979; Samson 1979; Schukman 1993; Speirs and Orenstein 1975; Taylor and Taylor 1979; Temple et al. 1979; Weeks 1979, 2020).

Brennen and Schnell (2007) used Breeding Bird Survey (BBS) data from the south-central states to determine landscape-level features affecting the Eastern Phoebe. It was most abundant in relatively undisturbed areas with a high ratio of edge to interior. Population numbers tended to be higher in densely wooded areas and lower in more sparsely wooded locations.

In Kansas, the Eastern Phoebe nested mostly along primary and secondary streams and only infrequently along tertiary streams. It was predominantly a forest and edge species that nested along a habitat gradient from woodland streams to draws with sparse or no woodland, but chose the former preferentially (Schukman et al. 2011).

Nests are on either a ledge or vertical surface, greatly limiting the number of natural nest sites. Much of the nest is constructed of mud, so there must be a nearby source of water and the nest must have overhead protection from the elements or it falls down or disintegrates during rain. In Ontario, 96% of nests were on human-made structures, especially buildings and bridges.

Approximately half were on or in buildings on ledges, eaves, beams and posts, electrical fixtures and wires, ceilings and roofs, drain pipes and eavestroughs, and stovepipes. About 30% were on bridges and culverts, 3% on cliffs and in caves, 1.7% under earthen-bank overhangs, and 0.2% in tree roots and stubs. Unusual nest sites included a pitchfork handle, a hanging pile of harness, the seat of a canoe, a piece of loose wallpaper, a hanging electric motor, a metal can, a gate, a partially sunken boat, a mailbox, a cattle-feeding trough, in an old well, and in an overturned car. Old nests were often reused, with 1 used 8 consecutive years. Occasionally, old Barn Swallow or American Robin nests were repaired and used, and nesting frequently occurs near Barn and Cliff swallow colonies (Peck and James 1987). Mills (1981) reported a nest in a hole in an earthen road embankment near Snug Harbour. In Elgin County, the phoebe has nested in natural habitat several times. In these cases, nests were built into root masses of upturned trees or were in cavities in steep ravine slopes (Lancaster et al. 2004). In the Kingston area, 88 nests were on cottages, 23 were on natural rock outcrops, 46 were on human-made structures no longer frequented by humans (abandoned barns and cabins, old cars), and 35 were on outbuildings (Conrad and Robertson 1993a). Ontario nests on buildings were 0.8-9 m from ground, with most 2.1-3 m up. On bridges and culverts, nest heights ranged from 0.3-9 m (average 1.2-2.4 m). Nests on rock faces were 0.6-7.6 m from the ground (average 1.2-2.4 m). Most nests were against a vertical surface and were therefore flat on 1 side and circular on the remainder. Two- and 5-tier nests were reported resulting from materials being added in subsequent years (Peck and James 1987, 1997).

In heavily forested areas such as the Appalachians, nests are as likely to be in natural situations as on human-made features. In areas dominated by open habitats, over 90% of nests are on human-made structures. A Wisconsin study found that all nests under bridges were at the end of the bridge that had the deepest water, and all but one were within 2 m of the upstream edge of the bridge. Nests over deeper water may be better protected from predators. Unusual nest locations include in a woodpile and in a vertical cave about 2 m in diameter. The birds had to drop 2-3 m into the cave entrance to reach the nest. In Kentucky, nests were found in all large cave entrances examined. Typically 50-75% of nests present at the beginning of a season are reused. New material is always added, resulting in nests with as many as 6 tiers. Old nests are usually reused for second broods. Some nest sites have been used for 15-30 consecutive years. The phoebe readily uses nesting platforms placed in culverts (Campbell et al. 1997; Faanes 1980; Fitch 1958; Graber et al. 1974; Hill 1987; Hill and Gates 1988; McClure 1946; McIlwraith 1894; Palmer-Ball and MacGregor 1989; Tyler in Bent 1942; Weeks 1977, 1978, 1979, 2020).

The phoebe is highly territorial, particularly early in the breeding season, and territorial disputes may be common. Due to its special requirements for nest sites, territories often are not contiguous and large areas of apparently suitable habitat may be devoid of phoebes. Usually only 1 nest is present on a structure and, when 2 nests are present, this has been attributed to polygynous nesting. Three occupied nests were found on an Ontario bridge. Nests have been found as close together as 75 m on buildings and 13 m on a cliff. Limited information is available on territory size. One territory in an Illinois floodplain forest was estimated at 0.3 ha; 2 Kansas territories were 1.3 and 2.9 ha. There is no information on home range size, but it has been assumed to be larger than 3 ha. In Indiana, breeding adults were never seen further than 100 m from the nest, so the home range was less than

3 ha (Fitch 1958; Graber et al. 1974; Hill and Gates 1988; Johnston 1971; Peck and James 1987; Weeks 2020).

Natal philopatry has been reported to be very low in areas other than Ontario. In Indiana, only 1 of 11,847 nestlings bred at its natal site and only 218 (1.8%) were subsequently found breeding on the 250 km^2 study area (Weeks 2020). Three of 167 nestlings (1.8%) returned to a Kansas study area. One young banded in Virginia was recovered during the breeding season in Alberta, approximately 1,100 km from its natal area (Brewer et al. 2018). Near Kingston, 24% of young returned. In the same study area, 38% of adults returned the next year, and 25% of adults returned in Kansas. In Indiana, 40% of both males and females returned; multiple-brooded birds were more likely to return than those that had a single brood the previous year. Most retained the same territory for their entire life. Weeks (2020) stated that site fidelity by adults was very high, probably in excess of 80%, and that it was likely that all surviving adults returned to the same area. During a breeding season, adults seldom move from the original territory to renest or raise a second brood. In Indiana, only 15.7% of birds dispersed to another territory between years, and 0.9% dispersed within a breeding season (usually birds that had failed to raise the previous brood) (Beheler et al. 2003; Conrad and Robertson 1993b; Peck and James 1987; Schukman 1993; Weeks 2020).

Limiting Factors

Eggs have been found in Ontario nests from early April until early August, with most present from the last week of May until the last week of June (Peck and James 1987). In Algonquin Park, nests are under construction from mid-April to late May, eggs are present from mid-April to mid-July, nestlings are present from late May to mid-August, and fledglings have been observed from early June to early September (Tozer 2012).

Nest building begins shortly after pair formation and takes 7-14 days. If an old nest is used, it may be repaired and completed in 2-5 days. Nests built for second broods may be finished 5 days quicker than new first nests. After the nest is complete, 1 or 2 weeks pass before the first egg is laid, but occasionally as long as 3 weeks elapse. One egg is laid a day, but a day may rarely be missed. The incubation periods of 45 Ontario nests ranged from 13 to 18 days with most eggs hatching in 14 or 15 days. Eggs were present in 2 nests 21 and 22 days, suggesting that onset of incubation was delayed. Elsewhere, the incubation period has been reported as 14-17 days (average 16 days). Incubation begins with the laying of the last egg, but does not start in earnest until the next day. Eggs may hatch over a 1-3-day period with hatching asynchrony greater in second clutches. Young fledge when they are 13-20 days old, usually in 15-17 days. Approximately 10 days pass between fledging of the first brood and initiation of the second clutch. It takes about 45 days to raise a single brood and 117 days to raise 2 broods (Conrad and Robertson 1993a; Faanes 1980; Graber et al. 1974; Hill and Gates 1988; Keast 1990; Lemieux and Rail in Gauthier and Aubry 1996; Murphy 1994; Peck and James 1987, 1997; Smith 1942; Tyler in Bent 1942; Weeks 1978, 1979, 2020).

The phoebe may raise 1, 2, or even 3 broods a season, and renesting is common if the first clutch is lost. Females that lose the first brood to predation are more likely to forego nesting until the next year. Usually it raises 2 broods a year, but only one may be raised depending on age of the female and whether the first nest was successful. In the Kingston area, about half of females attempted second broods. Both yearlings and older birds tried to raise 2 broods, but almost all single-brooded

females were yearlings. All successful older females attempted a second brood compared with 69% for unsuccessful birds. Three triple broods have been reported. Clutches of 2-8 eggs have been found in Ontario, with 4- and 5-egg clutches constituting more than 82% of clutches; other clutch sizes were rare. Elsewhere, clutches of 2-8 eggs have been reported, with the normal clutch size 3-5 eggs. In many studies, over 90% of nests contained 4 or 5 eggs. Clutches larger than 6 eggs may be due to intraspecific parasitism. Second clutches may average slightly smaller than first ones, but usually this difference is not significant. Clutches of replacement nests are significantly smaller than those of first and second nestings (Beheler et al. 2003; Conrad and Robertson 1993a, 1993b, 1993c; Conrad et al. 1998; Faanes 1980; Graber et al. 1974; Hill and Gates 1988; Lemieux and Rail in Gauthier and Aubry 1996; Murphy 1994; Peck and James 1987; Schukman 1993; Tyler in Bent 1942; Weeks 1978, 1979, 2020).

The age at first breeding is 1 year. The phoebe is typically monogamous, with pairs remaining mated for the entire breeding season. In Indiana, 2.4% of females and 4.8% of males divorced and remated for their next breeding attempt within the year. Many pairs remate and nest in the same location over multiple years. Polygyny occurs rarely. In New York, 2 females had a common mate, nested 20 m apart, and successfully fledged full broods. Neither female attempted a second brood (Gretch 1999; Weeks 2020). In Indiana, 17.2% of nests contained extra-pair young in at least 1 brood. Overall, 9.2% of broods contained extra-pair young and 5.1% of nestlings were extra-pair. Second broods were significantly more likely to contain extra-pair young (13.8%) than first broods (4.6%). In first broods, only 1 nestling was not related to the female's mate compared with more than 50% of nestlings in second broods. This genetic study also revealed 2 instances of intraspecific parasitism where young were not related to either adult attending the nest (Beheler and Rhodes 2003).

The Eastern Phoebe forages mostly from a perch less than 10 m from ground, typically in the lower half of the canopy. Perches are in edge habitats or lower limbs of closed-canopy forest. In Illinois, most perches were in hawthorns, willows, black cherry, and apple. In British Columbia, perches were usually dead branches of trembling aspen, willow, or snags. Foraging occurs mostly in the morning, and flycatching is the typical method of capturing prey. When it flycatches, about 75% of food is caught by hawking and the remainder by hover-gleaning from twigs and leaves. During winter in Texas, 54.1% of foraging movements were aerial hawks, 29.5% were sally gleans, and 15.6% were perch-to-ground sallies. It rarely took prey from the surface of water. The percentage of foraging movements that involved aerial hawking increased with ambient temperature. Temperature probably affects phoebe foraging techniques in Ontario during cold spring and early autumn periods. Average perch height in Texas was 3.77 m. The phoebe occasionally pursues flying insects to the ground or pounces on ground-dwelling invertebrates. Rarely, it perches on humans and deer and flycatches insects attracted to them. It occasionally fishes by perching 50-60 cm above water and diving or hover-diving to catch fish once they come within 5-8 cm of the surface. Typically, only the bird's head and breast touch the water. It was observed hawking moths at night during autumn migration under the bright lights of a football stadium (Binford 1957; Campbell et al. 1997; Fitch 1958; Graber et al. 1974; Lebbin et al. 2007; McKenzie and Noble 1975; Troy and Baccus 2009; Weeks 2020).

Near Kingston, nestlings of first nests were fed different prey than second broods due to changing availability of invertebrates. First broods were fed mostly beetles and flies; second broods were fed caterpillars, moths, caddisflies, and damselflies. Other food items brought to nestlings included oligochaetes, snails, spiders, midges, and hymenopterans (Keast 1990). Near Cambridge, Sandilands and Morningstar (2018) analyzed prey items in nestlings' feces collected under a nest. Each of the 2 broods consumed 15 taxa of invertebrates for a total of 24 taxa. Only 6 taxa (25.0%) were consumed by both broods. These included stream mayflies, dobsonflies, gypsy moths, oblique-banded leafrollers (a moth), and blow flies. Fowl mites occurred in samples of both broods, but it is possible that these dropped or were dropped on the feces rather than being ingested. The first brood consumed narrow-winged damselflies and skimmers (Odonates), earwigs, tiger and owlet moths, spruce budworms, giant casemaker caddisflies, flesh flies, and horse flies. The second brood consumed leafhoppers, crambid snout moths, tiger moths, root-maggot flies, frit flies, and flesh flies. Results of both Ontario studies indicate that the 2 broods have differing diets probably because of differing seasonal prey availability. The food items fed to the broods were different in Kingston and Cambridge, suggesting that adults capture prey opportunistically based upon its local abundance.

Limited information is available on the adults' diet, with the most definitive analysis completed more than a century ago. This study found that 89.2% of the diet was animal material, mostly insects. Hymenopterans were the most important food, comprising 26.7% of the diet, constituting the largest percentage of the diet in almost every month. Beetles comprised 15.3% of the diet and were eaten year round, but mostly in spring and early summer. Orthopterans constituted 12.9% of the diet, bugs 18.5%, lepidopterans 8.9%, flies 6.9%, and spiders, ticks, and millipedes 5.8%. The phoebe frequently eats dragonflies and readily adapts to outbreaks of insects such as cicadas and forest tent caterpillars. It actively selects beetles 2-10 mm long. Other animal foods it has eaten include mosquitoes, skippers (butterflies), small frogs, and fish as long as 6 cm. Vegetation is eaten chiefly early in spring and autumn, but also during unfavourable weather. It eats mostly seeds and berries, including pokeweed, wild cherries, elderberries, raspberries and blackberries, and juniper berries (Beal 1897a; Binford 1957; Graber et al. 1974; Hespenheide 1971b; Keast 1990; McKenzie and Noble 1975; Tyler in Bent 1942; Weeks 2020).

The phoebe is commonly parasitized by the Brown-headed Cowbird. The phoebe is a receptor species, rarely ejecting an egg, burying it in the lining, or abandoning the nest. About 10% of parasitized nests fledge both phoebes and cowbirds although fewer phoebes fledge from parasitized than unparasitized nests. Cowbirds frequently remove a phoebe egg prior to depositing an egg of their own, thereby reducing production even in successful nests. Parasitism rates depend on timing of phoebe nesting, nest location, and whether the nest has previously been parasitized. In New York over 2 years, parasitism rates of first phoebe nest attempts were 37% and 42% compared with 11% and 13% for later nests. Parasitism rates under eaves were 46% and 57% compared with 11% and 6.7% under bridges, and 50% of nests parasitized the previous year were parasitized again compared with 6.2% for nests that were not previously parasitized. Parasitism rates vary greatly depending on habitat, relative abundance of host and parasite, and sample size. In Ontario, 179 of 1,498 nests (11.9%) were parasitized. Other parasitism rates include 0%, 14%, 29%,

and 33% in 4 Illinois study areas; 1% in southern Wisconsin and Tennessee; 15%, 24%, and 18.2-36% in Kansas; 11% and 14% in Michigan; 5% in Indiana; and 0% in Maryland and British Columbia (Campbell et al. 1997; Faanes 1980; Graber et al. 1974; Hauber 2001; Peck and James 1997; Rivers et al. 2010; Weeks 1979, 2020). In Maryland, parasitism rates of phoebe nests were dependent upon the habitat where the nest was situated. In field and edge habitats, 0 of 22 nests were parasitized compared with 8 of 19 nests (42.1%) within forest habitat (Hahn and Hatfield 1995). In New York, Wagner et al. (2013) examined phoebe nests for parasitism from 2009 to 2011, observing the same nest sites that had been studied 1999-2002. Nests that were more likely to be parasitized in the later period had also been parasitized more frequently from 1999 to 2002. Cowbirds demonstrate a consistent preference for particular phoebe nest sites, even across generations of birds.

The greatest limiting factor to phoebes is availability of suitable nest sites. Consequently, many birds capable of mating are forced to be floaters. When a mated bird dies, it is replaced very quickly. Replacement males may attempt to kill the female's young to increase the likelihood of raising their own young. Large areas of otherwise suitable habitat may not be used if there are no appropriate nest sites. Good nest sites may become unusable if adjacent woody vegetation is removed. Out of necessity, some nests are placed in less than ideal situations where they are not totally protected from precipitation and dampness. These nests are vulnerable to falling. Nests under bridges are more likely to fall than those under eaves. Initial human settlement greatly increased nest-site availability. Nest sites are now declining due to replacement of old cement and wooden culverts and bridges with corrugated pipes and removal of derelict buildings (Badzinski 2000; Fitch 1958; Hauber 2001; Lemieux and Rail in Gauthier and Aubry 1996; Ritchison and Ritchison 2010; Sheppard et al. 1936; Weeks 2020).

Cold weather may have adverse effects on phoebes. Severe winters in the south may result in population crashes. In 1958, early spring storms occurred in the southern states and declines were noted in the Kingston area in 1958 and 1959. Periodic population declines have occurred since. Weather may also affect the breeding cycle. Timing of initiation of first clutches varies significantly year to year, depending on temperatures. Nest-building activities appear to cease when temperatures drop below 10°C. Cold spring weather may result in nesting delays as long as 3 weeks. This may affect clutch size or the number of broods that may be raised (Badzinski 2000; Graber et al. 1974; Murphy 1994; Weeks 1979, 2020; Weir 2008).

Insect abundance may affect timing and success of nesting. Studies in the Kingston area found that insects were scarce until late April or early May, abundant mid-May to mid-June, and scarce after mid-June. A similar pattern was documented in Kansas. If insects are particularly scarce in spring, nest initiation may be delayed. With the rapid spring increase in arthropods, there is ample food for nestlings of the first brood. Food may be limited when the second clutch hatches, and nestling starvation occasionally occurs. Hatching asynchrony is greatest in second broods, and this appears related to the relative scarcity of food. Spraying of pesticides may further reduce insect availability (Keast 1990; Lemieux and Rail in Gauthier and Aubry 1996; Murphy 1994).

Nests in culverts and under bridges may be washed away during floods (Schukman 1993; Weeks 1978, 1979). Peak flow rates in many Ontario streams have increased as a result of deforestation, urbanization, and other land-use practices.

In North Carolina, abundance of the phoebe was correlated with temperature, suggesting that it would benefit from climate change (Lumpkin and Pearson 2013). DesGranges and Morneau (2010) considered it highly sensitive to climate change in Quebec where it is near the northern extent of its range.

Status

The phoebe is undoubtedly more common now than prior to European settlement. Human-made structures have increased availability of nest sites and allowed it to inhabit much more area. McIlwraith (1894) considered it common in southern Ontario and Baillie and Harrington (1937) considered it common north to the transcontinental railway and west to the Lake of the Woods area. Baillie and Hope (1943, 1947) determined that it was rare along the northeast shore of Lake Superior but common in the Sudbury area. Smith (1957) considered it rare in the Clay Belt. During the first atlas, the Eastern Phoebe was widespread south of the Canadian Shield and in the Great Lakes–St. Lawrence Forest Region in the Shield. There were gaps in its distribution in the unbroken forests of Algonquin Park, Chatham-Kent where there are few wooded patches, and the alvars of Manitoulin Island. The most northerly record was at Pickle Lake (Helleiner in Cadman et al. 1987). James (1991) stated that it was common in the south but rare and local in heavily forested areas north to Pickle Lake and Timmins.

The second atlas indicated little change in the distribution of the phoebe since the first atlas. It was seen in many more squares in extreme southwestern Ontario and on Manitoulin Island than during the first atlas. Its probability of observation increased during the second atlas province-wide and in the Carolinian and Great Lakes–St. Lawrence forest regions. There were 2 areas in the province where it exhibited high abundance. The largest area was along the southern edge of the Canadian Shield from Renfrew County to Lake Ontario to the southern portion of Georgian Bay, and inland through Muskoka District. The other area was the Bruce Peninsula and Manitoulin Island. These areas support considerable forest cover and numerous bridges and buildings that could provide potential nest sites. Density was low in the Boreal Forest Region and the Algonquin Highlands, possibly due to extensive forest cover with a scarcity of bridges and buildings, and in extreme southwestern Ontario, possibly due to scarcity of forest cover (McLaren in Cadman et al. 2007).

Long-term (1970-2021) BBS data indicated annual decreases of 1.43% in Canada and 0.376% in Ontario. Over the short-term (2011-21), there were annual decreases of 2.16% in Canada and 1.89% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings occasionally return to the nest when they are young and continue to be fed by the adults for 2-3 weeks after fledging. Adults leave the territory shortly after the last brood fledges, usually in early July, looking for more diverse habitats where invertebrates are more abundant (Weeks 2020).

In Ohio, adult and juvenile Eastern Phoebes used densely regenerating clear-cuts during the postbreeding period. These and other early successional habitats may be important sources of dense cover and abundant food late in the breeding season (Vitz and Rodewald 2006, 2007). In Michigan, 86% of juvenile phoebes were captured in riparian forests during the postbreeding period; 14% occurred in upland forests. Riparian forests had a dense woody understorey whereas

upland forests had sparse coverage by shrubs and saplings (Akresh et al. 2009). During the postfledging period in Pennsylvania, Stoleson (2013) captured 1 adult and 9 fledglings in clear-cuts compared with 1 adult and 0 fledgling in mature, closed-canopy forest. Shrub density did not differ between clear-cuts and forests, but clear-cuts supported a high density of fruit-bearing shrubs.

MIGRATION

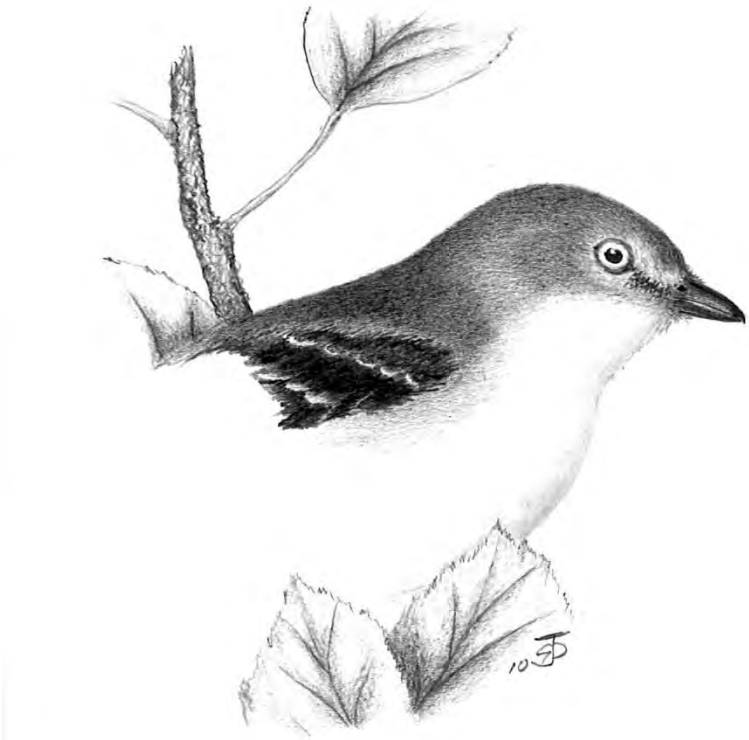
The phoebe is a solitary migrant and it is uncertain if it migrates diurnally, nocturnally, or both (Graber et al. 1974; Weeks 2020). In spring, it appears to follow the frost line and insect emergence northward. In much of its range, first birds arrive in March, although it may not occur in the northernmost portions of its range until early May. Males are thought to arrive before females, but this has yet to be confirmed. First arrivals may precede the peak of migration by more than a month. It arrives in Ontario in early April or late March, with the peak of migration in mid-April and stragglers continuing until about the end of May (Keast 1990; Weeks 2020). In the Kingston area, some autumn migrants appear in mid-July, including juveniles and adults, and another wave of juveniles occurs in mid-August. Autumn migration begins in earnest in mid-September and continues until the end of October, with the peak from the very end of September until mid-October. The phoebe moves southward gradually as insect numbers decline and may often remain in the province until early November (Keast 1990; Weeks 2020; Weir 2008).

During migration, the phoebe occurs in a variety of habitats. These include woodlands typical of breeding habitat; riparian growth along rivers, lakes, marshes, and beaver ponds; edges of deciduous and mixed forest; agricultural land; and rural residential areas. Presence of water appears to be more important during spring migration (Campbell et al. 1997; Weeks 2020).

The Eastern Phoebe is common during migration in Ontario (James 1991). Long Point migration data indicate that it has increased significantly at a rate of 4% annually since 1961. There was an increase in the 1960s, a decline in the 1970s, and a steady increase throughout the 1980s and 1990s (Badzinski 2000; Hussell et al. 1992).

White-eyed Vireo

Vireo griseus



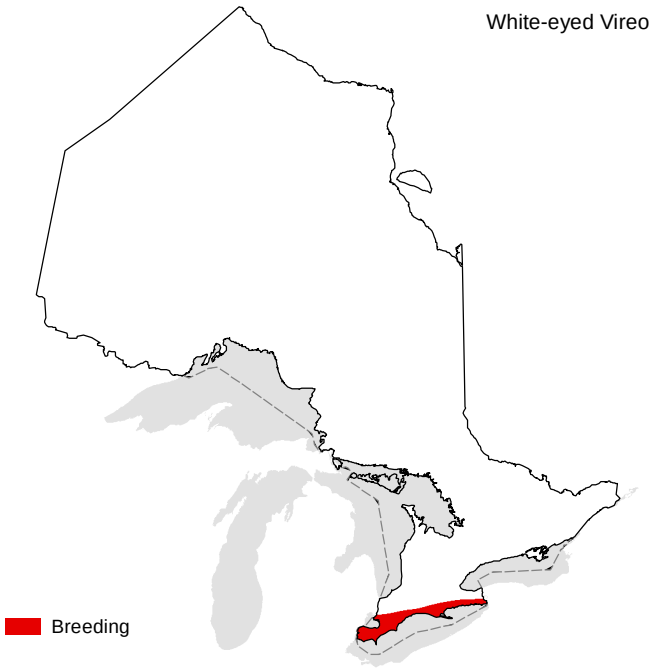
BREEDING SEASON

Habitat Requirements

In Ontario, the White-eyed Vireo has nested in thickets, savannahs, a dense tamarack stand near a marsh, overgrown fields, young second-growth woodlands, open shrubby beaches, woodland edges and clearings, and open swampy forests (Austen et al. 1994; Peck and James 1987).

Throughout its range, the White-eyed Vireo demonstrates a preference for overgrown old fields, young regenerating forests, and thickets along streams. In addition to habitats used in Ontario, it may nest in shrub thicket swamps, shrubs adjacent to marshes, near tree-fall gaps in deciduous forests, very dense second growth, cleared hydro rights-of-way, and abandoned pastures and cemeteries. In Illinois, it preferred successional fields, with numbers peaking on old farmland 44 years after abandonment. It did not appear on strip-mined areas until 18-20 years after mining. It occurred in small numbers in forested areas, preferring lowland forests. In Texas, it nested in low, shrubby vegetation with very high foliage density 0-1 m from ground, with a high diversity of shrub species.

Its density was inversely related to increased vegetation height, foliage density at 12-15 m, density of pole-sized trees, and percent canopy closure. In New Jersey, the White-eyed Vireo was significantly more abundant in hardwood swamp than in oak-pine forest. In Indiana, it nested in fields of grasses with blackberry thickets that contained numerous dense stands of small trees 1-7 m tall, and shrubby fields where about half the ground was shaded during part of the day either by saplings about 7 m tall or by nearly continuous stands of dense hawthorns. In Illinois and Virginia, 20-50-year-old abandoned pastures supported highest densities. It preferred areas with maple and elm saplings and a variety of other small trees and shrubs such as chokecherry, plum, witch-hazel, dogwoods, willows, and blackberries. Overall, it prefers variable habitat with extensive undergrowth, shrubs, raspberries, and saplings interspersed with taller trees on 10-20% of the area (Bent 1950; Bradley 1980; Fitch 1958; Graber et al. 1985; Hopp et al. 2020; Nolan 1963; Remson et al. 1998; Rich et al. 1994).



In Texas, abundance of the White-eyed Vireo was positively correlated with the number of shrub species, number of shrub stems, and foliage density at 1 and 3 m. It was negatively correlated with vegetation height, canopy closure, foliage density at 12-15 m, percent coverage by pines 17-32 cm diameter at breast height (DBH), and the number of tree stems 17-32 cm DBH (Conner et al. 1983). In the mid-Atlantic states, it was positively associated with foliage density 1-2 m tall, number of trees larger than 3 cm DBH per ha, and number of trees larger than 38 cm DBH per ha. It was negatively associated with percent ground cover and number of trees in a 0.04-ha circle at the pointing count (Robbins et al. 1989). In Texas, it was equally abundant in shrublands and woodlands with an understorey of oaks. It tended to nest in taller, more closed, later successional (woodland-like) habitat than the Black-capped Vireo, although there was considerable overlap in habitat (Kovar et al. 2018).

Lindell et al. (2007) summarized studies that determined species' abundance in relation to forest edge. The White-eyed Vireo was found to exploit edges and avoid forest interior. In South Carolina, almost all records were from forest edges and gaps during spring and autumn migration and the breeding and postbreeding seasons. There were very few records from forest interior (Bowen et al. 2007). In shrubby clear-cuts in Ohio, Rodewald and Vitz (2005) set mist nets 20, 50, and 80 m from the edge of a mature forest. There were no significant differences in its abundance at different distances from edge.

In forested riparian corridors in Georgia, the White-eyed Vireo was significantly more abundant in medium-sized (440-610 m) than narrow (36-330 m) or wide (1,320-2,088) corridors. It was negatively associated with basal area and canopy cover and positively associated with shrub cover (Hodges and Krementz 1996).

Shake et al. (2012) studied the White-eyed Vireo in shrublands in North Carolina to determine if it was area sensitive or affected by the shape of the habitat patch. They found no significant correlations between these parameters and its abundance. In Ohio, Lehnen and Rodewald (2009a) observed no evidence of area sensitivity by this vireo in clear-cuts. Patch size had no effect on annual survival or juvenile recruitment. Rodewald and Vitz (2005) found no difference in its abundance in small (4-8 ha) or large (13-16 ha) clear-cuts in Ohio.

Ontario nests were about 1 m from the ground in chokecherry, oak saplings, gray dogwood, raspberry, tamarack, and white pine (Peck and James 1987, 1997; Rayner 1988a). The nest site is often a Y-shaped horizontal deciduous branch close to ground, and the nest is usually surrounded by dense vegetation. Most often the nest is within a few metres of the edge of the territory. A high diversity of tree and shrub species is used for nesting. The species of plant may be unimportant provided that there is an abundance of stems and leaves for foraging close to the ground. Species commonly used for nesting include poison ivy, arrowwood, red cedar, multiflora rose, dogwood, plum, blackberry, blue beech, hawthorn, and saplings of elm, oak, sugar maple, hophornbeam, sassafras, hackberry, yellow birch, and cherry. Nests are close to ground, with an overall range of 0.2-2.6 m. Most are less than 1 m up, with average heights of 0.70 m, 0.74 m, 0.8 m, 0.94 m, and 1.45 m reported from Indiana, Kansas, Illinois, Virginia, and Texas, respectively (Bent 1950; Fitch 1958; Graber et al. 1985; Hopp et al. 2020; Kovar et al. 2018; Nolan 1963).

Males are territorial, but females may tolerate other females. Territory size varies depending on habitat quality, if there are neighbouring pairs, and on the experience of the bird. In Florida, some males defended lone territories surrounded by unsuitable habitat; others had many neighbours. In a 14-ha patch, there were 11 territories, a mean size of 1.3 ha. Two territories in Illinois averaged 0.14 ha; another Illinois territory in a swamp thicket was 0.13 ha and one in forest edge was 1.4 ha. Another territory in Illinois that contained 3 ponds surrounded by young second-growth forest was 0.13 ha. In Virginia, 16 territories averaged 1.03 ha (range 0.6-1.8 ha). In Kansas, 1 territory was 2.6 ha 1 year and 2.1 ha the next, but covered the same general area (Bradley 1980; Brewer 1955; Fitch 1958; Graber et al. 1985; Hopp et al. 1999, 2020).

Natal site fidelity appears to be low. None of 42 young returned in Virginia; in Massachusetts, 1 yearling was recovered breeding 20 km from its natal area. In Ohio, 7 of 273 juveniles (2.8%) returned as adults, and 6 of the 7 were encountered again at the natal site. Adult site fidelity is high, particularly for males. Of 74 male adults in Virginia, 54% returned the year after banding, 26% 2 years later, 7% 3 years later, 4% 4 years later, 3% 5 years later, and 0% 6 years later. Of returning males, 67 of 69 (97%) returned to their previous territory. The other 2 remained within 800 m of their original territory. Of 5 females, 3 returned the year after banding and 1 each returned in the second and third years. None of the females returned to the same territory and none paired with the same male in subsequent years. The nearest female movement was to the adjacent territory and the furthest was 3 territories away, a distance of 750 m. In Ohio shrubland habitat, 67 of 285 adults (23.5%) returned

and 66 of these were encountered at the same site (Hopp et al. 1999, 2020; Lehnen and Rodewald 2009b).

Limiting Factors

Eggs are most likely to be present in Ontario nests from mid-May until the end of June (Peck and James 1987, 1997). Nest building is initiated shortly after courtship and takes 3-5 days. Egg laying begins 1-3 days after the nest is complete. Eggs are laid at the rate of 1 a day but occasionally a day is skipped. Incubation begins with the laying of the third or fourth egg. If cowbird eggs are present in the nest, incubation may begin with the second vireo egg. The incubation period at 1 Ontario nest was 11 or 12 days. Elsewhere, the incubation period has been reported as 12-16 days, with most eggs taking 13-15 days to hatch. Fledging occurs at age 9-11 days (Bent 1950; Bradley 1980; Graber et al. 1985; Hopp et al. 2020; Kovar et al. 2018; Peck and James 1997; Nolan 1963; Saunders 1915).

In Virginia, the White-eyed Vireo frequently produces 2 broods a year, but it is unknown if double broods occur as far north as Ontario. It is a persistent renester and may attempt as many as 4 clutches if earlier attempts are unsuccessful. After an Ontario nest failed, a new nest was built approximately 300 m away for the second clutch. Ontario clutches contained 3 or 4 eggs. Five-egg clutches are rare and the mean North American clutch size is 3.74 eggs (Bent 1950; Hopp et al. 2020; Peck and James 1997; Rayner 1988a).

The breeding system is monogamous and the age at first breeding is 1 year. Some yearling males fail to attract mates. Once breeding is initiated, it occurs every year (Hopp et al. 2020).

The White-eyed Vireo forages in deciduous trees, shrubs, and vines at low to intermediate heights. It forages from the ground to 15 m, but captured 90% of food 0.6-6 m from ground in 1 study and 87% between 1.2 and 10.7 m in another study. In the latter study, average height of trees used for foraging was 10.0 m and 64.5% of foraging occurred in the middle portion of the tree. It forages by gleaning from vegetation by picking or hovering. In 1 study, 61.5% of captures were made while perched and the remainder by aerial hovering. Eighty-five percent of prey was captured on leaves. In Maryland, most foraging was by gleaning, less frequently by hovering and pecking; hawking was not observed (Hopp et al. 2020; Nolan and Wooldridge 1962; Williamson 1971).

The diet consists of 90% animals, mostly insects; caterpillars are especially important. Some fruit is eaten year round, but particularly in early spring, autumn, and winter when insects are less available. Lepidopterans may constitute a third of the diet yearly, being consumed every month, with peaks in April, May, June, and August. Beetles (weevils and ground, lady, click, long-horned, metallic wood-boring, and leaf beetles) and bugs (stink bugs, leafhoppers, and scale insects) are important prey. Other invertebrates commonly eaten include ichneumonid and other wasps, bees, flies, grasshoppers, and spiders and their egg cases. Miscellaneous insects occasionally eaten include dragonflies, damselflies, walkingsticks, stoneflies, and lacewings. Snails and lizards are rarely consumed. Plant food includes fruit of sumac, dogwood, poison ivy, pokeweed, and wild grape (Chapin 1925; Hopp et al. 2020; Nolan and Wooldridge 1962).

The White-eyed Vireo is an acceptor of Brown-headed Cowbird eggs, and the rate of parasitism is very high, about 50% overall. Cowbirds typically lay in the first 2 days of laying by vireos and lay 1 or 2 eggs. Some parasitized nests are abandoned. In Ontario, 4 of 7 nests (57%) were parasitized.

Parasitism rates in other areas include: 40% in Louisiana, 48.9% in Virginia, 50% in Indiana, 83% in Illinois, and 11.1% in Georgia and South Carolina (Bent 1950; Hopp et al. 2020; Kilgo and Moorman 2003; Lowther 1997; Peck and James 1997; Rayner 1988a).

Habitat availability and loss may be limiting factors. Suitable habitat is patchy and unevenly distributed. The White-eyed Vireo has expanded its range northward in Ontario since 1950, primarily due to habitat creation through abandonment of marginal farmland. This new habitat may be temporary because much of it may regenerate naturally into forest. Its preferred habitat is usually not considered significant by humans and is often converted to other land uses (Austen et al. 1994; Hopp et al. 2020; James in Cadman et al. 1987).

Robinson and Robinson (1998) cut openings of 0.02-0.4 ha within a 2,000-ha forest in Illinois. The White-eyed Vireo was common in recent cuts, rare in older cuts, and absent in uncut forest.

Price (2004) predicted that the breeding range of the White-eyed Vireo would increase in Ontario if the average summer temperature increased by 2°C.

Status

In the late 1800s and early 1900s, the White-eyed Vireo was considered accidental in Ontario. The first record was an autumn migrant collected near Listowel in 1890. In the same year, breeding was reported in Welland County and it was reported nesting near Toronto in 1898. These early breeding records were never substantiated and are probably in error. Excluding these records, only 7 had been confirmed in the province by 1939. These were all spring or autumn records. In addition to the Listowel record, it was documented at Woodstock, Mount Forest, Ashbridges Bay in Toronto, Point Pelee, and on Pelee Island. Breeding was first confirmed in 1971 when 2 unsuccessful nests were found near Rondeau Provincial Park. One or 2 pairs may breed annually near the park, but some years none breed successfully. It is a rare to local breeder near Lake Erie, with the largest population near Point Pelee, where at least 6 pairs nested in 1992. Several pairs have been recorded near Fish Point on Pelee Island, but breeding has not been confirmed on the island. Other sites where it has bred include the Fingal Wildlife Management Area in Elgin County, the St. Williams forest, and at Long Point. Isolated pairs may nest sporadically anywhere within the Carolinian Forest Region. It is a rare to locally uncommon breeder in extreme southwestern Ontario (Austen et al. 1994; James in Cadman et al. 1987; James 1991; Lewis 1948; Mowat 1947; Rayner 1988a).

The second atlas indicated that there had been no changes in the distribution or probability of observation of the White-eyed Vireo since the first atlas. It is a regular but rare breeder in the Carolinian Forest Region, with most breeding records along the northern shore of Lake Erie, particularly at Point Pelee, Rondeau, and Long Point (James in Cadman et al. 2007).

POSTFLEDGING PERIOD

In Florida, juveniles often followed the male around the territory and helped to defend it. Juveniles continue to sing after dispersal from the natal territory and may establish and defend a vacant or abandoned territory (Hopp et al. 2020).

Vitz and Rodewald (2006) captured 79 adult and 178 juvenile White-eyed Vireos in regenerating clear-cuts in Ohio during the postbreeding period. They did not state whether it nested in this

habitat. Dense shrubby areas may be important during the postfledging period. In Missouri, Porneluzi et al. (2014) netted birds during the postfledging period 2-15 years after an oak-pine-hickory forest was clear-cut. The White-eyed Vireo was the third most abundant species captured. Its numbers peaked shortly after cutting and declined annually thereafter.

MIGRATION

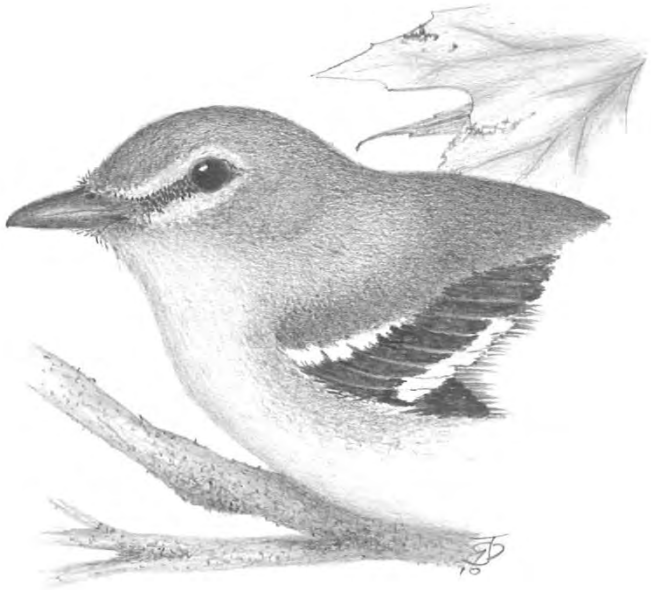
Based on kills at television towers, it has been presumed that the White-eyed Vireo migrates nocturnally. During migration, it prefers habitat similar to that used during the breeding season. During migration in Illinois, numbers were highest in forest edge and shrub habitats. It also occurred in lowland and upland forests (Graber et al. 1985; Hopp et al. 2020; Nolan and Wooldridge 1962).

In spring, older birds arrive sooner than yearlings, but only by a couple of days. The White-eyed Vireo typically arrives in the province in early May, but has occurred in early April. In autumn, juveniles leave first. Migration in Ontario occurs from mid-September to mid-October, with stragglers rarely remaining until late December (Hopp et al. 1999, 2020; James 1991).

James (1991) considered the White-eyed Vireo a rare migrant in the south and a vagrant in the north.

Yellow-throated Vireo

Vireo flavifrons

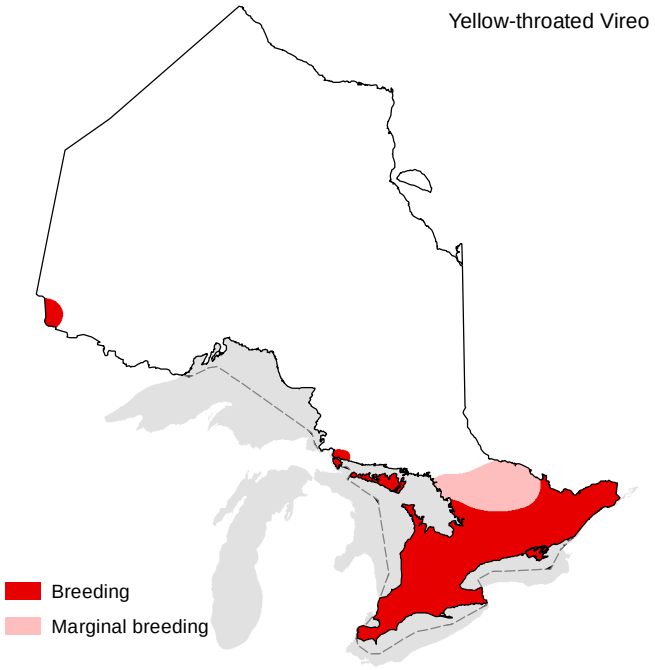


BREEDING SEASON

Habitat Requirements

In Ontario, the Yellow-throated Warbler breeds in deciduous and mixed woods that are usually semi-open, or near clearings and edges. It also nests in beaver ponds with scattered trees, in swamps with standing water, in treed fencerows and roadsides, along streams, in aspen-poplar groves, and seldom in treed village streets and campus parking lots (Peck and James 1987). It particularly favours red oak upland forests and lowland maple swamps (James in Cadman et al. 2007).

Older Ontario data suggested that the Yellow-throated Vireo preferred forests dominated by beech (McIlwraith 1894) and mature sugar maple–beech (Speirs and Orenstein 1975), and that it occasionally nested in parks in towns (Baillie and Harrington 1937). More detailed information was presented by James (1979b). It typically inhabits very open deciduous forests with mature trees. Habitat used in southern Ontario varies from mature deciduous forest to open woodlands with scattered large trees. Usually there are tall mature trees and scattered trees of varying ages, and there are often patches of grassland among tree groves. Nesting areas are often open, allowing growth of trees and shrubs that do not normally occur in forests. Dominant trees in Ontario territories were sugar maple, white elm, white oak, balsam poplar, trembling aspen, and white birch.



Other species included hemlock, basswood, ash, white pine, black walnut, hophornbeam, white cedar, hickory, beech, cherry, hawthorn, butternut, and apple. Detailed habitat characteristics in Ontario and Pennsylvania, respectively, were: trees per ha, 297 and 525; mean distance between trees, 5.8 m and 4.4 m; basal area, 16.8 m^2 and 23.5 m^2; mean crown volume per tree, 140.7 m^2 and 80.8 m^2; canopy cover, 62% and 90%. In Ontario, habitat always contains tall, old trees. Based on crown volume, Pennsylvania habitat was almost twice as dense as in Ontario. When it nests near other vireo species, it may adjust its habitat usage. Near Eastern Warbling-Vireos, both species nest in open habitats. Near Red-eyed Vireos, the Yellow-throated Vireo tends to occupy more open areas of forests or areas with little understorey. In these situations, it may have a preference for large oak trees (James 1976).

Habitat preferences elsewhere are similar to those in Ontario. The Yellow-throated Vireo prefers lowland and upland deciduous and mixed forests and avoids coniferous forests. Mature, open stands are selected, or edges and openings in closed stands are preferred. It typically nests on edges of forests created by watercourses, swamps, and roads, but may breed near forest gaps caused by treefall. Although it formerly nested in towns, suburban areas, orchards, and cities, these habitats were abandoned early in the 20th century. In Louisiana, habitat included tall trees in open woodlands, usually at edges, and at forest-interior openings large enough to create a sunny edge within the forest. In the mid-Atlantic states, it was positively correlated with the number of trees with diameter at breast height (DBH) larger than 38 cm, basal area, amount of foliage density between 0.3 and 1.0 m, and mean canopy height. It was negatively correlated with the number of dead standing trees and presence of conifers in the canopy. In southern Wisconsin, breeding territories had more large trees 37-52 cm DBH, more white oaks, and fewer shrubs 1-3-m tall than random areas. In Missouri, habitat surrounding singing perches was characterized by canopies taller than 16 m, 70-90% canopy closure, and 50-90% subcanopy coverage. Because of its preference for open canopy, the Yellow-throated Vireo is positively associated with shrub density, but negatively with forest isolation. Although typically associated with mature forests, it tolerates younger stands if there are scattered older trees. It breeds in a variety of deciduous and mixed forest communities including oak-hickory, sugar maple–hickory, sugar maple–basswood, sugar maple–yellow birch, pine-oak barrens that are almost forest, bur oak–green ash, oak–black gum, oak-poplar, elm-ash-cottonwood, sugar maple–beech-birch, white oak–tulip-poplar, and sycamore-ash-elm. In Illinois, it preferred woodlands with high numbers of large trees (Bent 1950; Bond 1957; Bushman and Therres 1988; Cyr and Henderson in Gauthier and Aubry 1996; Faanes and Andrew 1983; Graber et al. 1985;

Hoffman 1989a; Lynch 1987; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991; Noon et al. 1979; Remson et al. 1998; Robbins et al. 1989; Rodewald and James 2020; Samson 1979; Sutton 1949; Temple et al. 1979).

The Yellow-throated Vireo preferred landscapes with 51-75% forest cover in North Dakota; no areas had more than 75% forest cover (Cunningham and Johnson 2019). In North Dakota 400-m landscapes with less than 30% tree cover, its probability of occurrence increased greatly with increasing tree cover within 100 m and was 0% at 0-18% tree cover, 5% at 40% tree cover, and almost 15% at 70% tree cover. It also increased with increasing tree cover in landscapes with more than 30% tree cover, but less dramatically. Its probability of occurrence was 3% at 30-70% tree cover, increasing to 8% at 90% tree cover (Cunningham and Johnson 2016).

With the exception of Hayden et al. (1985), most researchers consider the Yellow-throated Vireo area sensitive. Even though it nests on forest edges, it requires large tracts and has disappeared or declined significantly where forest sizes have diminished. In Wisconsin, it was found in woodlots as small as 6.5 ha, but was at least 50% more common in larger woodlands. In western Maryland, it was only encountered in forests larger than 4,000 ha; in Wisconsin, highest frequencies were in woodlots larger than 32 ha; in Illinois, it occurred in woodlots 6-16 ha in area; in eastern Maryland, it disappeared from woodlands smaller than 70 ha; in Connecticut, average patch size it occurred in was 1,366 ha, and the minimum woodlot size it occurred in was 347 ha. In Maryland, it was estimated that 100 ha of forest as well as a high percentage of regional forest cover with large, deciduous trees were required to support a viable population. In Texas, it was absent in riparian forests with widths less than 70 m (Askins et al. 1987; Bond 1957; Bushman and Therres 1988; Robbins 1979; Rodewald and James 2020). Although it occasionally occurs in Ontario woodlands smaller than 100 ha, it is unknown if self-sustaining populations occur in smaller areas.

Ontario nests were in deciduous trees and all but one were living. Large, mature trees were greatly preferred for nesting. Trees selected for nesting, in order of preference, were maples, poplars, oaks, and elms. DBH of 3 nest trees was 36, 41, and 41 cm. Nests were usually in forks of horizontal branches. Their positions ranged from near the trunk (77%) to ends of branches at the tree periphery (23%). Distances from trunk were 0.3-3 m, mostly 0.6-1.2 m. Nests were 1.2-24 m from the ground, with most 7.5-13.5 m up (Peck and James 1987). Nest height may be influenced by presence of the Red-eyed Vireo. Overall average height of Ontario nests was 11.2 m; 14.4 m when the Red-eyed Vireo was present and 9.5 m when it was absent, a significant difference (James 1997a).

Throughout its range, the Yellow-throated Vireo nests almost exclusively in deciduous trees, rarely in conifers, usually at the edge of mature forests or in widely spaced trees near woodlands. It nests mostly in maples and oaks, but also in beech and elm, and in pines in the south. Other nest tree species include hickory, black cherry, apple, honey locust, balsam poplar, trembling aspen, large-toothed aspen, and black walnut. Nests are usually suspended from prongs of a forked twig in the crown of a tree. Most are well concealed, but some may be exposed; exposed nests are still in shade most of the time. Occasionally nests overhung cottages, outbuildings, or parking lots. Nests tend to be at a height of 0.5-0.75 of the tree height, and closer to the centre of the tree than the outside. Nests were reported 1-24 m from the ground with most more than 10 m up (Bent 1950; James 1976, 1979b, 1999b; Rodewald and James 2020; Sutton 1949; Whitelaw 1997).

The Yellow-throated Vireo is only mildly territorial. Intruders are expelled, but usually only when they land in the same tree. Some territories may be close to the ground; others are high in the canopy. It is possible that 1 territory may be over another. Due to its scattered distribution, most territories have no neighbours and there is no need for defence. When neighbours are present, they are tolerated within close range; 2 active nests in Oxford County were only 15 m apart. Eastern Warbling- and Red-eyed vireos are tolerated unless they approach very close to the nest. Nests have been found within 25 m of a Red-eyed Vireo nest and nest trees of Yellow-throated and Eastern Warbling- vireos had intertwining branches. No information on home range is available. One territory in the eastern states was estimated at 4 ha. Four Illinois territories averaged 0.8 ha (range 0.7- 1.0 ha), and Williamson (1971) reported a territory size of about 4 ha in Maryland. Once Ontario birds are mated, they seldom stray further than 100 m from the nest (3 ha), but may travel 500 m if the habitat is irregular or linear (Cyr and Henderson in Gauthier and Aubry 1996; James 1976, 1996a, 1999b; Peck and James 1997; Rodewald and James 2020; Smith et al. 1978; Sutton 1949).

There is limited information on site fidelity. One bird banded during the breeding season in Maryland was recaptured at the same site 6 years later (Rodewald and James 2020).

Limiting Factors

Eggs have been found in Ontario nests from the last week of May until mid-July, with most present in the first half of June (Peck and James 1987). Once females arrive, pairing occurs quickly and nest initiation is within 4-12 hours. The first nest takes about 8 days to complete. Nests for second attempts may be built in 5 days or take as long as the first nest. Egg laying begins the day after the nest is finished, and 1 egg is laid a day. Incubation starts once the clutch is complete. The incubation period is usually 12 or 13 days, but may be 15-16 days when cowbird eggs are present. One of 3 eggs in an Elgin County nest hatched in 10 days; there was a delay of at least 5 days between laying of the first and third eggs in this nest. Young leave the nest when they are 13-15 days old, but can fly only weakly (Bent 1950; Cyr and Henderson in Gauthier and Aubry 1996; James 1978a, 1996a, 1996b, 1997a, 1997b, 1999c; Peck and James 1987, 1997; Rodewald and James 2020).

Although Sutton (1949) stated that the Yellow-throated Vireo typically reared 2 broods in Michigan, Rodewald and James (2020) and James (1999c) concluded that it only raises 1 brood annually. This was based on the lengthy dependency of young on adults and the fact that second broods have not actually been confirmed. Renesting is common if a clutch is lost and as many as 3 nesting attempts may be made. Renesting occurs in a new nest, often within 100 m of the first nest but occasionally as far as 400 m away. Typical clutch size is 4 eggs, sometimes 3 eggs, rarely 5. Nests parasitized by cowbirds may contain only 1 or 2 vireo eggs (Bent 1950; Cyr and Henderson in Gauthier and Aubry 1996; James 1997b; Peck and James 1987; Rodewald and James 2020; Sutton 1949).

The age at first breeding is 1 year, and breeding occurs every year thereafter if a mate is obtained. The mating system is monogamous (Rodewald and James 2020).

The Yellow-throated Vireo forages mostly on branches in the interior of trees in Ontario. In Maryland, it foraged on the outer portions of trees early in the season and moved more towards the interior later. It chooses trees significantly shorter than expected for feeding. Males forage at

significantly higher heights than females. Overall mean foraging heights were 6.7 m in Ontario, 11.7 m in Pennsylvania, and 16.1 m in Arkansas. It forages around 0.5-0.75 of tree height, at greater heights than Red-eyed and Eastern Warbling- vireos, and forages higher when Red-eyed Vireos are present. The Yellow-throated Vireo rarely feeds on the ground. It forages on every tree species in the territory, including conifers, often in proportion to their availability. In Ontario and Pennsylvania, important trees for foraging were sugar maple, white elm, white oak, and balsam poplar; trembling aspen, ash, and hawthorn were also frequently used. In Illinois, it exhibited selectivity in the tree species that it foraged in. Of tree species found in Ontario, in order of decreasing preference, pin oak, sycamore, white elm, bitternut hickory, Shumard oak, black gum, and Manitoba maple were used more than their availability. In order of decreasing avoidance, pumpkin ash, red maple, blue beech, silver maple, green ash, and shellbark hickory were used less than their availability. Bitternut hickory was selected, yet it was 19th and last in abundance of tree species. Pumpkin ash and blue beech were avoided, but they were second and seventh in abundance, respectively. In Ontario and Pennsylvania, canopy closure at foraging sites averaged 62% (range 30-90%), significantly more than for the Eastern Warbling-Vireo and significantly less than for the Red-eyed Vireo. The Yellow-throated Vireo preferred to forage on dead limbs and favoured completely dead trees or oaks or aspens, which often have large numbers of dead lower limbs. Foraging perches were 76.5% dead, 21.5% unfoliated, and 2.0% foliaged. It gleans most food from tree bark. Foraging is concentrated on basal portion of limbs, and it frequently moves near and around the trunk in a spiral fashion. Eight-four percent of food is taken from branches and the rest from leaves. Over 80% of food is taken centrally in trees, the remainder from the periphery. About 55-69% of food is obtained by stalking and gleaning (significantly different from Red-eyed and Eastern Warbling- vireos), 23-29% by sallying and hovering (significantly different from Red-eyed and Eastern Warbling- vireos), and 2-5% by hawking (Gabbe et al. 2002; Hamilton 1958; James 1976, 1979b; Rodewald and James 2020; Williamson 1971).

Nestlings are initially fed mostly soft-bodied green caterpillars, but later a wider variety of arthropods including moths and dragonflies. Most food brought is fresh, but adults occasionally regurgitate food for young nestlings. The diet of adults consisted of more than 98% animals: 95.8% insects, 2.4% spiders, and 0.06% other invertebrates (based on a sample of 160 stomachs). Over 42% of the diet consisted of lepidopterans including 23.1% caterpillars and 19.4% moths; butterflies were seldom consumed. Other invertebrates it ate included 12.9% beetles (weevils and lady, metallic wood-boring, leaf, click, dung, and scarab beetles), 7.4% flies (midges and horse flies), 5.1% hymenopterans (bees, sawflies, and ichneumonid wasps), 4.9% other insects (grasshoppers, crickets, locusts, and dragonflies), and snails. It eats plant material only in late summer and autumn, including sassafras berries, wild grape, pokeweed berries, lamb's-quarters seeds, and multiflora rose hips (Chapin 1925; James 1999c; Rodewald and James 2020; Sutton 1949).

Many nests are parasitized by Brown-headed Cowbirds, including replacement nests. The incidence of parasitism varies geographically; in Ontario, 23 of 48 nests (47.9%) were parasitized. Twenty-seven of 95 nests (28%) throughout the Yellow-throated Vireo's range were parasitized. It is a cowbird egg acceptor. Very rarely, it abandons a parasitized nest or buries cowbird eggs. Cowbirds frequently remove vireo eggs from nests, and there may be as many as 3 cowbird eggs in a nest. Vireo production in parasitized nests is low. Unless a vireo is hatched first, it usually dies due to

squashing or being out-competed for food. Parasitized nests average 0.6 vireo fledglings compared with 3.4 for unparasitized nests (Bent 1950; James 1997b; Lowther 1997; Peck and James 1997; Robinson 1992; Rodewald and James 2020; Sutton 1949).

Habitat loss and degradation may affect populations. Forest fragmentation may result in woodlands becoming too small to support a viable population. Effects of logging are uncertain, although extensive clear-cutting is detrimental. With its preference for an open canopy, the Yellow-throated Vireo may tolerate a broad range of silvicultural practices. Selective logging that creates small canopy openings may be beneficial, but may make nests more vulnerable to cowbird parasitism. Selective thinning tends to remove mature trees, which are important to the Yellow-throated Vireo (Bushman and Therres 1988; Cyr and Henderson in Gauthier and Aubry 1996; Rodewald and James 2020).

Current impacts of pesticides and contaminants are unknown. The Yellow-throated Vireo suffered direct mortality and local extirpations due to spraying for Dutch elm disease and gypsy moths. These practices are thought to have been responsible for its disappearance as a breeding species from towns, suburban areas, cities, and orchards (Bent 1950; Rodewald and James 2020).

In New Jersey and Pennsylvania over a 15-year period, hemlock declined from 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The Yellow-throated Vireo responded positively to hemlock decline and increased (Toenies et al. 2018).

Human disturbance may be a factor, depending on the stage of nesting. If disturbed during pair formation and early nest building, the nest site is typically abandoned and the female may desert the male. Once incubation starts, the Yellow-throated Vireo is insensitive to disturbance. Once adults cease to brood young, they become much more agitated by humans and other predators (James 1996b, 1999c; Rodewald and James 2020).

Price (2004) predicted that the range of the Yellow-throated Vireo could expand in southern Ontario if the average summer temperature increased by 2°C.

Status

The Yellow-throated Vireo has never been common in Ontario. McIlwraith (1894) considered it uncommon but generally distributed in the south, with records from London and Ottawa. The first record for the Kingston area was in 1919 (Weir 2008). Baillie and Harrington (1937) considered it uncommon in extreme southern Ontario, breeding north and east to Peterborough and Ottawa. They also had summer records from Grey County, Muskoka and Parry Sound districts, the Lake Nipissing area, Kenora, and Sault Ste. Marie. During the first atlas, it was uncommon in the south, with highest numbers along the southern edge of the Canadian Shield and along the Niagara Escarpment (James 1996a; James in Cadman et al. 1987). James (1991) considered it uncommon to locally common in the south north to Bruce County and Ottawa and occasional and rare to Sault Ste. Marie and Manitoulin Island and in western Rainy River District. A nest reported from Sudbury District in 1996 is the most northerly one confirmed to date (Peck and James 1997; Whitelaw 1997). James (in Cadman et al. 1987) concluded that it probably declined with settlement and forest

fragmentation, but that populations were stable at that time. It suffered a significant decline in the first half of the 20th century due to pesticide spraying.

The second atlas revealed that there was no significant change in the breeding distribution of the Yellow-throated Vireo, although there were more northern records in the Canadian Shield south of the North Bay area. This may represent a real range extension, or may be mostly singing territorial males that are unmated and contribute little to the population. There was significant turnover in the squares in which it was detected between atlases. This may reflect changes in forest cover or be related to a small and dispersed population shifting around. There was no significant change in its probability of observation province-wide between atlases, but there was a significant decline in the Carolinian Forest Region. The Frontenac Axis was the largest area of high abundance, with patches of high abundance along the southern edge of the Shield and on the Bruce Peninsula. In the Carolinian Forest Region, the larger areas of mature forests in northern Lambton County and in Norfolk County supported high densities (James in Cadman et al. 2007).

Long-term (1970-2021) population trends determined from Breeding Bird Survey results indicate increases of 0.903% annually in Canada and 0.5% in Ontario. The short-term (2011-21) trends were annual increases of 5.09% in Canada and 5.51% in Ontario. The long-term trends were highly reliable. The short-term results were of medium reliability for Canada and low reliability for Ontario (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings remain near the nest site most of the summer. They are typically within 100 m of the nest the first week, 200 m by the second week, and still within 400-500 m by late summer. After fledging, each adult cares for 1 or 2 young. Fledglings start looking for food 16 days after leaving the nest, but are occasionally fed by adults until a month after fledging. Family groups may remain on the breeding territory until autumn departure (Rodewald and James 2020).

In Ohio, adult and juvenile Yellow-throated Vireos used densely regenerating clear-cuts during the postbreeding period. These and other early successional habitats may be important in providing dense cover and abundant food (Vitz and Rodewald 2006, 2007). In Missouri, Porneluzi et al. (2014) netted birds during the postfledging period in an oak-pine-hickory forest 2-15 years after it had been clear-cut. Twenty Yellow-throated Vireos were captured during this period.

MIGRATION

Most migration is nocturnal, but some daytime movement occurs. The Yellow-throated Vireo typically migrates solely or in mixed flocks of chickadees and warblers (Bent 1950; Rodewald and James 2020).

In Ontario and southern Quebec, the Yellow-throated Vireo may arrive as early as late April, but most arrive in May with the peak in the last two thirds of May. Adult males arrive a few days before females (Cyr and Henderson in Gauthier and Aubry 1996; James 1996a; Rodewald and James 2020). Autumn departure timing is not well known, but is from mid- or late August to mid-September. Stragglers have occurred in the province until mid-November (James 1991; Rodewald and James 2020).

During migration, the Yellow-throated Vireo uses a variety of habitats, some of which may not be used during the breeding season. It may occur anywhere there are trees. It is most frequent in a variety of deciduous and mixed woods, usually at forest edge. It may also occur away from forests, such as on shrubby beach barriers (Bent 1950; Rodewald and James 2020) and along treed roadsides (personal observation). In Illinois, spring densities were higher in bottomland forests than upland forests (Graber et al. 1985). In Ohio, there was no difference in its abundance during spring migration in riparian forests and upland forests (Rodewald and Matthews 2005).

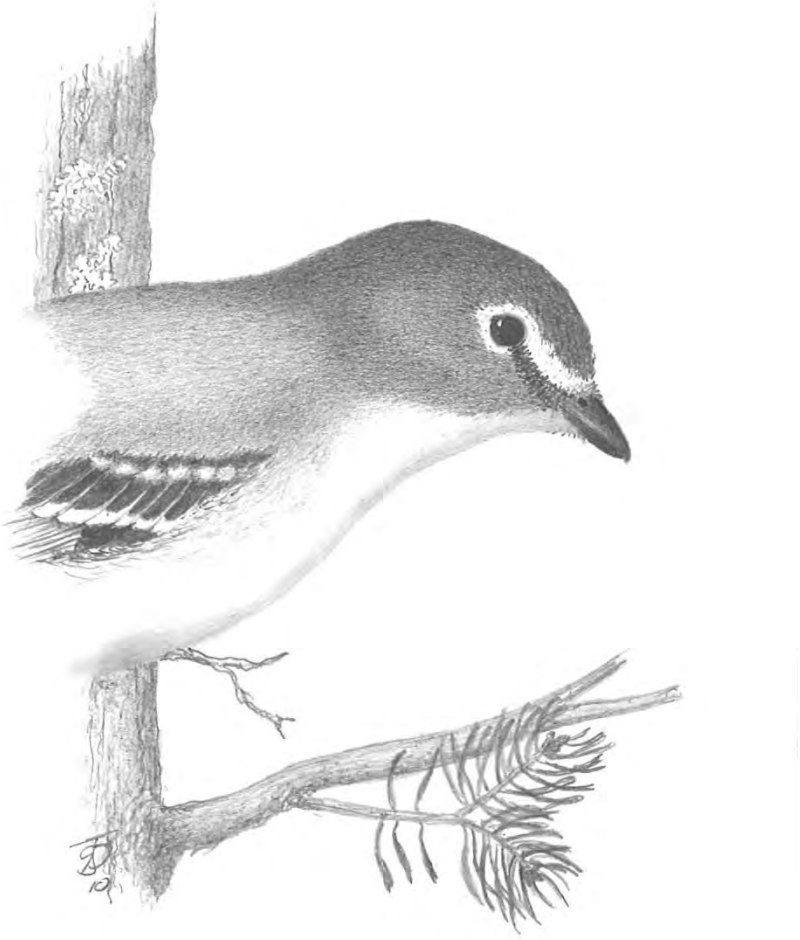
The Yellow-throated Vireo is often killed at structures at night while migrating, but kills are much less common than for most other species. Eighteen were reported killed at the Lennox Generating Station chimneys (Rodewald and James 2020; Weir 2008).

The Yellow-throated Vireo is a rare migrant. It tends to fly straight to the breeding territories in spring, remain there until autumn then depart abruptly. It is seldom seen outside of breeding areas (James 1991).

Data from the Haldimand Bird Observatory's Ruthven banding station indicated that the Yellow-throated Vireo may be increasing. This is the only banding station in Ontario that detects sufficient individuals to generate a trend (James in Cadman et al. 2007).

Blue-headed Vireo

Vireo solitarius



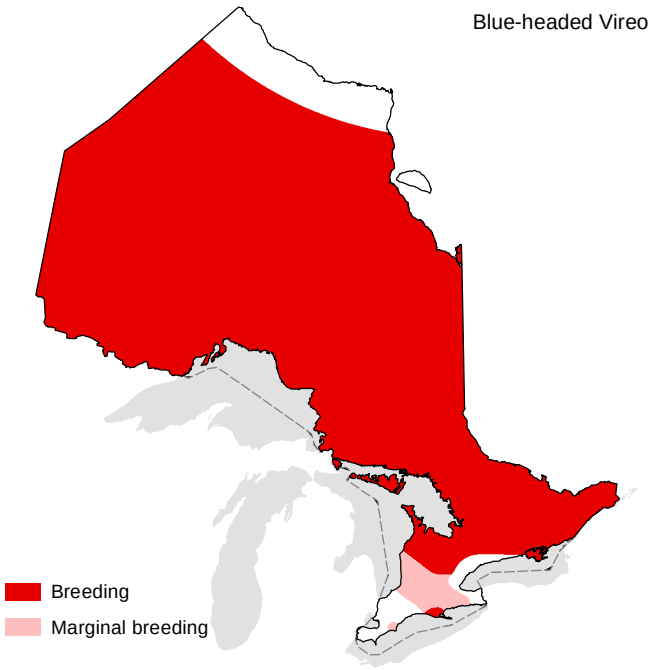
BREEDING SEASON

Habitat Requirements

The Blue-headed Vireo nests mostly in woodlands in Ontario, preferring mixed stands above coniferous stands and seldom nesting in deciduous woods. Two nests were in open areas: a dry rock ridge and an overgrown pasture. Several nests were near water, but it is uncertain if it prefers sites near water or if this was a reflection of the habitat preference of conifers (Peck and James 1987).

In northwestern Ontario in the Boreal Forest Region, the Blue-headed Vireo occurred in coniferous shrubs, mixed shrubs, coniferous forest, and deciduous forest (McLaren and McLaren 1981). Near Pickle Lake, it occurred regularly in low numbers in coniferous forest (James 1980). Near Hearst, it occurred at low densities in 5- and 6-year-old clear-cuts in upland mixed forest and in

uncut upland stands. It was not detected in upland clear-cuts that were 3 and 9-24 years old and it was absent in uncut and cut lowland conifer stands (Welsh and Fillman 1980). In jack pine stands near White River, it was significantly more frequent in stands 40-100 years old than in stands 3-25 years old. It was an indicator of mature forest (Venier and Pearce 2005). In the Clay Belt, it was most frequent in wet stands with a rich nutrient status (Welsh and Lougheed 1996). In the Boreal Forest Region of Ontario, it did not have any strong associations for the variables that Rempel (2007) tested. It tended to be associated with low edge amounts and relatively intact forests of moderate age with more coniferous than deciduous trees.



In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Blue-headed Vireo nests in both mature and old-growth white pine stands. Presence of super-canopy trees was important to it as was presence of large to medium-sized pines (Kirk et al. 2012). Near Gogama, it was characteristic of jack pine stands yet uncommon, rarely straying into adjacent mixed forest. It first began to nest when trees reached approximately 10 m in height, and nested and foraged where canopy closure was greater than 75%. It was most numerous in mature forest and absent in stands younger than 20 years old (James and Peck 1995a). Near Parry Sound, it occurred in low density in a mixed jack pine stand 10 m tall with 50% canopy closure, but was absent in stands with more open canopy (James 1979a). In Algonquin Park, Martin (1960) considered it characteristic of hemlock stands, where it occurred only in mature stands. It was absent in birch-poplar, birch-poplar-fir-spruce, fir-spruce, immature white pine, fir-spruce-hardwood, and hardwood stands. Near Dwight, it occurred predominantly in mixed forests. Often these forests were on slopes with deciduous trees at the top gradually replaced by conifers down gradient. Canopy closure was 90% and trees were always tall and usually old. Forests used for nesting had a moderately dense understorey, often of balsam fir, but it avoided areas with dense or no understorey. It also avoided young forest stands. The 4 main tree species in territories were sugar maple, balsam fir, yellow birch, and hemlock. It appeared to prefer greater tree density than the Yellow-throated Vireo (James 1979b).

In the Carolinian Forest Region, the Blue-headed Vireo has recently begun to nest in the Hamilton area in maturing coniferous plantations (Curry 2006). In southern Ontario, it occurs mostly in large, mature coniferous plantations that have developed an understorey (James in Cadman et al. 1987).

Morton and James (2020) summarized the Canada-wide habitat preferences of the Blue-headed Vireo. It usually occurs where trees are intermediate-aged to mature, where there is more than 75% canopy closure, where there is some (but not dense) understorey of shrubs or saplings, and often near small openings or edges of wetlands and lakes. It is normally associated with coniferous or mixed forests with spruce, fir, hemlock, or pine. Common deciduous associates are poplar, birch, and maple. It is most frequent in landscapes dominated by forests. In boreal Canada, Erskine (1977) considered it characteristic of coniferous forests, particularly spruce stands with deciduous species in the understorey. It is also characteristic of balsam fir stands and frequent in jack pine forests. It may occur in swamps and floodplains dominated by balsam poplar with willows and alders, plus patches of conifers. In Quebec, it was common in 60-year-old second-growth forests dominated by balsam fir, black spruce, white spruce, and white birch. It was significantly more frequent in well-forested landscapes. Remnant patches sufficiently large (5 ha) to support a territory were inadequate in clear-cut-dominated landscapes and were not occupied (Drolet et al. 1999). In Quebec balsam fir–white cedar forests, the Blue-headed Vireo was significantly more abundant in riparian than nonriparian stands; there were no differences in the vegetative structure of the 2 types of stands (LaRue et al. 1995). In Quebec, it appeared to prefer young, mature, and overmature spruce stands with openings. It also nested in mixed and deciduous forests with clearings and underbrush and in coniferous plantations. It was less common in deciduous forests and avoided densely populated areas (Langevin and Lafontaine in Gauthier and Aubry 1996). In British Columbia, it appears to prefer more open forests. Mixed forests on dry rocky sites, pine forests, poplar-pine-spruce stands, and intermediate-aged regenerating forests on dry sites are preferred (Campbell et al. 1997). In the northeastern United States, it may nest in pure deciduous stands of beech, maple, oak, and hickory (Morton and James 2020). Other authors reported it nesting in stands of white pine, aspen, birch–white cedar, hemlock, sugar maple–beech-hemlock with considerable understorey, pine-oak barrens with large patches of pine-dominated savannah, coniferous plantations, natural pine stands, spruce, and spruce-fir stands (Beals 1960; Bent 1950; Bielefeldt and Rosenfield 1994; Capen 1979; Crawford and Titterington 1979; Mossman et al. 1991; Niemi and Pfannmuller 1979; Noon et al. 1979; Temple et al. 1979; Thompson and Capen 1988).

Brooks and Bonter (2010) surveyed the number of Blue-headed Vireo territories in a field, a forest, and a managed Christmas tree plantation where natural succession occurred over 35 years. The number of territories increased significantly in the successional field but did not change in the forest; it was absent in the Christmas tree plantation.

In New Jersey, Benzinger (1994) considered the Blue-headed Vireo an obligate hemlock species, closely associated with the Black-throated Green Warbler. It occupies deciduous forests and coniferous plantations more frequently than the warbler. He considered its habitat associations as approximately 75% hemlock, 20% hardwoods with pine, and 5% coniferous plantation. It occupied a wide range of forest types from spruce-fir to pine, to pure deciduous. It exhibited an aversion for stands with dense undergrowth. In New Hampshire and Maine, it showed a significant affinity for sawtimber-sized trees and hemlock stands (DeGraaf and Chadwick 1987). In Maryland, it was strongly associated with hemlock bottomland forest (Gates and Giffen 1991). In New Jersey and Pennsylvania over a 15-year period, hemlock declined from representing 56% of the total basal area

to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. It was adversely affected by the decline of hemlock and also declined (Toenies et al. 2018).

In Pennsylvania, the Blue-headed Vireo breeds in pure deciduous stands, often with Yellow-throated Vireos. Although the Blue-headed Vireo occurs there mostly in mature stands, it also nests in younger stands with some understorey (James 1979b). Haney (1999) considered it an old-growth associate in Pennsylvania, rather than an obligate. It occurred in 100% of old-growth forests, 48% of forests on the Appalachian Plateau, and 30% of statewide forests.

In New Hampshire subalpine communities, streams were a key component of territories (Sabo 1980). This may have been incidental rather than a habitat requirement. In subalpine areas of New Hampshire, abundance of the Blue-headed Vireo was negatively correlated with the number of deciduous trees 2-10 cm diameter at breast height (DBH) and the total foliage volume of coniferous stems smaller than 2 cm DBH (DeGraaf et al. 1998). From Virginia southward, it uses more deciduous species such as hazel, chokecherry, birch, oak, maple, hickory, and beech. It usually occurs in large forests in a shady humid environment, but often near natural edges or small openings (Morton and James 2020).

Lindell et al. (2007) summarized studies that determined abundance of the Blue-headed Vireo in relation to edge. In 1 study, it showed no response to edge; in another it avoided edge.

Ontario nests were in trees, and all but one in a dead white cedar were in living trees. Coniferous trees (85.5% of nests) were preferred to deciduous trees. Trees selected, in order of preference, were balsam fir, spruce, and hemlock. Nests were suspended from horizontal branches, usually near the tip of the branch but occasionally closer to the trunk. Nest distances from tree trunks ranged from 0.07 to 3 m, mostly 0.3-1.8 m. Two thirds of nests were in small trees and saplings rather than large trees, and they were more frequently near the tops of small trees than in lower branches of bigger trees. Nest heights ranged from 0.9 to 11 m, averaging 2-4.3 m (James 1997a; Morton and James 2020; Peck and James 1987). One nest in Elgin County was 3 m up in a black cherry sapling (Lancaster et al. 2004).

In the northern part of its range, the Blue-headed Vireo typically nests in conifers, particularly spruce, balsam fir, and hemlock, but also in jack pine, sugar maple, yellow birch, and hophornbeam. In New Jersey, half of nests were in young hemlock. In Pennsylvania, all nests were in hemlock or pine. Further south, it may nest in oaks, pines, white cedar, magnolia, pear, apple, gray birch, beech, hickory, and walnut. Nests have been reported 1.2-18.9 m from ground, but most are 2-5 m up. It is not known to reuse nests (Bent 1950; Benzinger 1994; James 1978a; Morton and James 2020).

Males arrive before females and wander as far as 800 m from a central point over several days and as far as 400 m in a day. Unmated males may have territories as large as 50-200 ha. As soon as birds are mated, the territory immediately shrinks to a radius of about 100 m (3 ha), provided that the surrounding habitat is suitable. In New Hampshire, where territories were linear along watercourses, territory size was about 5 ha (James 1978a, 1996a; Sabo 1980). Pairs tend to be well spaced, with little conflict among them. Much apparently suitable habitat is unoccupied. Once nesting is underway, territorial defence is essentially non-existent (James 1996a; Morton and James 2020). Blue-headed and Red-eyed vireo territories frequently overlap and the 2 species have

structurally similar habitats. These species forage and nest at the same heights without conflict, and have been observed foraging together in the same tree. Nesting in conifers by the Blue-headed Vireos may be a mechanism for avoiding competition with the Red-eyed Vireo (Hudman and Chandler 2002; James 1997a, 1999b; Morton and James 2020).

No information is available on natal philopatry. Early returns to territories occupied the previous year suggest some adult site fidelity, but there are no data to confirm this (Morton and James 2020).

Limiting Factors

Eggs may be present in Ontario nests from mid-May until early August, mostly in the first 3 weeks of June (Peck and James 1987). Later egg dates may represent replacement clutches or second broods. In Algonquin Park, nests are under construction from early May to mid-June, eggs are present from late May to early July, nestlings are present from early June to mid-August, and dependent fledglings are present from mid-June to mid-September (Tozer 2012).

Pairing occurs almost immediately after the females arrive. The first nest takes 8 days to complete. Nests for replacement clutches may be built in 4-5 days or may take as long as the first nest to build. The first egg is laid the day after the nest is complete, and one is laid a day. Continuous incubation starts when the clutch is complete. The incubation period is typically 13 or 14 days, but may be 15 days in cold weather. Young fledge when they are 12 or 13 days old, but can fly only weakly (James 1978a, 1996a, 1996b, 1997a, 1997b, 1999c; Morton and James 2020; Peck and James 1987).

One brood is typically raised in Ontario; a second brood is rarely raised. In Pennsylvania, second broods occurred in 2 or 3 pairs of 37; double broods are probably common in the southern Appalachians. Renesting is typical if the first clutch or brood is lost. A new nest is built for replacement clutches, often within 100 m of the first but rarely as far away as 400 m. Clutches of 3-5 eggs have been reported in Ontario, with most containing 4 eggs. This is typical throughout the Blue-headed Vireo's range, with 5-egg clutches rare (Bent 1950; James 1997b, 1999b; Morton and James 2020; Peck and James 1987, 1997).

The age at first breeding is unknown, but the Blue-headed Vireo is probably capable of breeding at age 1 year. It is likely that breeding occurs every year provided that birds are successful in attracting a mate. The nesting system is monogamous (James 1996a; Morton and James 2020) and there are no records of extra-pair copulations or young (Morton and James 2020).

The Blue-headed Vireo searches slowly on inner branches, foliage, and tree trunks for prey. In New Hampshire, it captured 55.2% of prey on bark and 38.2% on leaves. In Ontario, 68% of foraging was in the interior of a tree and 32% at the periphery. In Pennsylvania, 81% of foraging was in the interior of trees compared with 43% in New Hampshire. In Saskatchewan, it foraged in conifers significantly more on the inner and middle portions of branches and less near the tops of trees than lower areas. Trees selected for foraging were significantly shorter than random and shorter than those selected by Yellow-throated Vireos. There was no difference in foraging heights of the sexes. Mean foraging height in Ontario was 7.7 m at 55.7% of tree height; mean foraging height in Pennsylvania was 56.1% of tree height. In Saskatchewan, mean foraging height was 6.1 m in coniferous trees and 6.3 m in deciduous trees. It seldom forages near treetops or the ground. It

forages on any tree species within the territory, often in proportion to availability. But in Saskatchewan, it foraged more in balsam fir than expected and less than expected in trembling aspen. It used deciduous trees more than their availability in mixed forests in Ontario, exhibited high use of conifers in New Hampshire, and fed preferentially on yellow birch probably because insect densities were highest on this species. It takes 55-60% of prey from branches and most of the rest from leaves. It uses live branches for foraging 50-80% of the time. Usually 45-65% of food is captured by short sallies. Average sally distances were 0.8 m in Maine, 0.6-1.2 m in New Hampshire, and 1.5 m in Virginia. The proportion of food taken by sallying varies depending upon types of insects available. In Maine 95% of food items were captured by sallying but only 15% were captured by this method in New Hampshire. It captures most other prey at a perch, but about 5% may be taken by flycatching. Apparent flycatching is used near the nest to deceive potential predators. When nestlings are present, adults often appear to flycatch immediately before attending the nest, but prey is taken only a small proportion of the time (Cumming 2004; James 1979b, 1979c; Morton and James 2020; Robinson and Holmes 1982; Sabo 1980).

The young are initially fed mostly soft-bodied green caterpillars. Larger food is brought once they are older, including large dragonflies. Occasionally, adults regurgitate food to older nestlings. An analysis of more than 300 stomachs determined that adults ate in excess of 95% animal matter, almost all insects. In spring, the Blue-headed Vireo may feed heavily on tent caterpillars. Lepidopterans dominated the diet and they were mostly caterpillars; they comprised more than 30% of the diet annually and 40% certain months. The diet also consisted of about 20% bugs (predominately stink bugs), 13.5% beetles (weevils, and lady, metallic wood-boring, and click beetles), 6.9% hymenopterans (sawflies and ants), and 4.3% flies and miscellaneous insects (stoneflies, dragonflies, grasshoppers, crickets, and locusts). Miscellaneous invertebrates eaten include spiders and snails. The vegetable matter it consumes is mostly fleshy fruits such as wild grape, dogwood, viburnums, greenbrier, sumac, and elderberry (Bent 1950; Chapin 1925; James 1999c; Morton and James 2020; Remsen et al. 1998; Robinson and Holmes 1982). In New Hampshire and Maine, the Blue-headed Vireo ate few spruce budworms when they occurred at low density, but increased consumption exponentially as budworm numbers increased. The abundance of vireos and budworms was not correlated (Crawford and Jennings 1989). Venier et al. (2009) noted that the response of the Blue-headed Vireo to spruce budworms was inconsistent, with some studies reporting that it increased with increasing budworm populations but no response was observed in other studies. In their study area near Manitouwadge, the number of territories in mature black spruce–balsam fir–aspen stands increased significantly from 3.7 to 7.75 when budworms became numerous. Response was limited in young and intermediate-aged stands. In New Brunswick, it exhibited no response to spruce budworm populations (Morris et al. 1958). Over 2 years in Maine, spruce budworm larvae and pupae constituted 34% of the invertebrates consumed in both years (Mitchell 1952).

In the north, the Blue-headed Vireo is infrequently parasitized by cowbirds because it nests in extensively forested areas. It usually accepts cowbird eggs, rarely abandoning the nest or burying the parasitic egg in the nest lining. Eggs removed by cowbirds are not replaced. In Ontario, 4 of 50 nests (8%) were parasitized. In the northern United States and eastern Canada, 13.5% of nests were

parasitized. Parasitism rates in other areas include 21.2% and 46.5% of nests in 2 Virginia areas and 42.1% of nests in the southern United States. Parasitism greatly reduces nest success. In eastern Canada and northern United States, a mean of 2.9 young fledged in unparasitized nests; 0 fledged in parasitized nests (James 1997b; Morton and James 2020; Peck and James 1997).

The distribution of the Blue-headed Vireo in southern Ontario is limited by forest clearing and fragmentation. It was probably more widespread prior to settlement. It is now starting to reoccupy areas that were reforested, notably in the St. Williams forest in Norfolk County and the Oak Ridges Moraine. Local declines may result from forest clearing or death of trees due to acidification. It tolerates light timber harvesting, although pairing rates may decline. Heavy forest thinning promotes dense growth of understorey, making habitat unsuitable. In southern Ontario and further south, its distribution is patchy due to the distribution of suitable habitat. In New Jersey, where it is a hemlock obligate, increasing fragmentation of hemlock growth makes it more difficult for dispersing birds to locate suitable habitat, leading to reduced site occupancy and possibly local extinctions (Benzinger 1994; Morton and James 2020).

Forestry practices have varying effects depending on the harvest prescription used. Tozer et al. (2010) studied the effects of group-selection harvesting of timber in Algonquin Park. Typical group-selection consisted of cutting about 5% of the stand; intensive group-selection affected 20% of the stand area. Neither treatment had any effect on the abundance of the Blue-headed Vireo. Vanderwel et al. (2009) examined the effects of partial tree harvesting in the Boreal Forest Region of Ontario. It decreased when 30 or 50% of tree cover was removed, but was relatively unaffected when 70% of trees were cut. In Ontario in the Canadian Shield, there was no difference in its abundance in early successional stands after clear-cutting or fire. It was significantly less abundant in mid-successional clear-cuts than in similarly aged stands after fire. There was no difference in its abundance in early successional and mature stands but it was significantly more abundant in mid-successional than mature stands (Zimmerling et al. 2017). In Nova Scotia hardwood forests, the Blue-headed Vireo was common, but it was absent in clear-cuts and thinned plots and much less common in strip-cut plots (Freedman et al. 1981). Also in Nova Scotia, it was absent or present only in trace numbers in hardwood forests younger than 40 years (Morgan and Freedman 1986). In Vermont, territories encompassed both uncut and clear-cut hardwood forest (Lent and Capen 1995). In Virginia, the ability of males to find a mate after group-selection harvest was less than 50% over 2 years compared with more than 80% in unharvested forest over 3 years (Morton and James 2020). In New York, Keller et al. (2003) recorded bird species usage of clear-cuts for several years after harvest. The Blue-headed Vireo was in a guild with 3 warbler species and all 4 species were associated predominantly with hemlock. This tree did not become prominent in the canopy and subcanopy until 55-75 years after cutting. This guild was absent in stands younger than 55 years but ranked third in abundance from 75 years postharvest onward.

In Minnesota, blowdown of spruce-fir forest resulted in an 80% decline in canopy cover and a 100% increase in shrubs. The Blue-headed Vireo nested in the blowdown area but was absent from the control plots (Burris and Haney 2005).

Rose and Simons (2016) studied the effects of fire in North Carolina pine-oak forests. The Blue-headed Vireo generally responded negatively to fires, but did occur more frequently after low-severity burns.

The Blue-headed Vireo is very sensitive to human disturbance during pairing and early nest building. If disturbed, the female readily abandons the nest and occasionally her mate. Once eggs are laid and during incubation, it is very tolerant of human intrusion, and may allow humans to touch it on the nest. If nestlings are removed from the nest for banding in the presence of the female, she will abandon the nest; the young then die of exposure. Once the female ceases brooding nestlings, it becomes sensitive to disturbance again. It is sensitive only to humans that pay attention to the nest and may nest in busy locations such as campgrounds if the nest is not disturbed (Bent 1950; James 1996b, 1999b; Morton and James 2020).

In Alberta, Bayne et al. (2016) studied the effects of forest fragmentation by energy-sector facilities on the Blue-headed Vireo. There were no significant differences in its abundance at seismic lines and pipelines than in forest interior adjacent to these features. It was significant less abundant at well pads than in adjacent forest interior. Farwell et al. (2019) detected no significant responses to well pads, access roads, and pipelines in extensive forest in West Virginia.

Price (2004) concluded that the breeding range of the Blue-headed Vireo might exclude southern Ontario if the average summer temperature increased by 2°C. In Quebec and Labrador, its abundance was associated with increasing numbers of growing-degree days, or areas experiencing the warmest summer weather (DesGranges and LeBlanc 2012). This suggests that climate warming may be beneficial to this species where it is near the northern extent of its range. In North Carolina, its abundance was negatively correlated with temperature, suggesting that climate change could be detrimental to it in this area (Lumpkin and Pearson 2013).

Status

McIlwraith (1894) had no breeding records for the Blue-headed Vireo, but it probably bred through much of southern Ontario prior to European settlement. Most of his records were from southern Ontario, and it undoubtedly nested in the Canadian Shield at that time. Baillie and Harrington (1937) considered it an uncommon breeder in central Ontario from Muskoka District and Algonquin Park north to the intercontinental railway. Their only definite breeding records were from Thunder Bay, Chapleau, and Algonquin Park. They noted 1 summer record from Fisher Glen in Norfolk County, where it still breeds. In 1991, it was confirmed breeding in Elgin County for the first time, the most southwesterly breeding record (Lancaster et al. 2004). During the first atlas, James (in Cadman et al. 1987) concluded that habitat was suitable in the Shield from central Georgian Bay and Ottawa northward. He considered it common in the Shield, becoming scarce or absent in the northern portion of the Hudson Bay Lowland where trees are scattered, with isolated birds occurring in the agricultural south.

The second atlas indicated that the probability of observation of the Blue-headed Vireo increased significantly since the first atlas. Increases occurred province-wide and in all regions, and all increases were significant except in the Carolinian Forest Region where it remained rare. The greatest increase, almost 300%, occurred in the Great Lakes–St. Lawrence Forest Region south of the

Canadian Shield. Increases may be related to maturation of coniferous plantations. It was most abundant in the Shield, with lower densities in the Clay Belt, the Hudson Bay Lowland, and south of the Shield (James in Cadman et al. 2007).

Long-term (1970-2021) population trends determined by the Breeding Bird Survey indicate annual increases of 3.04% in Canada and 2.71% in Ontario. The short-term (2011-21) trends were annual increases of 17% in Canada and 1.98% in Ontario. Results were of medium reliability, except for the short-term Ontario results, which were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young are fully dependent on the adults for the first week after fledging then the adults split up, each taking half the young. Fledglings are partially dependent for 2-4 weeks, and usually remain with the adults within 1 km of the nest until autumn migration (Morton and James 2020).

During the postfledging period in Pennsylvania, Stoleson (2013) netted 18 adults and 8 fledglings in clear-cuts compared with 4 adults and 0 fledgling in forest habitat.

MIGRATION

The Blue-headed Vireo is probably a nocturnal migrant. It travels singly or in mixed flocks of warblers and kinglets, but not in flocks of its own species (James 1999c; Morton and James 2020).

Adult males arrive in spring a few days before females. The Blue-headed Vireo typically arrives in mid-April with large numbers present by early May; some arrive in late March. Despite its early arrival, some males do not find mates until early June. Some birds remain on or near the territory until the first week of September, others are moving south at that time, and most have moved south by mid-September (James 1991, 1996a, 1999c; Morton and James 2020).

During migration, the Blue-headed Vireo may occur in any type of wooded area, from shrubs to treetops. Deciduous, mixed, coniferous, open to dense, and dry to moist woodlands are used. It seldom occurs away from wooded areas, but it rarely uses well-treed urban areas and rural lots (Morton and James 2020).

During autumn migration in Pennsylvania, the Blue-headed Vireo was most abundant at forest edges including hydro rights-of-way, open-canopy forest roads, and edges of forest cuts. It was second in abundance in forest interior, suburban forest, and areas of shrubs and saplings. There were no statistical differences in usage of the top 4 habitats. Other habitats used to a lesser extent were pole-stage forest and forest-agriculture edges. Structurally heterogeneous habitats were used most (Rodewald and Brittingham 2002). Suomala et al. (2010) examined abundance of the Blue-headed Vireo on 2 islands in the Gulf of Maine during migration. During spring migration, it was most abundant on the island dominated by trees. It was more abundant on the shrub-dominated island in autumn. In Pennsylvania, it was significantly more abundant in forest than shrub habitats during spring migration (Smith and Hatch 2008). In Ohio, it occurred significantly more in mature upland forest than mature riparian forest during spring migration (Rodewald and Matthews 2005).

The Blue-headed Vireo is occasionally killed at tall structures during migration, but in low numbers. It represented less than 0.01% of the total kill at lighted office towers in Toronto, and 19 were killed at the Lennox chimneys near Kingston. It is one of the species least vulnerable to striking

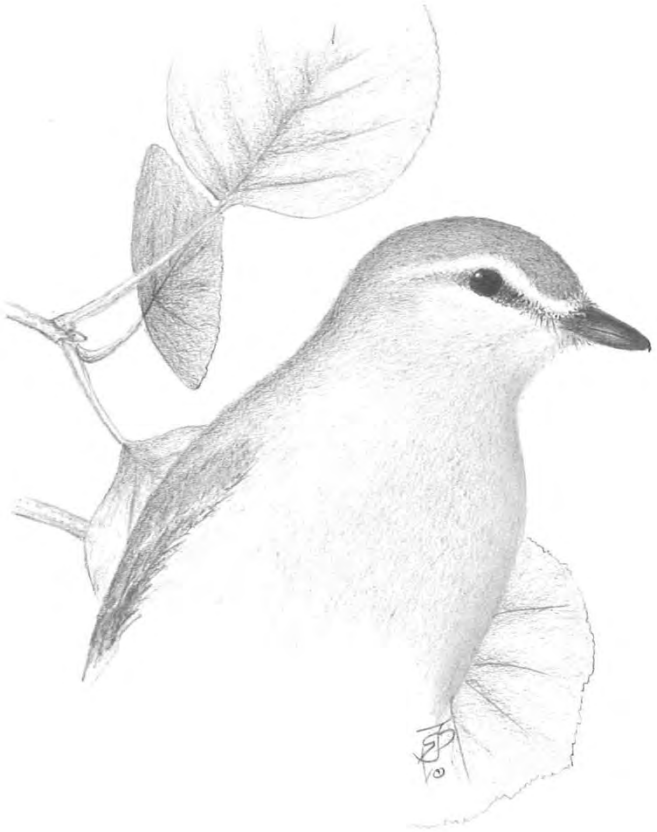
high-rise buildings in Toronto (Colling et al. 2022; Morton and James 2020; Remsen et al. 1996; Weir 2008).

In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season during 1888-1939 and 1967-2012. There was limited climate change during the first period but significant warming during the second period. The Blue-headed Vireo arrived significantly earlier in the second period but there were no differences between periods for autumn departure dates and length of the breeding season.

The Blue-headed Vireo is uncommon during migration (James 1991). Migration data at Long Point Bird Observatory showed a nonsignificant 1.0% annual increase 1979-88 (Hussell et al. 1992).

Philadelphia Vireo

Vireo philadelphicus

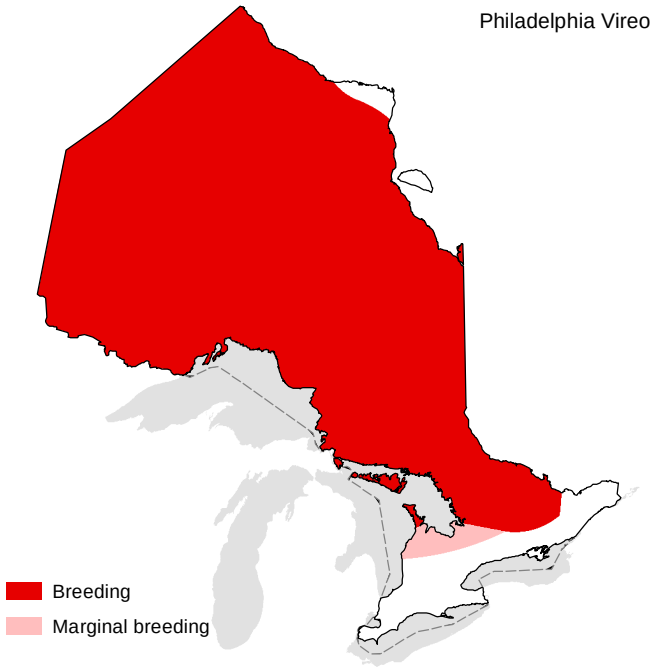


BREEDING SEASON

Habitat Requirements

In Ontario, the Philadelphia Vireo nests primarily in deciduous forests dominated by poplars and sometimes birch, less frequently in mixed woods of poplar and spruce, and occasionally in alder thickets that often contain dogwoods and willows. Forested areas where breeding occurred often had an understorey of alder. Breeding was confirmed in 1 southern deciduous forest dominated by maple (Peck and James 1987).

In the Englehart area, the Philadelphia Vireo was restricted to alder thickets and aspen or yellow birch groves, usually with an understory of these same species or alder (Barlow and Power 1970; Barlow and Rice 1977). In northern Ontario, Schueler et al. (1974) found it primarily in tall stands of balsam poplar. On the northeast shore of Lake Superior, it preferred moist alder patches to drier poplar and birch woods (Baillie and Hope 1943). In the Clay Belt, Smith (1957) considered it a species of wet alder patches. In this region, it was associated with rich, wet stands (Welsh and Lougheed



1996). Near Gogama, it was common only in deciduous portions of older mixed forests where trees were taller than 10 m. It showed a strong preference for trembling aspen; rarely, white birch constituted a third of the trees in a territory (James and Peck 1995a). Near Hearst, it occurred in 9- and 24-year-old clear-cuts in upland mixed forests. It was not observed in lowland coniferous forests that were intact or clear-cut, in upland uncut forests, or upland clear-cuts 3-6 and 11-19 years old (Welsh and Fillman 1980).

Throughout its range, the Philadelphia Vireo inhabits early to mid-successional forests and forest edges, aspen parklands, and shrub thickets, with preference for aspen, birch, alder, and ash. It also nests in mixed woods and older forests as long as the favoured tree species are present. Second growth of aspens and birches on burned and logged areas, young cherry coppices, and willow and alder thickets along streams are good habitat. It may inhabit dense patches of mountain maple. It usually avoids residences but 1 Quebec nest was in a rural yard at the edge of 5-7 km^2 of open forest of red oak and white birch. In Quebec, it was uncommon in landscapes dominated by extensive black spruce forest. It was documented only in recent clear-cuts where shrubs and saplings were less than 2 m tall. In the Boreal Forest Region of Canada, it was absent in black spruce and species-poor jack pine stands, and was associated with mesic mixed and deciduous stands with moderate nutrient richness. It occurred in 50% of aspen stands 0-9 years old, 33% of 15-20-year-old aspen stands, 67% of 40-year-old stands, and 3.3% of 80-year-old stands. It was associated with openings or young stands, and occupied shrubs in open areas as well as tall, deciduous shrubs under a dense poplar canopy. Typical British Columbia habitat consists of dense, tall, rapidly growing young stands of trembling aspen or balsam poplar with 80% canopy closure and an understorey of highbush cranberry, alder, and willow. Riparian forest is important breeding habitat. In Quebec, it is typical of second-growth forests of trembling aspen saplings and shrubs. Sugar maple stands and agricultural areas in the St. Lawrence River plain are less suitable habitat. In New Hampshire, it inhabited late-successional hardwoods dominated by sugar maple–beech, and yellow birch with occasional ash. It preferred areas where there were several openings in the canopy created by fallen trees and where white ash and yellow birch were abundant. As this forest community matured, the Philadelphia Vireo disappeared (Back 1979; Bent 1950; Brewster 1903; Campbell et al. 1997; Erskine 1977; Faanes and Andrew 1983; Hobson and Bayne 2000; Imbeau et al. 1999; Kirk et al. 1996; Lewis 1921; Moskoff and Robinson 2020; Robinson 1981; Robinson and Holmes 1984; Villard in Gauthier and Aubry 1996).

Moskoff and Robinson (2020) thought that the Philadelphia Vireo may require large forest tracts to avoid high rates of nest predation and parasitism. In Saskatchewan, it was randomly distributed within a fragmented landscape and its abundance was unaffected by forest fragment size or amount of forest cover within a radius of 5 km. It was more common than expected in fragmented landscapes (Hobson and Bayne 2000).

Most Ontario nests (77.8%) were in trees, but some were in shrubs. Poplar species were favoured nest sites, supporting 70% of nests, followed by alder (24%), birch (2.7%), and maple (2.7%). Most nests were suspended from horizontal forks of lateral branches from very near the trunk to 1.5 m from it. Two nests were at the periphery of very large aspen trees. Nests were 1.8-21 m from the ground, mostly 3-15 m up (Peck and James 1987).

Few nests have been reported outside Ontario, and most were similar in placement. Nests in trees are almost always very near the top. Nests are frequently near water. The Philadelphia Vireo apparently does not use materials from old nests and old nests are not reused (Bent 1950; Brewster 1903; Campbell et al. 1997; Levin 1921; Moskoff and Robinson 2020).

Territorial defence begins as soon as birds arrive on the breeding grounds. Peaks in territoriality occur when territories are being established and during the nestling stage when there is competition for food resources. Territories are usually exclusive, but may overlap considerably when food is abundant. Territory size varies considerably among study areas and years due to breeding density and habitat quality. Near North Bay and Englehart, 54 territories averaged 0.3 ha; territories as large as 0.8 ha have been reported in Ontario. New Hampshire territories were 0.5-4 ha (Barlow and Rice 1977; Moskoff and Robinson 2020; Rice 1978a, 1978b).

The Philadelphia Vireo has a complicated relationship with the Red-eyed Vireo. The 2 species' songs are very similar. It appears as though the Philadelphia Vireo can discriminate between them but the Red-eyed Vireo cannot. Near Englehart, there were no significant differences between the species in their habitat preferences or foraging behaviours or heights. Their territories appeared to be mutually exclusive, with Philadelphia Vireos involved in as many territorial disputes with Red-eyed as Philadelphia vireos. In other areas, including Gogama, territories may overlap. Where overlap occurs, the Philadelphia Vireo nests and forages above the Red-eyed Vireo, so that the species are separated vertically. During the late nestling period, vertical separation disappears as adult Philadelphia Vireos expand their foraging range to include the shrub and sapling layers. Fledglings spend their first 2-5 days out of the nest among shrubs. During these periods, aggression between the 2 species may be intense and physical. The Red-eyed Vireo is usually dominant at this time (Barlow and Power 1970; James and Peck 1986; Moskoff and Robinson 2020; Rice 1978b, 1978c; Robinson 1981).

No information is available on natal philopatry. Adult site fidelity occurs, but its extent is unknown. Some adults reoccupy the same territories in consecutive years. Near Englehart, no areas were consistently occupied over a 3-year study (Moskoff and Robinson 2020; Rice 1978c).

Limiting Factors

Eggs have been found in Ontario nests from mid-May to mid-July, with most present in the first half of June (Peck and James 1987). In Algonquin Park, nest construction occurs in mid-May, eggs are present from mid-June to early July, nestlings are present from late June to mid-July, and dependent fledglings have been seen from late July to mid-August (Tozer 2012).

The female selects the nest site and builds the nest in about 6 days. Eggs are laid at the rate of one a day and incubation starts with laying of the first egg. The incubation period of 1 Ontario clutch was 11-13 days; incubation periods of 11-14 days have been reported. Hatching is asynchronous, with as long as 2 days between hatching of the first and last eggs. Nestlings fledge in approximately 14 days (Barlow and Rice 1977; Bent 1950; Lewis 1921; Moskoff and Robinson 2020).

A single brood is raised annually. Moskoff and Robinson (2020) suggested that second broods might occur during major caterpillar outbreaks, but this has not been confirmed. Renesting occurs if a clutch is lost or abandoned. Clutches of 3 and 4 eggs have been found in Ontario, with 70% containing 4 eggs. Normally 3 or 4 eggs are laid and most clutches contain 4 eggs; 5-egg clutches are rare (Bent 1950; Campbell et al. 1997; Moskoff and Robinson 2020).

The mating system is seasonally monogamous. At least 1 pair remained together for 2 breeding seasons. There is no information available on age at first breeding, but breeding probably occurs in the first year (Moskoff and Robinson 2020).

The Philadelphia Vireo usually forages on deciduous leaves high in the canopy, more often at the periphery of a tree than near its centre. In Ontario, it captured most food on foliage while perched; in New Hampshire, it obtained most food by sally-gleaning. In the Clay Belt of Ontario, all foraging occurred in deciduous species, and 83% of foraging occurred in foliage. Foraging techniques included 68.6% aerial attacks, 8.5% hanging, and 19.0% hovering. The mean foraging height was 13.7 m. In New Hampshire, 83.2% of attacks were on leaves and 10.5% on bark; most food was taken from the lower surface of leaves by hovering. It attacked prey in beech and yellow birch in proportion to caterpillar abundance and more in sugar maple than expected. Within the canopy, it attacked prey almost 3 times more often in ash and yellow birch than in beech. In the subcanopy layer, its attack rate was higher in sugar maple and yellow birch than beech. In Ontario, there were no significant differences in foraging heights or techniques between Red-eyed and Philadelphia vireos, other than for rarely used techniques. This was in an area where the 2 species had mutually exclusive territories. Male Philadelphia Vireos tended to forage higher than females, but not significantly. In New Hampshire, these differences were significant with males foraging at a mean height of 14.6 m compared with 13.5 m for females. There were no significant differences in the foraging techniques of the sexes, but males foraged more in sugar maple and less in white ash than females. In a New Hampshire study area, where territories of the 2 species overlapped, there were differences in foraging habits. The Philadelphia Vireo foraged preferentially on yellow birch and white ash in the canopy; the Red-eyed Vireo foraged in all tree species. In the subcanopy-sapling

layer, the Philadelphia Vireo foraged significantly less in beech and there was no difference in the sapling-shrub layer. Mean foraging height for the Philadelphia Vireo during territory establishment was 18.9 m (12.6 m for Red-eyed Vireo), 21.9 m during incubation and early nesting (13.4 m for Red-eyed Vireo), 11.2 m in the late nestling and early fledging stages (10.5 m for Red-eyed Vireo), and 18.7 m during late fledging (10.3 m for Red-eyed Vireo). The New Hampshire study area was not typical breeding habitat (Holmes 1986; Holmes and Schutz 1988; Moskoff and Robinson 2020; Rice 1978c; Robinson 1981; Robinson and Holmes 1982, 1984).

The young are fed mostly hairless caterpillars but also a variety of flying insects, including mayflies; small snails are rarely fed to young. One study examined 75 stomachs of adults that contained 92.5% animal material and 7.2% plant material. Insects comprised 88.4% of the diet and spiders constituted the remainder of the animal food. Lepidopterans were most important in the diet, forming 26.3% of the overall diet (24.1% caterpillars). More were eaten as the breeding season progressed to a high of 45.5% in September. Beetles were important in the diet at 24.8%, mostly leaf and lady beetles, but also scarab beetles and weevils, with small numbers of click, long-horned, and metallic wood-boring beetles. Fourteen percent of the diet consisted of wasps, bees, and other hymenopterans (ichneumonid and chalcid wasps, ants, and sawflies). Flies totalled 11.8% of the diet, mostly midges; 10.5% were bugs, especially stink bugs; and 1.1% were miscellaneous insects. Another study found that the diet consisted of 54.2% lepidopterans (50% larvae), 20.8% bugs, 4.2% hymenopterans, 8.3% beetles, 4.1% flies, 4.1% spiders, and 4.1% miscellaneous. The Philadelphia Vireo consumes fruit late in the breeding season and early autumn, including rough-leaved dogwood berries, rose hips, grapes, spicebush berries, and Virginia creeper berries (Barlow and Rice 1977; Chapin 1925; Graber et al. 1985; Lewis 1921; Moskoff and Robinson 2020; Remsen et al. 1998). Near Manitouwadge, it tended to increase with increasing populations of spruce budworms, but not significantly (Venier et al. 2009).

Cowbird parasitism has been documented in Ontario, but apparently not elsewhere. A male vireo was observed feeding an almost fully-grown cowbird fledgling in Sudbury District. Two of 14 Ontario nests (14.3%) were parasitized (Baillie and Hope 1947; Moskoff and Robinson 2020; Peck and James 1997).

The Philadelphia Vireo prefers poplar stands, so clear-cutting, logging, and fire may all be beneficial. The current practice of planting clear-cuts with conifer seedlings may be detrimental. Forest maturation may make habitat unsuitable (Holmes and Sherry 2001; James in Cadman et al. 2007; Moskoff and Robinson 2020; Villard in Gauthier and Aubry 1996). In the Canadian Shield of Ontario, it was significantly less abundant in early successional clear-cuts than in early successional burns, but there was no difference in its abundance in mid-successional clear-cuts and burns. There was no difference in its abundance in early successional and mature stands, but it was significantly more abundant in mid-successional than mature stands (Zimmerling et al. 2017).

In Alberta, the Philadelphia Vireo was significantly more abundant at pipelines than in adjacent forest interior. There was no difference in its abundance at seismic lines and well pads than in forest interior adjacent to these features (Bayne et al. 2016).

Price (2004) concluded that the Philadelphia Vireo could disappear as a breeding species from southern Ontario if the average summer temperature increased by 2°C. In Quebec, DesGranges and Morneau (2010) concluded that it was very sensitive to climate change.

Status

The status of the Philadelphia Vireo is somewhat difficult to determine due to the similarity of its song to the Red-eyed Vireo and its habit of remaining high in the canopy. The first Ontario record was a bird taken in May 1884 in Hamilton (McIlwraith 1894). Baillie and Harrington (1937) concluded that it was a more or less common breeder from northern Lennox and Addington County north to Moose Factory and west to Lac Seul. Schueler et al. (1974) considered it fairly common at Attawapiskat. Near Pickle Lake, it was uncommon, but more numerous than the Red-eyed Vireo (James 1980). It is a rare breeder in the Kingston area in the Canadian Shield (Weir 2008). James (in Cadman et al. 1987) stated that it was widespread and common in northern Ontario, reaching its greatest abundance in the Boreal Forest Region. At Moosonee, it outnumbers the Red-eyed Vireo 2:1. James (1991) considered it an uncommon to common breeder across the north to Big Trout Lake and Attawapiskat, and possibly Fort Severn, and occasional and rare in the south as far south as the Bruce Peninsula and central Peterborough and northern Leeds counties.

The second atlas indicated that the Philadelphia Vireo had extended its range both northward and southward since the first atlas. It was found in several 100-km blocks north of where it was detected during the first atlas. In the south, it occurred in many more squares in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, and also south of the Shield and notably on Manitoulin Island. The reasons for its northward range extension are uncertain but may be due in part to better coverage. Expansion southward may be due to increasing amounts of poplar on abandoned farmland. As these stands evolve to tolerant hardwoods, the Philadelphia Vireo may retract its range in the south. It was most abundant in the Boreal Forest Region in a broad band between latitudes 49°N and 53°N, from south of James Bay to the angle of the western border with Manitoba (James in Cadman et al. 2007).

Long-term (1970-2021) population trends determined by the Breeding Bird Survey indicated annual increases of 1.9% in Canada and 2.5% in Ontario. Short-term (2011-21) trends included an annual increase of 4.13% in Canada and an annual decrease of 0.255% in Ontario. Results were of medium reliability for the long-term trends and of low reliability for the short-term trends (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings remain with the parents for about 10 days after leaving the nest, with the brood split between the parents (Moskoff and Robinson 2020).

Major and Desrochers (2012) captured Philadelphia Vireos in clear-cuts in Quebec during the postfledging period. There was no difference in usage between control plots and those in which the fruit had been removed.

MIGRATION

The Philadelphia Vireo migrates nocturnally singly or in small groups of 3-5 and frequently joins mixed-species flocks. The average stopover period for autumn migrants in Maine was 3.4 days

(range 1-8 days). Birds gained significant weight during this period indicating that stopover areas are important in providing resources for migration (Bent 1950; Moskoff and Robinson 2020).

Both sexes arrive on the breeding grounds together and all usually arrive within a short period. The Philadelphia Vireo typically arrives in the province in mid-May, but has been seen in late April. In Muskoka and Parry Sound districts, it starts moving southward in late July. Autumn migrants are evident in Algonquin Park from mid-August until mid-September. Most leave the province by late September with stragglers remaining until early November (James 1991; Mills 1981; Tozer 2012).

During migration, the Philadelphia Vireo appears to prefer deciduous second growth, thickets, forest edges, and particularly shrubs along streams or marshes. It shows a strong preference for willow thickets during migration. In Illinois, it was 10 times more abundant in mid-successional forests and thickets than old fields or mature forests. During autumn migration in Pennsylvania, it occurred in all habitats studied (forest interior, forest edge, forest-agricultural edge, suburban forest, pole-stage forest, shrub-sapling forest), but numbers observed were insufficient to determine preferences. In urban areas of Ohio, there was no significant difference in its abundance during spring migration in mature riparian forests and mature upland forests. In British Columbia, it prefers woodlands and thickets during migration and is seldom seen in suburban or rural habitats (Bent 1950; Campbell et al. 1997; Graber et al. 1985; Moskoff and Robinson 2020; Rodewald and Matthews 2005; Rodewald and Brittingham 2002).

The Philadelphia Vireo is occasionally killed at television towers and other tall structures during migration. From 1972 to 1982, 189 were killed at the Lennox chimneys near Kingston (Graber et al. 1985; Moskoff and Robinson 2020; Weir 2008).

The Philadelphia Vireo is uncommon in Ontario during migration (James 1991).

Eastern Warbling-Vireo

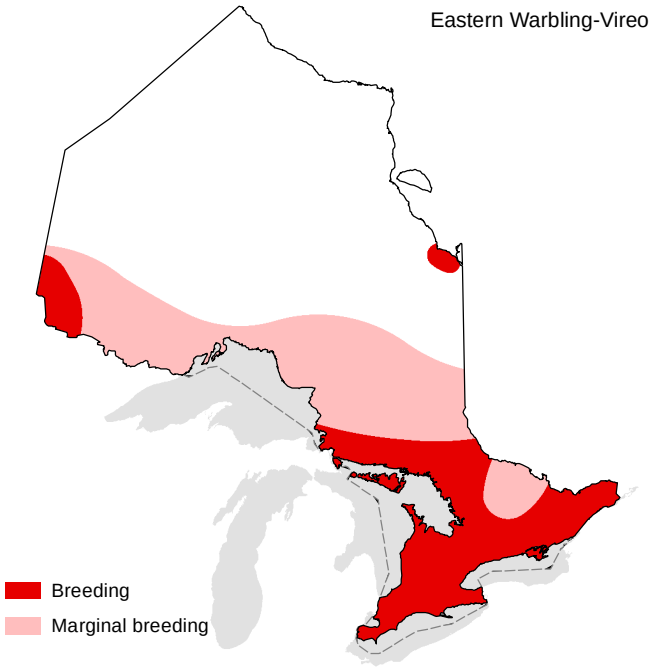
Vireo gilvus

BREEDING SEASON

Habitat Requirements

In 2025, the Warbling Vireo was split into 2 species, the Eastern Warbling-Vireo and Western Warbling-Vireo. The Eastern Warbling-Vireo nests from central Alberta eastward and the Western Warbling-Vireo nests further west. The 2 new species were identified due to differences in genetics, morphology, song, moult and migration, and response to brood parasitism (Chesser et al. 2025b). Because there are no known differences in the habitat preferences of the 2 species, relevant information on the western species is also included in the species account.

The Eastern Warbling-Vireo nests mostly in deciduous and mixed woodlands in Ontario (64% of nests), usually at edges or openings (65.5% of woodland nests). Other nesting habitat includes urban parks and gardens (19.8%), in agricultural habitat and fencerows (15.1%), and an aspen clump in a pine plantation (1.2%). Most nests were in edge habitats such as roadsides, pond and river



shorelines, swamp and marsh openings, beaver ponds, and cottage clearings (Peck and James 1987). McIlwraith (1894) stated that it preferred isolated ornamental trees in parks and gardens and shade trees in cities. In the Kingston area, it is present wherever there are mature deciduous trees, including those along city streets and highways, and in parks (Weir 2008). More detailed studies were completed by James (1976, 1979a). In the south, it nested in open habitat such as parkland with isolated trees, small groves, and forest edges. It selected habitat based on its structure rather than tree species composition. Habitat selected by Eastern Warbling-Vireos was more open than that of Yellow-throated Vireos, although not significantly, and significantly more open than Red-eyed Vireo habitat. In Parry Sound District, the Eastern Warbling-Vireo was absent in pure jack pine stands, but present in an immature open (less than 25% canopy closure) jack pine stand mixed with trembling aspen, white birch, white pine, and silver maple. In southern Ontario, it frequently occurs in small riparian stands dominated by poplars or willow trees (personal observation).

Throughout its range, the warbling-vireo inhabits a variety of deciduous and mixed forest types, with a strong penchant for riparian areas. During the breeding season in British Columbia, 70% of observations were in riparian habitats compared with 60% during spring migration and almost 90% during autumn migration. It exhibits a strong preference for mature deciduous woodlands, especially along streams, ponds, marshes, and lakes, but occasionally inhabits upland areas away from water. Nesting also occurs in young deciduous stands regenerating after clear-cuts or fires, in treed suburban areas, urban parks, orchards, and farm fencerows. It is strongly associated with poplar throughout its range but silver maple stands are important in Illinois. It keys in on overall habitat structure, selecting large, deciduous trees with a semi-open canopy (usually less than 75% canopy closure), and appears fairly indifferent to understorey density. It is most common in edges and small, disjunct patches, and is not area sensitive. In Washington, it was more abundant along large streams than small ones, possibly due to a more contiguous band of deciduous trees. In Colorado montane areas, it was associated with aspen stands and avoided riparian willow stands. In British Columbia, all nests in 1 study area were within 15 m of forest edge, and all but 4 were within 5 m of edge. When it nests in coniferous stands or plantations, it selects patches with more deciduous vegetation for nesting than is generally available. It avoids extensively forested areas. Historically, it was probably restricted to riparian areas and recent burns. It occurs in almost all age classes of deciduous stands, but reaches highest densities in mature and old-growth stands; mature poplar and aspen stands may be as young as 50 years. In Michigan, it nested in fringes of trees along

low, wet areas and preferred scattered poplars, ash, elm, and silver maple. Overall, it is associated with early successional, open or scattered forest, typically adjacent to water. In addition to poplar, aspen, and cottonwood stands, it breeds in ash-basswood, birches, sugar maple, silver maple, Manitoba maple, green ash, and willow. It is the most abundant species in most western aspen forests. In California, it nests regularly in coniferous forests and is most abundant and productive at mid-elevation areas where cowbird parasitism is absent or rare (Bent 1950; Campbell et al. 1997; Easton and Martin 2002; Erskine 1977; Faanes and Andrew 1983; Flack 1976; Gardali and Ballard 2020; Glass and Floyd 2015; Graber et al. 1985; James in Cadman et al. 2007; Kirk et al. 1996; Mossman 1988; Mossman et al. 1991; Noon et al. 1979; Paradis in Gauthier and Aubry 1996; Purcell 2006, 2007; Rumble and Gobeille 1998; Samson 1978; Sutton 1949; Temple et al. 1979; Ward and Smith 2000; Wiebe and Martin 1998).

At the landscape level, the warbling-vireo preferred areas that were 10-34% forested in North Dakota (Cunningham and Johnson 2019).

In North Dakota aspen stands, the probability of occurrence of the warbling-vireo was positively correlated with the percentage of ground cover (Grant and Berkey 1999). High percentages of ground cover are typically associated with open sites, forest edges, and woodlands with fairly open canopies. Whitmore (1977) considered the warbling-vireo a habitat specialist in Utah, preferring forests with low ground cover and high shrub density, also an indication of open-canopy stands.

Ontario nests were in deciduous trees and shrubs. The most common species used were poplar (41.2% of nests), maple (39.2%), elm (7.2%), birch (6.2%), and oak (6.2%). Nests were pensile and in forks of lateral limbs, usually near the end of the branch and periphery of the tree, occasionally close to the trunk. Distances of nests from trunks were 0.3-6 m, mostly 1.2-3 m. Nests were 1.4-18 m from the ground, mostly 6-9 m (James 1976; Peck and James 1987).

The warbling-vireo typically nests in deciduous trees and shrubs, although the western species occasionally nests in pines. In California, 69% of nests at 1 study area were in conifers, although deciduous trees were used for nest sites more than their availability. Nests are most frequently in aspens and poplars, particularly trembling aspen, but also balsam poplar, large-toothed aspen, cottonwood, and black poplar. In Manitoba, 17.6% of nests were in cottonwoods, but they were only 0.9% of trees present and occurred in clumps. Other nest-tree species include white ash, elm, basswood, sugar maple, silver maple, Manitoba maple, willow, black walnut, sycamore, apple, and pear. In Manitoba, peach-leaved willow was the dominant tree, but was not used for nesting. The warbling-vireo may nest in shrubs and saplings including red-osier dogwood, elderberries, willows, and poplars. In California, trees selected for nesting were taller, had larger diameters, and had higher foliage density than randomly selected trees. Basal area and canopy cover at nest sites did not differ from random sites and nest orientation was random. Nests are usually in the upper and middle periphery of trees, less frequently in the upper central portion or lower periphery. Nests tend to be at an average of 65% or more of tree height. Overall nest heights reported are 1.1-37 m. Nest height varies considerably depending on availability of trees and shrubs. Average heights were 2.1 m in 1 Arizona study area and 13.2 m in another, 8.3 m in 1 California study and 7 m and 15.7 m in 2 others, 6.2 m in 1 British Columbia study and 61% between 2 and 6 m for the province, and 8.4 m and 12.6 m in Manitoba. Some nests were situated where they received little shade. In Arizona, 2.4 times more

sky was visible on east halves of nests than west halves. This resulted in 90% more exposure to sunlight in the morning and was thought to be an adaptation to reduce afternoon heat stress (Bent 1950; Campbell et al. 1997; Easton and Martin 2002; Gardali and Ballard 2020; Graber et al. 1985; James 1976; MacKenzie et al. 1982; Purcell 2007; Sutton 1949; Ward and Smith 2000).

The warbling-vireo is not strongly territorial. Territoriality is most evident prior to nest building, dropping off sharply during nest building and largely ceasing thereafter. Females may forage outside males' territories and steal nest materials from other warbling-vireos; these intruders may be attacked. Two nests were in a single tree in Ontario. Limited information is available on territory size. Two pairs in Arizona had territories of 1.2 ha each, 9 territories in California averaged 1.45 ha, 19 in California averaged 1.2 ha, 1 in Illinois was 1.2 ha, 3 in southern Ontario were 1.2-1.5 ha, 2 in Alberta were 1.5 ha each. No information is available on home range size. When nesting in open habitat, it frequently flies as far as 100 m to find suitable foraging areas, suggesting a home range size of about 3 ha (Gardali and Ballard 2020; Howes-Jones 1985a; James 1976; Peck and James 1987).

Limited data suggest that natal philopatry is low. One percent of young were recovered from 19 years of mist-net data in California. Of 38 adults in British Columbia, 13 (34.2%) returned, all males. All males returned to their original territory and 3 returned the subsequent year (Gardali and Ballard 2020; Ward and Smith 2000). Two birds banded in Alberta during the breeding season were recaptured in another breeding season at the original banding site, suggesting site fidelity (Brewer et al. 2018).

Limiting Factors

Eggs have been found in Ontario nests from mid-May to mid-July, with most present in the first half of June (Peck and James 1987). About a week after arrival, the female starts to look for potential nest sites. Females may begin and abandon 1-3 nests before completing the final nest. Abandoned nests were worked on for 1-3 days. First Ontario nests took an average of 7.2 days to complete and usually 1-2 days elapsed after they were completed before egg laying was initiated. Replacement nests took an average of 6.0 days to complete and egg laying commenced as soon as they were complete. Occasionally the old nest was dismantled and its materials were used to construct the next one. Material may be taken from Yellow Warbler nests. Ontario replacement nests averaged 33 m from the first nest, except for one 30 cm away. In Montana, nest construction took an average of 5.4 days; elsewhere, 1 nest took 8 days to build. Eggs are laid at the rate of 1 per day. Incubation may begin with laying of the second egg. The incubation period at Ontario nests was 13 or 14 days. In Arizona, Idaho, and Montana, the mean incubation period was 12.5 days (range 10.5-16 days, mode 12 days). Fledging occurred at an average of 12 days in Ontario. In Arizona, Idaho, and Montana, mean fledging age was 14 days, with a range of 10.5-19 days and a mode of 13 days (Bent 1950; Gardali and Ballard 2020; Howes-Jones 1985a, 1985b).

Double broods have been reported in Montana and California, and double-brooding is probably common in areas with a long breeding season. Double broods have not been reported in Ontario or the eastern population. Renesting may occur, particularly in warmer areas. In California, females may lay as many as 5 clutches in an attempt to raise young. In Ontario, 1 renest may occur but a replacement clutch may not be attempted if loss occurs during late incubation. Clutches of 1-4 eggs have been reported in Ontario, mostly 3 or 4 eggs; 25 of 54 clutches (46.3%) contained 4 eggs.

Clutches of 1-5 eggs have been documented throughout the warbling-vireo's range, with about two thirds containing 3 or 4 eggs; 4 eggs is the most frequent clutch size (Bent 1950; Campbell et al. 1997; Gardali and Ballard 2020; Howes-Jones 1985a, 1985b; Peck and James 1997; Ward and Smith 2000).

The mating system is monogamous. The age at first breeding is unknown, but is probably 1 year (Gardali and Ballard 2020).

James (1976) studied the Eastern Warbling-Vireo's foraging behaviour in southern Ontario. Its foraging techniques and locations were similar to those of the Red-eyed Vireo but significantly different from the Yellow-throated Vireo: 32.0% by stalking, 59.0% by hovering, and 10.0% by hawking. It captured 97% of food items on leaves and 3.0% on branches. In California, 80% of prey was taken from twigs suggesting that it is opportunistic (Gardali and Ballard 2020). In Ontario, 88% of foraging was in the periphery of a tree (40% in the upper portion, 40% in the middle, 8% in the lower portion) and 12% in the centre of a tree (6% upper, 6% middle, 0% lower). Foraging perches were 51.5% unfoliated, 39.0% foliated, and 9.5% dead. It spent much time foraging within an individual tree, feeding mainly on tips of live branches. It foraged in almost all tree species in territories (sugar maple, white elm, red oak, balsam poplar, trembling aspen, white birch, ash, apple, basswood, hophornbeam, hickory, walnut, cherry) except for beech, willow, spruce, and white pine. Mean foraging height was 7.7 m (range 0.15-21 m) on trees a mean height of 10.0 m, mostly in trees 12-15 m tall (James 1976). In addition to foraging for invertebrates, the warbling-vireo drinks from wet vegetation and small streams (Gardali and Ballard 2020). In the Northwest Territories, 94.3% of foraging occurred in deciduous species and 5.7% occurred in conifers. Ninety percent of foraging occurred on foliage and the mean foraging height was 8.2 m (Greenberg et al. 1999).

The main food delivered to nestlings appears to be small green caterpillars, but also dogwood berries and large moths after the wings are torn off. An analysis of 340 adult stomachs indicated that the warbling-vireo ate 94.2% animal food, almost all insects, and 5.8% plant material. Lepidopterans dominated the diet at 40.4% (35.4% caterpillars). Beetles comprised 15.5% of food, especially lady beetles, but also weevils and metallic wood-boring and leaf beetles. The remainder of the diet consisted of 16.7% bugs (mostly stink bugs), 9.5% flies, 6.0% hymenopterans, 4.4% grasshoppers and other insects, and trace amounts of spiders and snails. Vegetation consumed included fruits of cherry, sassafras, and blackberry. Another study reported similar results: 95% insects of which lepidopterans were most important at 43% (mostly caterpillars but also moth pupae). Other prey included 21% bugs, 19% lady beetles, 7% other beetles, 4% other insects, and 2% spiders. In Illinois, 3 spring migrants ate 79% caterpillars and 15% beetles, of which about a third were ground beetles. In autumn, the warbling-vireo may also eat elderberries and pokeweed berries (Bent 1950; Chapin 1925; Gardali and Ballard 2020; Graber et al. 1985).

The Western Warbling-Vireo typically accepts cowbird eggs whereas the Eastern Warbling-Vireo usually rejects them. The Eastern Warbling-Vireo may eject cowbird eggs from the nest or abandon parasitized nests. In Manitoba, 0.13 vireo egg was lost per ejected cowbird egg; ejection greatly improved reproductive success over acceptance. The Western Warbling-Vireo is highly parasitized and is one of the most frequently parasitized species in British Columbia with an overall rate of 49%, and 75%, 79.1%, and 61.7% in 3 studies. Parasitism was so high in some areas that local vireo

extirpations would occur without immigration. Other western parasitism rates are 50% in Wyoming, 63% in Montana, 75% in Colorado, and 80% in California. In Oregon, 46% of nest failures were attributed to parasitism, the highest rate of the 5 species studied, and it was the only species for which parasitism losses were greater than those due to predation. The overall parasitism rate was 47%. Parasitism rates are much lower in the Eastern Warbling-Vireo, possibly because observers do not detect rejected eggs. The rate is 11.3% in Ontario and 3.6% in Manitoba. Parasitism has not been documented in Quebec, Michigan, Illinois, or Kansas. Cowbirds may remove vireo eggs, reducing clutch size. In Montana, clutch size averaged 3.8 eggs in unparasitized nests and 3.16 in parasitized nests. Results were 3.36 eggs in unparasitized nests and 2.75 eggs for parasitized nests in British Columbia. If a cowbird egg is accepted, typically the entire vireo brood is lost. The mean number of young surviving per parasitized nest was 0.1 in British Columbia; only 2.6% of parasitized Montana nests produced young. In the Sierra Nevada of California, Western Warbling-Vireo abundance was negatively correlated with cowbird abundance. In British Columbia, parasitism rate was not correlated with nest height (Bent 1950; Campbell et al. 1997; Gardali and Ballard 2020; Heltzel and Earnst 2006; Howes-Jones 1985a; Lowther 1997; Ortega and Ortega 2003; Peck and James 1997; Sealy 1996; Siegel and DeSante 2003; Sutton 1949; Underwood and Sealy 2011; Ward and Smith 2000).

Habitat loss does not appear to be a significant problem for the warbling-vireo. Clear-cutting coniferous stands and leaving deciduous trees in or near openings may be beneficial. Forest fragmentation in the south may have benefitted it (Gardali and Ballard 2020; Paradis in Gauthier and Aubry 1996). In California, it was more numerous in commercially thinned forests than unthinned forests (Siegel and DeSante 2003). Further loss of forest fragments and drainage of wetland pockets in the south may be detrimental. Vanderwel et al. (2007, 2009) summarized studies that examined the effects of partial forest harvest on breeding birds in the Boreal Forest Region, with an emphasis on Ontario. They concluded that there was no change in abundance of the warbling-vireo when 30%, 50%, or 70% of trees were removed. Bayne et al. (2016) examined bird responses to forest fragmentation due to energy sector disturbances in the western boreal forest. The Western Warbling-Vireo was significantly more abundant along pipelines than in forest interior.

In Oregon, abundance of the Western Warbling-Vireo increased significantly after cattle were excluded from grazing in riparian trembling aspen stands. Significant regeneration of aspen occurred once grazing ceased (Earnst et al. 2012). It is possible that grazing by white-tailed deer could adversely affect habitat for it in southern Ontario.

Price (2004) predicted that the range of the Eastern Warbling-Vireo could contract in southern Ontario if the average summer temperature increased by 2°C. DesGranges and Morneau (2010) considered the Eastern Warbling-Vireo very sensitive to climate change in Quebec.

Status

McIlwraith (1894) considered the Eastern Warbling-Vireo very common during the breeding season. It was common in eastern Ontario in the latter part of the 19th century, having moved northward as forests were cleared (Weir 2008). Baillie and Harrington (1937) reported that it was a widespread and common breeder in southern Ontario, particularly in urban centres. Breeding occurred north at that time to at least Parry Sound District and North Bay, northern Frontenac County, and Ottawa,

and in the Thunder Bay area. Breeding had been documented on the Manitoba side of Lake of the Woods, but not in Ontario. The first atlas demonstrated that it was well established in Rainy River District and that it had expanded its range northward to the Clay Belt. Population gaps were evident in the heavily treed Algonquin Highlands and in some squares in Essex County with essentially no tree cover (James in Cadman et al. 1987). James (1991) considered it common in the south, except for being absent from the Algonquin Highlands, and common in western Rainy River District.

The second atlas indicated that there had been little change in the distribution of the Eastern Warbling-Vireo since the first atlas. A small population became established in the Moosonee area, but there were few records from the Boreal Forest Region and the Algonquin Highlands. There was no difference in its probability of observation province-wide or in any atlas region except the southern Canadian Shield which experienced a significant decline that may have been related to forest maturation. Highest densities occurred along the shore of eastern Lake Ontario, on the southern edge of the Shield, along the St. Lawrence River, and in a small area east of Lake Huron (James in Cadman et al. 2007).

Long-term (1970-2021) population trends determined by the Breeding Bird Survey indicate that the warbling-vireo increased at annual rates of 0.841% in Canada and 1.24% in Ontario. The short-term (2011-21) trends were an annual increase of 0.255% in Canada and an annual decrease of 0.951% in Ontario. All results were highly reliable except that the Canadian long-term trend was of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

At Ontario nests, fledglings seldom ventured more than 10 m from the nest on the first day, were 30-100 m from the nest the second and third day, and by the fourth or fifth day were widely dispersed and often outside the territory. Within a week or 2 of fledging, young become independent and the family abandons the territory (Bent 1950; Howes-Jones 1985a, 1985b).

MIGRATION

The Eastern Warbling-Vireo migrates nocturnally either singly or joins mixed-species flocks. Of 20 pairs observed in Hamilton, both sexes of 13 pairs arrived together. The female arrived 1 day after the male in 5 cases, 3 days later in 1 case, and 4 days later in 1 case. Spring migrants usually arrive in early May, but some appear in mid-April. Some birds leave in August but many remain until mid- to late September with stragglers occurring into early October or rarely as late as mid-November (Curry 2006; Gardali and Ballard 2020; Howes-Jones 1985a; James 1991). In Idaho, adults arrived in autumn 21.1 days before juveniles (Carlisle et al. 2005).

During migration, the warbling-vireo uses a wide variety of forested and shrubby habitats, but avoids coniferous forests. It may occur in urban areas during migration (Campbell et al. 1997; Gardali and Ballard 2020). Favoured habitat during spring migration in Algonquin Park includes small patches and strips of trees along lakes and rivers, utility and road corridors, clearings, aspen stands, silver maple swamps, and floodplain groves (Tozer 2012). In Illinois, it was most abundant during spring migration in bottomland forests, forest edges, and shrubby areas (Graber et al. 1984). During spring migration in Wisconsin and Minnesota, it was significantly more abundant in floodplain forests than upland forests (Kirsch et al. 2013).

Keast (1980) studied the foraging strategies of the Eastern Warbling-Vireo during autumn migration at Prince Edward Point. Foraging substrates included 49% outer leaves, 7% twigs and inner leaves, 15% outer branches, 24% sapling foliage, 7% sapling branches, and 5% low shrubs. It did not forage in the air or on inner branches, tree trunks, or the ground. It foraged at heights of 1.4-12.9 m, most frequently at 7 m.

Carlisle et al. (2012) examined the diet of Western Warbling-Vireos during autumn migration in Idaho. Prey consumed more than expected based on their availability included bugs (mostly stink and spittle bugs), lepidopterans, and larvae. Prey consumed less than expected included spiders, stilt bugs, leafhoppers, jumping plant lice, hymenopterans (including ants, wasps, and yellowjackets), moths, and flies.

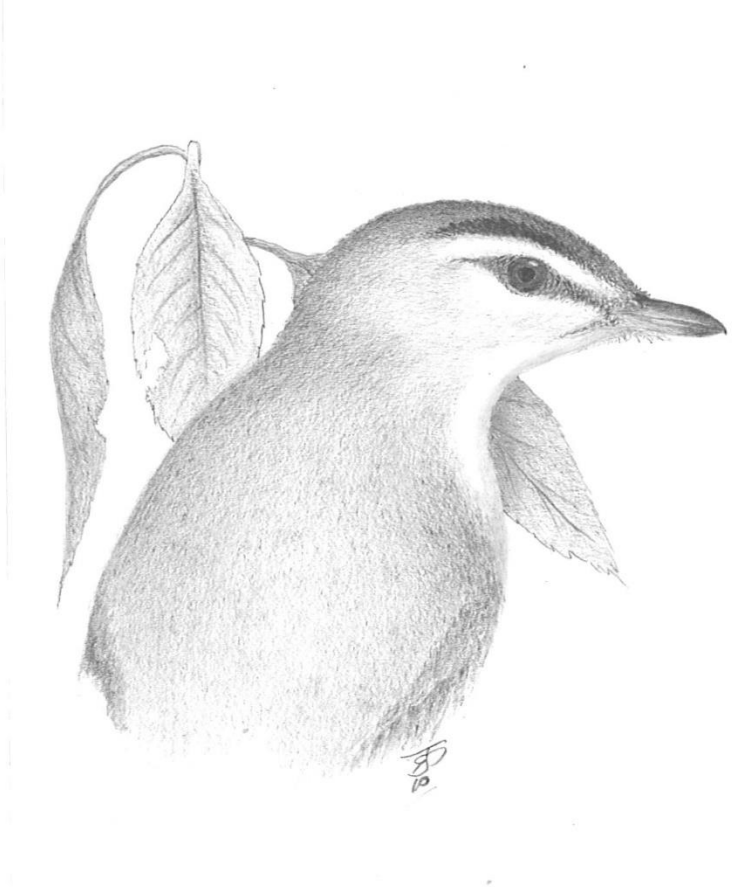
The warbling-vireo is occasionally killed at tall structures during migration, but typically in low numbers. Forty-two were reported killed at the Lennox chimneys near Kingston (Gardali and Ballard 2020; Weir 2008).

Ellwood et al. (2010) determined that spring arrival dates of the Eastern Warbling-Vireo were significantly correlated with temperature at Concord, Massachusetts. It was expected to arrive earlier in response to climate change. In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season for 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming during the second period. The Eastern Warbling-Vireo arrived significantly earlier in spring during the second period but there were no differences in its autumn departure dates or length of the breeding season.

James (1991) considered the Eastern Warbling-Vireo an uncommon migrant in Ontario.

Red-eyed Vireo

Vireo olivaceus

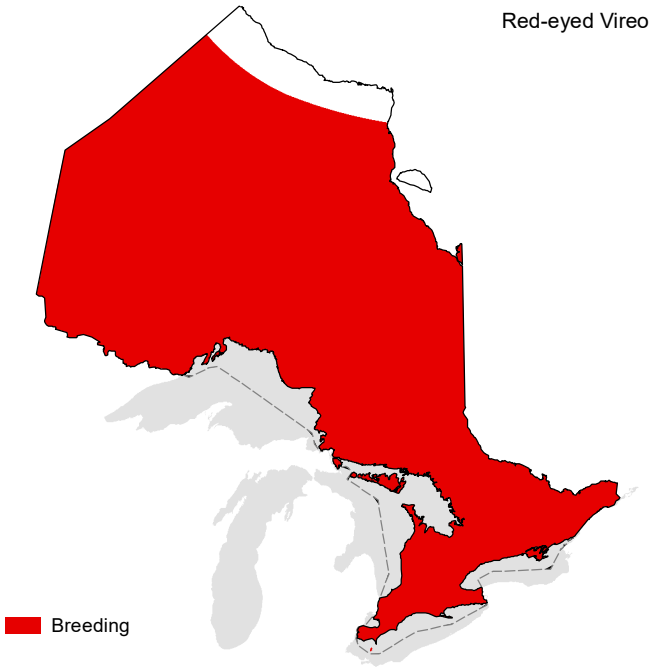


BREEDING SEASON

Habitat Requirements

In Ontario, the Red-eyed Vireo nests mostly in deciduous (38.7% of nests) and mixed woods (38.4%). It also nests in coniferous woods (1.5%); in gardens, cottage areas, campgrounds, and parks (11.9%); in overgrown fields and thickets (3.6%); in overgrown rocky outcroppings (3.3%); on road rights-of-way (0.9%); in mine clearings (0.3%); and in treed sand dunes (0.3%). Second-growth and mature stands were used for nesting as were open and closed stands. Many nests were at edges, along shorelines, or near roads or paths (Peck and James 1987). It may occur wherever tree canopy closure is 25% or more, and even in more open areas containing mature trees, such as city parks, savannahs, and rural gardens (James in Cadman et al. 2007).

In the Boreal Forest Region near Pickle Lake, the Red-eyed Vireo occurred in deciduous forests, mostly those dominated by poplar. It also occurred occasionally in coniferous forest and deciduous and mixed tall shrubs (James 1980; McLaren and McLaren 1981). In mixed-wood forests near Hearst, it occurred in upland clear-cuts 3-24 years old and in uncut stands. It was absent in most lowland coniferous stands, including uncut areas, but occurred in low density in 6- and 9-year-old lowland



clear-cuts (Welsh and Fillman 1980). In mixed jack pine forests near White River, it was significantly more abundant in 23-25-year-old stands than in younger (3-20 years) stands or mature uncut stands 40-100 years old. It was 1 of 4 significant indicator species of this forest age class and was most strongly associated with vertical structure in the 2.5-5 m stratum (Venier and Pearce 2005). It was common in the Clay Belt, where it preferred poplar woods (Smith 1957) and mid-succession forests (Welsh 1993). In the Ontario Boreal Forest Region, it occurred in immature to younger hardwoods with open conditions. It was associated with a high amount of edge, low amount and intactness of forest older than 80 years, and a high component of young hardwoods (Rempel 2007). It was associated with more disturbed, less intact, closed hardwood stands (Rempel et al. 2007).

Near Engelhart in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Red-eyed Vireo was present in deciduous and mixed forests and alder thickets, as well as in open stands with considerable regeneration and ash-elm riparian forest (Barlow and Power 1970; Barlow and Rice 1977; Rice 1978c). In Quetico Park, it was almost ubiquitous in forests. It was most dominant in stands to age approximately 75 years, but was also common in mature stands and present in old-growth forest (Apfelbaum and Haney 1985). In jack pine stands near Gogama and Parry Sound, it was absent as a breeder in pure pine forests, but occasionally wandered into them from adjacent deciduous areas. It always required some deciduous trees and was common in pure deciduous groves and in open, mixed stands. It first appeared once trees became 3-4 m tall, but preferred older forests (James 1979a; James and Peck 1995a). In the southern Boreal Forest Region and Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Red-eyed Vireo commonly nests in mature and old-growth white pine stands, where it is second in abundance to the Ovenbird (Kirk et al. 2012). Near Rutherglen, it occurred in extensive forest as well as woodlots in more open landscapes, and was also present in shade trees in North Bay. In forests, it preferred south and east slopes, and areas where water, rock outcrops, fires, or forestry had created openings. It was absent where undergrowth was totally lacking and where there was an absence or scarcity of deciduous trees in the overstorey (Lawrence 1953a). In Algonquin Park, it occurred in all treed habitats except bogs and pure stands of balsam fir and spruce; it was the most widely distributed bird species. It was the most abundant species in sugar maple–yellow birch stands, second in abundance in birch-poplar stands, and third in abundance in pure hemlock stands. Although density was lower in mixed birch-poplar-fir-spruce stands, it was still one of the more common species (MacLulich 1938; Martin 1960).

In Durham Region in the Great Lakes–St. Lawrence Forest Region south of the Shield, the Red-eyed Vireo occurred in all forest types and was the most abundant species in mature sugar maple–oak. Speirs and Orenstein (1975) considered it a late-succession, full canopy species, but other Ontario studies demonstrated that it uses all stages of succession and canopy closure. Near Ottawa, parameters that were of high importance to it were canopy cover, tree height, and percent deciduous species. Parameters of moderate importance were tree diameter at breast height (DBH), shrub height, tree density, and tree species richness. Percent living ground cover, leaf litter depth, and herb height were of low importance. Forest patch size was a significant predictor of abundance but the amount of surrounding forest was not (Lee et al. 2002).

In the Carolinian Forest Region in Halton Region, 9 of 10 nests were in forests with abundant understorey and the other was in a shrub near a grove of trees. Canopy closure at nest sites ranged from 50% to more than 90% and averaged 78%. Habitat appeared to be selected for its structure rather than tree species composition (James 1976). In the Walsingham Forest in Norfolk County, nests were associated with shrubs 0.3-1.0 m tall and increasing basal area of trees larger than 38 cm DBH (McCracken et al. 1998).

Habitat preferences reported elsewhere are very similar to those in Ontario. The Red-eyed Vireo occurs in virtually all types of deciduous and mixed forests and all age classes, but requires a moderate amount of shrubs and saplings in the subcanopy layer. Rarely, it breeds in coniferous plantations, tamarack bog forests, pine-hemlock stands, balsam fir–white cedar stands, and fir-pine stands. It tends to be absent in pure spruce or pine stands. In Georgia, it is one of the dominant species in climax pine stands, but these forests typically have an understorey of deciduous trees. Other than the requirement for shrubs, it is a habitat generalist, usually occupying the entirety of a woodlot with no other major habitat preferences. In New Hampshire and Maine, it occurred in all forest types but was most abundant in those dominated by white birch, northern hardwoods, swamp hardwoods, aspen, and hemlock. It was less common in white pine, spruce-fir, and balsam fir stands. It demonstrates increased abundance with age of stand and mesic soils. In eastern Quebec balsam fir–white cedar forests, it was significantly more abundant in nonriparian than riparian stands (LaRue et al. 1995). In Alberta aspen stands, it occurred in all age classes and was associated with the lower strata of the forest. In Missouri, the Red-eyed Vireo was most abundant in mature forests, followed by riparian forests and 9-year-old clear-cuts. It was absent in 3-year-old clear-cuts. In New York clear-cuts, its density was significantly correlated with the development of a deciduous canopy taller than 7 m. It was the dominant species in all stands 55-120 years old, with peak densities occurring in stands 75 and 100 years old. It is not typically an old-growth species. In Pennsylvania, it occurred in 100% of old-growth forests, but in 95.9% of forests in the Appalachians, and in 93.1% of forests in the state. In maple, birch, and aspen forests, it may be the dominant species, or be codominant with the Ovenbird. Although the Red-eyed Vireo occasionally occurs in suburban and urban areas, including parks and cemeteries, numbers in these habitats are usually quite low. In Illinois, it was most abundant in upland forests followed by floodplain forests and savannahs; it was not observed in urban habitats. In Indiana, most nested in deciduous forests but some nests were in grassy fields with thickets of blackberries that also contained dense stands of trees 1-7 m tall, and in shrubby fields where about half the ground was shaded part of the day either by saplings about

7 m tall or by dense hawthorns (Anderson and Shugart 1974; Back 1979; Beals 1960; Bielefeldt and Rosenfield 1994; Blake and Karr 1987; Bond 1957; Bushman and Therres 1988; Campbell et al. 1997; Crawford and Titterington 1979; Darveau in Gauthier and Aubry 1996; Darveau et al. 1992; DeGraaf et al. 1998; Erskine 1977; Faanes and Andrew 1983; Flack 1976; Graber et al. 1985; Haney 1999; Hoffman 1989a; Johnston and Odum 1956; Keller et al. 2003; Kirk et al. 1996; LaRue et al. 1995; Lent and Capen 1995; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991; Niemi and Pfannmuller 1979; Nolan 1963; Noon et al. 1979; Pagen et al. 2000; Schieck et al. 1995; Stauffer and Best 1980; Sutton 1949; Temple et al. 1979; Thompson and Capen 1988; Tyler in Bent 1950; Walk et al. 2011).

The Red-eyed Vireo preferred landscapes that were 59-75% forested in North Dakota; no areas were more than 75% forested. In New York, it preferred landscapes that were 82-100% forested (Cunningham and Johnson 2019). In North Dakota 400-m landscapes, it increased with increasing tree cover within 100 m but its probability of occurrence attained 50% in landscapes with more than 30% tree cover compared with 25% in landscapes with less than 30% tree cover (Cunningham and Johnson 2016).

In Pennsylvania, vegetation structure differed significantly between used and unused sites. Nests were closer to adjacent trees (4.99 m compared with 6.99 m), had greater canopy coverage (71.25% compared with 55.6%), less ground cover (31.94% compared with 46.25%), and fewer stems 0.5-1.0 m tall (2.03 compared with 3.40) than random sites. Coverage by ground vegetation was significantly lower at successful than unsuccessful nests (Siepielski et al. 2001). In Indiana, the Red-eyed Vireo was most abundant in forests with more than 90% canopy closure and in shrubby areas densely regenerating with oak saplings. It was next in abundance in savannahs and woodlands with 50-90% canopy closure and least abundant where there was less than 20% canopy closure (Grundel and Pavlovic 2007a). In the same state, it was common in 2-9-year-old regenerating clear-cuts. Its abundance was positively correlated with leaf litter depth (Ruhl et al. 2020). In New Hampshire and Maine, it was positively correlated with the total foliage volume of both deciduous and coniferous trees larger than 10 cm DBH and the total foliage volume of deciduous trees smaller than 2 cm and 2-10 cm DBH. It was negatively correlated with the number of coniferous trees larger than 10 cm DBH and the total foliage volume of coniferous trees smaller than 2 cm DBH (DeGraaf et al. 1998). In southern New Jersey, the Red-eyed Vireo was significantly more abundant in hardwood swamp than in oak-pine forest (Rich et al. 1994). In Texas, its abundance was positively correlated with vegetation height, number of tree and shrub species, canopy closure, foliage density at 7 m to greater than 20 m, percent coverage by hardwoods 5 cm to more than 32 cm DBH, and number of tree stems larger than 32 cm DBH. It was negatively correlated with percent coverage by pines 5-16 cm DBH. It used fairly mature pine-hardwood forests (Conner et al. 1983). In a Connecticut woodlot over 59 years, there was a progressive shift to larger trees, a sparser shrub layer, and a less diverse tree canopy dominated more by oaks and maples as a result of a severe decline in hemlock. There were no significant changes in the abundance of the Red-eyed Vireo (Buchanan et al. 2016).

The Red-eyed Vireo is not particularly area sensitive in Ontario. Near Peterborough, territories and nests were no further from edge than random, and nest success and parasitism and predation rates were unaffected by distance to edge, forest size, or amount of forest within 2- and 10-km radii.

Breeding density increased with the amount of forest cover within 2 km, but did not vary with forest size or amount of forest within 10 km (Dunford et al. 2002). Near Ottawa, its abundance was associated with forest size but not with the amount of forest cover (Lee et al. 2002). In southern Ontario, its probability of detection was positively correlated with the amount of forest 100 m or more from edge, the amount of forest within 2 km, and regional forest cover, but negatively correlated with forest size. The only significant associations were those with amount of local and regional forest cover, which were significant at the 0.10 level (Austen et al. 2001). Nol et al. (2005) studied the distribution of the Red-eyed Vireo in southern Ontario and found that occupancy of small woodlots by this species was not influenced by distance to the nearest large forest. Near Lake Simcoe, Red-eyed Vireos nested on 3 occasions in a sugar maple that had open habitat on 3 sides of it and 1 nested in an isolated white birch about 5 m from a house (Ross James, personal communication). These observations indicate that the Red-eyed Vireo is not an obligate area-sensitive or forest-interior species in Ontario.

It appears as though northern populations are not area sensitive, but area sensitivity increases southward. In western boreal Canada, distribution of the Red-eyed Vireo was influenced only by forest type, and not by forest size or the amount of forest within 5 km (Hobson and Bayne 2000). In Wisconsin, there was little evidence of it being affected by forest size, although when it occurred in more pioneer stands, it tended to be more abundant in larger woods (Bond 1957). Howe (1979) confirmed it breeding on islands as small as 0.4-1.1 ha in Wisconsin. Donovan et al. (1995) studied the Red-eyed Vireo in contiguous forests and fragmented woodlots in Wisconsin, Michigan, and Missouri. In the northern states, there was no difference in its abundance in contiguous and fragmented forests, but it was significantly more abundant in contiguous than fragmented forests in Missouri. In all 3 states, nest survival rates were greater in contiguous forests, which acted as sources; forest fragments were sinks. In Rhode Island, its distribution was unaffected by forest size, where Golet et al. (2001) concluded that the amount of forest in a landscape may be more important than forest size. A 2-year Illinois study found that its distribution was significantly correlated with forest size 1 year, but not the other (Blake and Karr 1987). In North Dakota, its probability of occurrence was positively correlated with forest size. Grant and Berkey (1999) considered it an area-sensitive species, despite the fact that its probability of occurrence was 100% in woodlots as small as 3 ha. Its probability of occurrence in 1-ha woodlots was 11%. In Maryland and the mid-Atlantic states, the Red-eyed Vireo was considered area sensitive. Its distribution was significantly correlated with forest size, and a sharp decline occurred in woodlands smaller than 4 ha. Although it occurred in most forests larger than 20 ha, it was predicted that 100 ha of forest were required to support a viable population. Despite these predictions, it occurred in woodlots as small as 0.1 ha, and was unaffected by forest size in Maine. In Pennsylvania, it was associated with unfragmented landscapes and larger woodlands (Bushman and Therres 1988; Keller and Yahner 2007; Lynch 1987; Robbins 1979; Robbins et al. 1989). Kilgo et al. (1997) considered the Red-eyed Vireo area sensitive in South Carolina. In Missouri, the smallest woodlot it was observed in was 4.6 ha, and it did not reach 100% occurrence until woodlands were larger than 340 ha (Hayden et al. 1985). There are some estimates of minimum widths of riparian forests to support Red-eyed Vireos. These are from more southern locations and are not directly relevant to Ontario where forest width may not be important. In Iowa, the minimum corridor width it was found in was 40 m (Stauffer and Best 1980). In Maryland and

Delaware, its probability of occurrence increased significantly with corridor width, from about 60% at 50 m to almost 100% at 300 m (Keller et al. 1993). In Georgia, it was more abundant in medium-sized than narrow or wide riparian forests, but the differences were not significant. Its abundance was positively correlated with basal area and canopy cover and negatively correlated with shrub cover (Hodges and Krementz 1996).

Villard et al. (2007) reclassified the Red-eyed Vireo as a forest-interior specialist because it consistently avoided edges in other studies reviewed by Villard (1998). In Saskatchewan, Villard et al. (2007) mapped Red-eyed Vireo territories before and after creating edge through clear-cutting. Significant edge avoidance by the Red-eyed Vireo was observed in 2 cases. They concluded that its response to edge will vary both with landscape context and time since edge creation. In Minnesota, it demonstrated no edge effect, with nest success unrelated to distance from edge (Hanski et al. 1996). In New Hampshire, it was significantly more abundant in forest interior than near clear-cut edges but its distribution did not differ from that of randomly placed simulated territories. The lower abundance in edge areas was not necessarily evidence of edge avoidance but may be due to the absence of suitable habitat beyond clear-cut borders (King et al. 1997). Lindell et al. (2007) completed a review of other studies and determined that some studies found that the Red-eyed Vireo avoided edges whereas others found that it exploited edges. In New Jersey, Rich et al. (1994) found no difference in its abundance in forest interior and along 3 types of open corridors with average widths of 8.3 m, 16.3 m, and 22.5 m, with an overall range of 6.2-41.0 m. In Tennessee, its breeding density increased with increasing distance from edge. Results were not significant and Kroodsma (1984) concluded that it did not demonstrate an edge effect.

Ontario nests were in live trees and shrubs, mostly in deciduous species (89.7%). Trees most commonly used were maples, less frequently birches, poplars, oaks, alder, and white cedar. Saplings and shrubs were used for nesting more than larger trees. Nests were pensile and suspended in horizontal forks, usually away from the trunk and often at the end of a limb. Distances of nests from trunks ranged from 0.3-6 m, mostly 1.1-2.4 m. Nests were 0.5-21 m from the ground, but mostly 1.8-3.7 m up (Peck and James 1987). Near Rutherglen, 77% of nests were in deciduous species and the remainder were in conifers. In order of frequency, nests were in white birch, beaked hazel, red maple, trembling aspen, white cedar, balsam fir, mountain maple, large-toothed aspen, juneberry, willow, and red pine. Nests were 0.9-16.8 m from the ground; 73% were lower than 4.6 m. Second and third nests tended to be higher than first nests. One pair nested at 2.4 m, 6.1 m, and 15.2 m; one at 1.5 m and 9.1 m; one at 2.4 m and 4.6 m; one at 5.5 m and 3.0 m; and one at 1.1 m and 1.1 m. Nests were at edges of clearings, along a lakeshore, or over water, but all had dense foliage beside or above the nest where birds could approach inconspicuously. Nests were often built close to the previous year's nest; old nests were not reused (Lawrence 1953a). A nest near Lake Nipigon was 9.8 m from the ground in a balsam fir (Kendeigh 1947). Of 10 southern Ontario nests, 3 were in the upper periphery of a tree, 4 in the middle periphery, 2 in the lower periphery, and 1 in the upper central. Nest trees included sugar maple, white elm, balsam poplar, beech, hickory, and hawthorn (James 1976). One Ontario nest was in a mountain-ash (MacLulich 1938).

In addition to species reported in Ontario, the Red-eyed Vireo has nested in hackberry, white ash, basswood, sassafras, black locust, sycamore, grape, honeysuckle, witch-hazel, chokecherry,

blackberry, bur oak, American chestnut, and hemlock. Nests are typically where they are completely shaded all day, but with an unobstructed view. Nests have been found 0.4-21.3 m from the ground, with average height ranging from 2.5 to 4.3 m, but averaging 10.7 m and 11.1 m in New Hampshire (Campbell et al. 1997; Cimprich et al. 2020; Darveau in Gauthier and Aubry 1996; Graber et al. 1985; Holmes et al. 1979; Robinson 1981; Sutton 1949; Tyler in Bent 1950; Williams 1946; Williamson 1971).

Near Englehart, males initially patrolled an area of about 2 ha, but the defended area declined to about 0.7 ha as more males arrived, with territory size varying with habitat. Mean size of more than 70 territories near Englehart and North Bay was 0.37 ha. In Algonquin Park, 139 territories averaged 0.19 ha (range 0.02-0.62 ha). Near Rutherglen, 5 territories averaged 0.57 ha 1 year; the next year 4 territories averaged 0.85 ha. There were 2 distinct portions to territories: the song area where the male spent most of his time, and the nest area. Near Lake Nipigon, 6 territories averaged 0.77 ha (range 0.61-0.85 ha). Nests may be near the edge of territories; active Ontario nests have been found as close together as 15 m, 18 m, and 30 m (Barlow and Rice 1977; Kendeigh 1947; Lawrence 1953a; Martin 1960; Peck and James 1987; Rice 1978b, 1979c). Illinois territory sizes averaged 1.2 ha in virgin floodplain forest, 0.7 ha in upland forest (range 0.3-1.0 ha), 0.6 ha in mature bottomland forest 1 year (range 0.2-1.0 ha), 0.8 ha the following year (range 0.8-1.0 ha), and 0.7 ha in an urban park. Territory size was inversely proportional to population size (Graber et al. 1985). Territories averaged 0.53 ha in Maryland and Florida (Williamson 1971) and ranged from 0.3-0.8 ha in Quebec (Darveau in Gauthier and Aubry 1996; DesGranges et al. 1987). One Kansas territory was 1.0 ha and adjoining territories averaged 0.58 ha (Fitch 1958). Mean territory size in Michigan aspen forests was 0.69 ha. In 1 Illinois study, territories were 3.0 ha in elm-maple forest 1 year but half this size when the number of territorial males doubled. Females range beyond the territory boundaries and have a larger home range (Cimprich et al. 2020). Near Quebec City, territories were aggregated together rather than spread uniformly through forested habitat. Forests may have to be larger than 1 territory size to support it (Bourque and Desrochers 2006).

Near Englehart, Red-eyed and Philadelphia vireos defended mutually exclusive territories. Red-eyed Vireos could not distinguish the songs of the 2 species, but Philadelphia Vireos could (Rice 1978b, 1978c). Near Gogama, territories of the 2 species overlapped although they may have been separated vertically with Philadelphia Vireos occupying space above Red-eyed Vireos (James and Peck 1986). In New Hampshire, territories of Red-eyed and Philadelphia vireos overlapped significantly. Overlap was 100% 1 year when Red-eyed Vireos occupied the entire study area; overlap other years was 40%, 50%, and 75%. Aggressive encounters occurred between the 2 species, most frequently during territory establishment and the late nestling and early fledgling stages. Aggression seldom occurred during incubation and the early nestling and late fledgling stages (Robinson 1981).

Little information is available on natal site fidelity. In 4,600 ha of the Ganaraska Forest in southeastern Ontario, 3 of 25 nestlings (12%) returned to breed. Of these, 1 male was found on territory 9,870 m from its natal nest, but no nest of this bird was found. One yearling male nested 70 m from its natal nest and a female nested 4,090 m from its natal nest (Walters and Nol 2011a). The return rate of 12% is high compared with the average of other studies (3.7%), but this may be due to the much larger than normal study area. None of 17 nestlings returned near Rutherglen (Lawrence 1953a).

In the Ganaraska Forest, 4 of 27 yearling birds (15%) and 5 of 56 older birds (9.0%) returned. Mean dispersal distances from the previous nest were 275 m for 2 second-year males (200 and 350 m), 210 m for 2 second-year females (170 and 250 m), and 540 m for 5 after-second-year males (range 40-2,040 m). In West Virginia, 49% of 96 males and 1 of 2 females returned; in Ontario, a single banded male returned the following year; in Illinois, 0 of 2 adults returned (Cimprich et al. 2020; Lawrence 1953a; Robinson 1992; Walters and Nol 2011a). Canadian banding records indicate high breeding season fidelity; 73% of encounters represent birds returning to the same breeding site in subsequent years (Brewer et al. 2018).

Limiting Factors

Eggs have been found in Ontario nests from late May until mid-August, with most present from mid-June through the first week of July (Peck and James 1987). In Algonquin Park, nests are under construction from late May to early July, eggs are present from late May to late July, nestlings are present from mid-June to early August, and dependent fledglings are present from late June to late September (Tozer 2012).

Females begin prospecting for a nest site shortly after arrival, but take 5 or 6 days to select one. For second nests, 3 or 4 days are spent selecting a site; third nests are typically well under construction a day after the second nest is abandoned. The female builds the nest within 4 or 5 days. Two to 4 days elapse between nest completion and laying of the first egg, and 1 egg is laid per day. Incubation begins with the laying of the third egg, even if there are 4 eggs in the clutch. The incubation period of Ontario nests was 11-15 days, mostly 12 or 13 days, typical of throughout its range. Most young left Ontario nests when they were 10 days old, but some remained another day. Elsewhere, some young remained in the nest 12 days (Barlow and Rice 1977; Campbell et al. 1997; Cimprich et al. 2020; Lawrence 1953a; Peck and James 1987; Tyler in Bent 1950).

Cimprich et al. (2020) concluded that 1 brood is raised per year south to Virginia, but 2 broods are raised in Louisiana. Near Rutherglen, Lawrence (1953a) observed 1 case of possible double brooding and Peck and James (1987) concluded that double broods might occur in Ontario. Graber et al. (1985) stated that the long laying period in Illinois suggested second broods, but this was not verified. Renesting occurs 4-9 days after a clutch is lost, and as many as 3 nesting attempts may be made. Clutches of 2-5 eggs have been reported in Ontario, mostly 3 or 4 eggs; 5-egg clutches were rare (1.2% of clutches). Clutches of 1-5 eggs have been documented elsewhere. The most frequent clutch size is 4 eggs, 3-egg clutches are common, and 5-egg clutches are rare. Second or third nesting attempts typically have a maximum of 3 eggs (Campbell et al. 1997; Cimprich et al. 2020; Graber et al. 1985; Lawrence 1953a; Tyler in Bent 1950; Williamson 1971).

The age at first breeding is 1 year and the mating system is typically monogamous (Cimprich et al. 2020). Mountjoy (1997) reported a possible case of polygyny in Nebraska. One male defended 2 distinct territories separated by the territory of another bird and unsuitable habitat. It participated in a nesting attempt on 1 territory and was associated with a female that may have had a nest in the other territory.

James (1976) studied the Red-eyed Vireo's foraging techniques in southern Ontario. It took 99% of food items from leaves and 1% from branches; 61% by hovering, 28% by stalking, and 11.5% by

hawking. Perches used for foraging were 65% unfoliated, 22% foliated, and 14% dead. Foraging occurred from the canopy to the ground, although it seldom occurred on the ground. Most (93.5%) foraging was in the periphery of trees (38.5% in the upper portion, 42% in the middle, and 13% in the lower portion), and 6.5% centrally (1.5% in the upper portion, 5.0 in the middle). Mean foraging height was 7.8 m in trees averaging 15.1 m tall. Significant and repeated use was made of the understorey for foraging. It foraged on most tree species within the territory except spruce, white pine, white cedar, and black walnut. No differences were noted in foraging heights of the sexes. Near Englehart, males foraged higher than females, but not significantly (Rice 1978c). Near Rutherglen, males foraged in the crowns of trees down to the middle branches and occasionally in the shrubbery when they accompanied females. Females foraged near or even on the ground (Lawrence 1953a). Mills (2007) studied the foraging strategies of the Red-eyed Vireo in central Ontario during the breeding season, in midsummer, and in autumn. During the breeding season, it was associated with early successional hardwoods. In midsummer, it was associated with hardwood forests and was highly associated with white birch in autumn. Foraging heights were similar during the breeding season and autumn and ranged from 4 to 14 m. It foraged predominantly by gleaning, with less frequent hovering and flycatching. In the Clay Belt of Ontario and near White River and Marathon, 91% of foraging occurred in deciduous species and 9% occurred in conifers. Foraging techniques included 70.7% aerial attacks, 14.0% hanging, and 14.1% hovering (Greenberg et al. 1999). In New Hampshire, females foraged significantly higher (12.5 m) than males (11.8 m). On leaves, males hovered more and gleaned less than females, and males foraged more on sugar maple and less on yellow birch and white ash than females (Holmes 1986). In New Hampshire, where it was sympatric with the Philadelphia Vireo, the Red-eyed Vireo was a bird of the middle and lower canopy, with the Philadelphia Vireo foraging in the upper canopy. The Red-eyed Vireo foraged in all tree species within its territory but the Philadelphia Vireo was more selective. During the late nestling and early fledgling stages, the Philadelphia Vireo foraged in the understorey and the 2 species appeared to be in direct competition. As in Ontario, the Red-eyed Vireo captured most prey from leaves in the outer periphery of the tree by hovering; 83.4% of attacks on prey were on leaves, 9.5% on bark (Robinson 1981; Robinson and Holmes 1982). Another New Hampshire study found that most prey was taken from the underside of leaves. Prey attacks in yellow birch were in proportion to caterpillar abundance, but greater than expected in beech and sugar maple (Holmes and Schultz 1988). Foraging techniques documented in Maryland, Florida, Louisiana, and Vermont were similar to those in Ontario. In Vermont, 30% of foraging was by hanging upside down to glean insects from leaves, and in Maryland and Florida a higher percentage (31%) of foraging occurred centrally near the trunk of the tree. There were significant differences in foraging heights of the sexes: mean 6-7 m for males compared with 3.7 m for females (Cimprich et al. 2020; Lent and Capen 1995; Williamson 1971). Hartung and Brawn (2005) studied Red-eyed Vireo foraging techniques in Illinois savannahs. Eighty-five percent of foraging was in oaks, 9% in hickory, 3% in black cherry, and 3% in other species, approximately in relation to tree availability. In closed-canopy forest, it exhibited strong preferences for tree species, using oak and hickory more than their availability and sugar maple, red elm, and black cherry less than their availability. Percent use of different foliage layers was 3% for 0-5 m, 20% for 6-10 m, 17% for 11-15 m, and 60% above 16 m in open-canopy forest. Percentages in closed-canopy forest were similar except that the 0-5 m layer was not used. More than 75% of foraging was

by gleaning, hovering, and hanging. Gabbe et al. (2002) examined tree-species preferences of foraging Red-eyed Vireos in Illinois floodplain forests. In order of preference, pin oak, Manitoba maple, black gum, shellbark hickory, silver maple, sycamore, green ash, and Shumard oak were used more than their availability. Species used less than their abundance, in declining order of avoidance, were pumpkin ash, blue beech, red maple, and bitternut hickory. Silver maple was one of the preferred trees, but was 18th in abundance. Pumpkin ash was strongly avoided but was the second-most abundant tree. Although it showed preferences for tree species, it was among the least selective of the bird species studied. There is 1 observation of a bird capturing prey by repeatedly diving into a shallow woodland pool from a branch 20 cm above the water (Tyler in Bent 1950).

Food delivered to nestlings at Rutherglen consisted of 65% caterpillars, 13% spiders, 16% dragonflies, 3% mayflies, and 3% flies. Similar food was presented to nestlings at Lake Opinicon, plus moths (Keast 1990; Lawrence 1953a). Chapin (1925) analyzed 569 stomachs of adults. The diet consisted of 85.28% animals and 14.72% vegetable matter. Lepidopterans constituted 32.4% of the diet; only 2.8% of these were adults. Caterpillars consumed frequently included those of sphinx moths, swallowtail butterflies, tent caterpillars, and codling moths. Other insects in the diet included 10.29% beetles (weevils and lady, leaf, scarab, click, ground, rove, metallic wood-boring, and long-horned beetles), 15.4% bugs (cicadas, scale insects, leafhoppers, and stink, squash, and assassin bugs), 10.7% hymenopterans (ants and ichneumonid wasps), 4.5% flies (crane flies and midges), and 4.6% other insects (katydids, stoneflies, and tree crickets). Other invertebrates eaten included a few small snails and 4.1% spiders. It eats fruit mostly from August on, including mulberries, barberries, currants, blackberries, elderberries, blueberries, spicebush, and Virginia creeper, plus some grass seeds and flower and leaf buds. Other studies noted its dependence on insects, particularly caterpillars, beetles, bugs, and flies early in the season, with increasing dependence on fruit as the summer passes. Other invertebrates its eats include walkingsticks, spittle bugs, treehoppers, sawflies, carpenter ants, and tussock moth egg masses. In declining sugar maple forests in Quebec, 44% of the diet was comprised of beetles (28% brown leaf weevils) and 29% was caterpillars. Near Rutherglen, nesting females fed mostly on small snails and ants. Other fruits reported in the diet include those of rough-leaved dogwood, prickly ash, black cherry, wild grape, pokeweed, multiflora rose, poison ivy, and northern arrowwood. It also consumes mountain-ash berries (personal observation). In New Hampshire and Maine and at Manitouwadge, the Red-eyed Vireo ate budworms but its abundance was not correlated with budworm abundance. It does not normally feed on low-density spruce budworm larval or pupal populations. In Maine over 2 years, spruce budworm larvae and pupae constituted 11.6% and 48% of the invertebrates it consumed (Cimprich et al. 2020; Crawford and Jennings 1989; DesGranges et al. 1987; Holt 1918; Lawrence 1953a; McIlwraith 1894; Mitchell 1952; Remsen et al. 1998; Tyler in Bent 1950; Venier et al. 2009; Williamson 1971).

The Red-eyed Vireo is one of the species most frequently parasitized by the Brown-headed Cowbird in North America. Parasitism rates vary considerably depending on the character of the landscape and relative abundance of cowbirds. In Indiana, the parasitism rate was 22% in forested landscapes and 80% in agricultural landscapes with twice as many young produced in forested areas. This appears to be true in Ontario, with higher parasitism rates in the agricultural south than

in the Canadian Shield. Of 387 Ontario nests, 154 (39.8%) were parasitized. In Waterloo Region, 10 of 13 nests (76.9%) were parasitized. Near Peterborough, 25.5% of nests were parasitized and 6% fledged only cowbirds; 23.9% were parasitized in south-central Ontario, including sites in and off the Shield. Parasitism resulted in a significant reduction in the number of vireo fledglings produced. Parasitism rates were significantly higher within 100 m of edge. Near Rutherglen, no nests were parasitized, although cowbirds were present and parasitized other species. Parasitism rates reported elsewhere are: British Columbia, 27%; Quebec, 42.7%; Michigan, 72%; Illinois, 83.3-100%; Minnesota, 13.6%; and Ohio, 42%. The Red-eyed Vireo is generally an acceptor of cowbird eggs and may continue incubation even if no vireo eggs are present. Parasitized nests may be abandoned early in the nesting cycle or if more than 1 cowbird egg is laid; it rarely buries cowbird eggs in the nest. Cowbirds may eject vireo eggs, thereby reducing vireo clutch size. Mean clutch size for unparasitized nests was 4.0 in Illinois compared with 2.5 for parasitized nests. Both vireos and cowbirds may fledge from parasitized nests, but vireo nest success in parasitized nests is less than half that of unparasitized nests. In Michigan 38-48% of parasitized nests fledged vireos, but usually only one fledged (Burke and Nol 2000; Campbell et al. 1997; Cimprich et al. 2020; Dunford et al. 2002; Ford et al. 2001; Graber et al. 1985; Hahn and Hatfield 1995; Hanski et al. 1996; Lawrence 1953a; Lowther 1985, 1997; Peck and James 1987, 1997; Rothstein 1975; Sutton 1949; Tyler in Bent 1950).

Habitat loss and degradation do not currently appear to be significant for the Red-eyed Vireo, although considerably more habitat was available prior to European settlement. Densities occasionally decline with maturation of forest as prolonged, complete canopy closure eventually eliminates the essential shrub and sapling layers. Rempel et al. (2007) modelled the potential impacts of forest management in the Ontario Boreal Forest Region when forest management guidelines for target species were applied. They predicted an increase in the Red-eyed Vireo relative to simulated natural variation in the forest. Vanderwel et al. (2007) summarized the effects of partial tree harvesting on the Red-eyed Vireo with particular reference to the Ontario portion of the Boreal Forest Region. Tree removal from forests had a negative impact on it. It experienced a 25% decrease in population when 40% of trees were removed and a 50% decrease when 67% of trees were removed. In the Canadian Shield of Ontario, there were no differences in its abundance in early successional and mid-successional clear-cuts and in similarly aged stands created by fire. There was no difference in its abundance in early successional, mid-successional, and mature stands (Zimmerling et al. 2017). In Algonquin Park, typical and intense group-selection timber harvesting had no effects on abundance of the Red-eyed Vireo, nor did single-tree selection (Jobes et al. 2004; Tozer et al. 2010). In the Carolinian Forest Region of Ontario, it was equally abundant in uncut forests, in those where selection cutting had occurred, and in woodlots that had been heavily harvested by diameter-limit cuts (Holmes et al. 2004). In Alberta, it declined significantly when 80-100% of trees in deciduous forests were removed. In Minnesota, partially harvested riparian buffers supported significantly more Red-eyed Vireos than unharvested riparian strips. A Pennsylvania study concluded that thinning of overstorey trees was deleterious because it selected areas where overstorey trees were close together and canopy closure was high. Another Pennsylvania study found that the Red-eyed Vireo declined by 72% in a forest where the density of tall shrubs increased but density of overstorey and subcanopy trees and short shrubs declined. It is tolerant of small canopy openings created by forest thinning, and usually recolonizes clear-cuts in less than 10 years. In Quebec,

densities were 30% lower in maple stands affected by die-back than in healthy stands (Bushman and Therres 1988; Cimprich et al. 2020; Darveau in Gauthier and Aubry 1996; DesGranges et al. 1987; Graber et al. 1985; Hanowski et al. 2002, 2005; Harrison et al. 2005; Litwin and Smith 1992; Morgan and Freedman 1986; Rohnke and Yahner 2008; Siepielski et al. 2001; Webb et al. 1977). In Illinois, Robinson and Robinson (1999) cut 0.02-0.4-ha openings within a 2,000-ha forest. The Red-eyed Vireo was significantly more abundant on uncut than cut ridges, but there was no significant difference in its abundance in cut and uncut areas in ravines. It was only 1 of 2 forest species that experienced a significant decline as a result of cutting. In Nova Scotia, it disappeared from forests that were clear-cut, but continued to be one of the dominant species in forests where strip-cutting occurred (Freedman et al. 1981). In Maine, it occurred in all seral stages from 2-year-old clear-cuts to dense overstoreys of conifers with an open forest floor. It was most characteristic of hardwood regeneration taller than 2 m with a well-developed but slower growing coniferous regeneration layer. These stands were 7-12 years post clear-cutting (Titterington et al. 1979). In Vermont, territories occurred in both undisturbed forest and in clear-cuts. It was the most abundant breeding bird and was associated with high abundance of sugar maple, moderate abundance of red maple, and low abundance of poplar and white pine (Lent and Capen 1995).

Forest size had a significant effect on the reproductive success of the Red-eyed Vireo in south-central Ontario. Burke and Nol (2000) examined forests ranging in size from 11.8 ha to more than 10,000 ha with core areas more than 100 m from edge of 0 ha to more than 5,000 ha. Local forest cover within a 10-km radius ranged from 13.8% to more than 80%. Nest predation rates were not affected by patch size or the amount of forest in the landscape. Failure due to nest abandonment was high: 32% in forest fragments and 6% in continuous forest. Parasitism rates did not vary with forest size or the amount of local forest, but no parasitism was observed in contiguous forest. Woodland size was the most important factor affecting reproductive success; the amount of local forest cover had no significant effect. Success was significantly higher in contiguous forest than in fragments, but birds breeding in small fragments were just as successful as those breeding in large fragments. Fecundity in forest fragments was less than half that in contiguous forest. Populations in forest fragments were sinks, with females not replacing themselves; populations in contiguous forests were close to being self-sustaining. Without constant immigration from contiguous forests, populations in fragments would become locally extirpated. Populations remained relatively constant suggesting a source-sink metapopulation.

The Red-eyed Vireo may be adversely affected by invasive shrub species such as honeysuckles and common buckthorn. In urban forests in Chicago, its abundance was positively correlated with the amount of litter but was negatively correlated with coverage by honeysuckles. Areas dominated by buckthorns had very little leaf litter (Schneider and Miller 2014).

Ford and Flaspohler (2010) studied abundance of birds in a cottage development along the Lake Superior shoreline and compared results to the undeveloped forested area across the road. The Red-eyed Vireo was significantly less abundant in the cottage development. In central Ontario, it was associated with deciduous woods with some understorey for singing posts and nest sites. Removal of shrubs and saplings associated with cottage lots could reduce habitat suitability for it

(Clark et al. 1983). In North Carolina, its abundance was negatively correlated with the number of houses and other buildings within 200 m (Lumpkin and Pearson 2013).

In New Jersey and Pennsylvania over a 15-year period, hemlock declined from 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. It responded positively to hemlock decline and increased in abundance (Toenies et al. 2019).

In Minnesota, blowdown of spruce-fir forest resulted in an 80% decline in canopy cover and a 100% increase in shrub cover. The Red-eyed Vireo was significantly more abundant in blowdown plots than control plots (Burris and Haney 2005).

Grundel and Pavlovic (2007b) studied the effects of habitat structure and fire on Indiana birds. Density of the Red-eyed Vireo increased as tree height increased from 8 m to 20 m and started to decline as trees continued to get taller. Density was greatest when fire frequency was 0 in 15 years and quickly declined to near 0 when there were 4 or more fires within 15 years. They concluded that it was strongly sensitive to fire frequency and that large changes in abundance could occur as a result of fire.

In Wisconsin and Michigan, the Red-eyed Vireo showed significant variation in numbers and densities over several years. Lowest populations were associated with dry periods, and it was one of the species most affected by drought (Blake et al. 1992).

In Alberta, the Red-eyed Vireo was equally abundant near noisy compressors and quiet well pads. It did not appear to be affected by chronic noise (Bayne et al. 2008).

In Alberta, the Red-eyed Vireo was more abundant in forest interior than near energy sector disturbances. It was 14-35% less abundant along seismic lines, 26-32% less abundant along pipelines, and 21-66% less abundant at well pads compared with adjacent forest interior (Bayne et al. 2016). Farwell et al. (2019) examined its response to shale gas infrastructure (well pads, access roads, and pipelines) in a contiguous forest in West Virginia. It was adversely affected and significantly more abundant with increasing distance from infrastructure.

In Delaware, there was no difference in abundance of the Red-eyed Vireo in areas supporting low, moderate, and high density of white-tailed deer (Tymkiw et al. 2013).

Status

The Red-eyed Vireo is one of the most abundant breeding birds in Ontario. McIlwraith (1894) termed it a very common summer resident. Baillie and Harrington (1937) stated that it bred throughout the province from the extreme south north to Lake of the Woods, Kapuskasing, and Lake Abitibi. North of this, it was very common along the Mattagami and Moose rivers, and they concluded that it probably bred north to southern James Bay. The first atlas demonstrated that it was abundant throughout the province, with probable or confirmed nesting as far north as Fort Albany and Big Trout Lake (James in Cadman et al. 1987). James (1991) considered it an abundant summer resident north to Big Trout Lake and Attawapiskat and probably to Fort Severn along major rivers in the west. In the Walsingham Forest in Norfolk County, it was the most abundant species, representing 14.75%

of all records. It and the Ovenbird accounted for over 75% of records, typical of this region and northeastern North America in general (McCracken et al. 1998).

The second atlas demonstrated that the range of the Red-eyed Vireo had not changed since the first atlas. Its probability of observation increased significantly province-wide and in the Canadian Shield. It was most abundant in the Shield in the Great Lakes–St. Lawrence Forest Region. There were also locally high concentrations on the Bruce Peninsula and on eastern Manitoulin Island. Numbers declined gradually northward, possibly due to greater abundance of coniferous cover, and south of the Shield due to habitat fragmentation by agriculture and urbanization (James in Cadman et al. 2007).

Long-term (1970-2021) population trends determined from the Breeding Bird Survey indicate annual increases of 1.08% in Canada and 0.85% in Ontario. The short-term (2011-21) trends were annual increases of 1.94% in Canada and 2.06% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young can only fly 5-10 m when they leave the nest and it is unknown when they become proficient fliers. Young may remain with the parents 25 days after fledging; 1 family remained together until autumn migration (Barlow and Rice 1977; Cimprich et al. 2020).

In Ohio, adult and juvenile Red-eyed Vireos made extensive use of densely regenerating clear-cuts during the postbreeding period. The most important factors determining its presence in clear-cuts, in descending order of importance, were abundance of low vegetation, presence of canopy and low vegetation, and amount of canopy. Early successional habitats may be important for it after breeding because they provide dense cover and abundant food (Vitz and Rodewald 2006, 2007). McDermott and Wood (2010) examined its abundance in West Virginia clear-cuts in varying stages of succession during the postbreeding period. It was positively associated with vertical complexity of the habitat and richness of arthropod abundance, but was negatively associated with basal area and understorey stem density. In Minnesota, Streby et al. (2011b) captured only 5 Red-eyed Vireos during the breeding season in regenerating clear-cuts, but caught 378 adults and 46 fledglings during the postbreeding period. In Missouri, the number of adult and juvenile Red-eyed Vireos in 3-4- and 9-year-old clear-cuts increased during the postfledging period. They were more common in early successional habitat than in mature or riparian forest (Pagen et al. 2000). Porneluzi et al. (2014) netted birds during the postfledging period in a Missouri oak-pine-hickory forest 2-15 years after it was clear-cut. The Red-eyed Vireo was the most abundant species captured. There was no significant change in its abundance during the sampling period. In Virginia and West Virginia, it was 1 of the 6 forest-breeding species that was most frequently captured in regenerating clear-cuts during the postfledging period. Four adult males captured in the clear-cut area during the postfledging period were located in forest plots during the breeding season in subsequent years. Their territories averaged 235 m (range 101-358 m) from the mist net where they were originally captured. Two of these were originally captured with dependent young during the postfledging period. This suggests that some birds move as family groups to early successional areas after young leave the nest. In Pennsylvania during the postfledging period, Stoleson (2013) captured 46 adults

and 19 juveniles in clear-cuts compared with 0 adult and 5 juveniles in mature forest with a dense understorey.

In Missouri, Burke et al. (2017) radiotracked juvenile Red-eyed Vireos that had been captured in 3-6-year-old deciduous clear-cuts. The mean distance travelled between relocations was 434 m (range 15.5-4,032.6 m). Forested areas were selected in addition to clear-cuts. The probability of use was greater for small-tree (52%) than pole (32%) or sawtimber (16%) stands. Probability of use was greater for clear-cuts (53%) than partial cuts (30%) or unharvested stands (17%). The bird that moved the greatest distance used locations that were split equally between pole-sized partial cuts and unharvested sawtimber stands; it appeared to alternate between these habitats in subsequent moves. It disappeared for 3 days then reappeared in a partial cut more than 4 km from any previous location. This vireo appears to make use of both early successional habitats and mature forests during the postfledging period.

MIGRATION

Migration is along a broad front and occurs at night (Cimprich et al. 2020). Birds mostly arrive in the province in mid-May, rarely by late April. The Red-eyed Vireo does not become common until the last week of May, and passage continues through the first week of June (James 1991). At Rutherglen, birds remained within the territory until they flew south. Adults migrate earlier in autumn, and there is no difference in timing by the sexes. Juveniles migrate over a much longer period than adults. At Rutherglen, most left in the first week of September. Near Kingston, migration begins in early August, but the main passage is in late August and early September (Cimprich et al. 2020; Lawrence 1953a; Weir 2008). During autumn migration at Long Point and 2 other locations in eastern North America, adults migrated significantly earlier than juveniles. Median passage dates for the 2 age classes differed by 21 days at Long Point (Woodrey and Chandler 1997).

During migration, the Red-eyed Vireo uses a wider variety of habitats than during the breeding season, but it still prefers deciduous cover. In addition to deciduous and mixed woods, it may be found in city parks, suburban and rural areas, open areas with scattered trees, along forest edges, and in deciduous shrubs. In British Columbia, it prefers groves of deciduous trees and shrubs in valley bottoms and riparian habitats, and avoids areas of continuous forest cover. It appears to have slightly different habitat preferences in spring than in autumn. In Illinois, it was much more frequent in forest interior than on edges in spring, but more frequent on forest edge in autumn. Preferences for forest edge during autumn were also demonstrated in Pennsylvania, Maryland, and Florida. In Pennsylvania, it occurred during autumn migration in all habitats studied. It was most abundant in forest edge, followed by forest-agricultural edge, forest interior, suburban forest, pole-stage forest, and shrub-sapling areas. Numbers were significantly lower in the latter 2 habitats. Follow-up work by the same authors found that it was most abundant in forest-agricultural edges and significantly more abundant than in forest interior and suburban forests. Abundance in pole-stage and shrub-sapling stage forests was intermediate. Another Pennsylvania study found that mist nets in shrubby areas caught Red-eyed Vireos at a significantly higher rate than those in forest, although it was observed on transects through forest significantly more than in shrub habitat. On 2 islands in the Gulf of Maine, it was significantly more common on an island dominated by trees than one dominated by shrubs during both spring and autumn migration. In Minnesota and Wisconsin, it was

more abundant in upland than floodplain forests during spring migration, but not significantly (Campbell et al. 1997; Cimprich et al. 2020; Graber et al. 1985; Kirsch et al. 2013; Rodewald and Brittingham 2002, 2004; Smith and Hatch 2008; Suomala et al. 2010; Williamson 1971).

The Red-eyed Vireo is less specific in its foraging techniques and substrates during migration than during the breeding season. It may forage on branches as much as leaves, often hangs upside down to capture prey, and forages at all heights in the vegetation and equally on the inner, middle, and outer portions of trees. Mean foraging height is lower than in the breeding season, averaging 4.4 m in Maryland and Florida, with a range of 0.9-16.8 m (Cimprich et al. 2020; Loria and Moore 1990; Rodewald and Brittingham 2002; Tyler in Bent 1950; Williamson 1971). Keast (1980) quantified the foraging substrates of the Red-eyed Vireo during autumn migration at Prince Edward Point. Fifty-one percent of foraging occurred on outer leaves of trees, 20% on sapling foliage, 15% on outer branches, 10% on twigs and inner leaves, and 5% on tree trunks. It did not forage aerially, on inner tree branches, on sapling branches, on low shrubs, or on the ground. Birds killed by striking an adjacent hydro tower had fed on plant material, snails, and beetles 12-16 mm long.

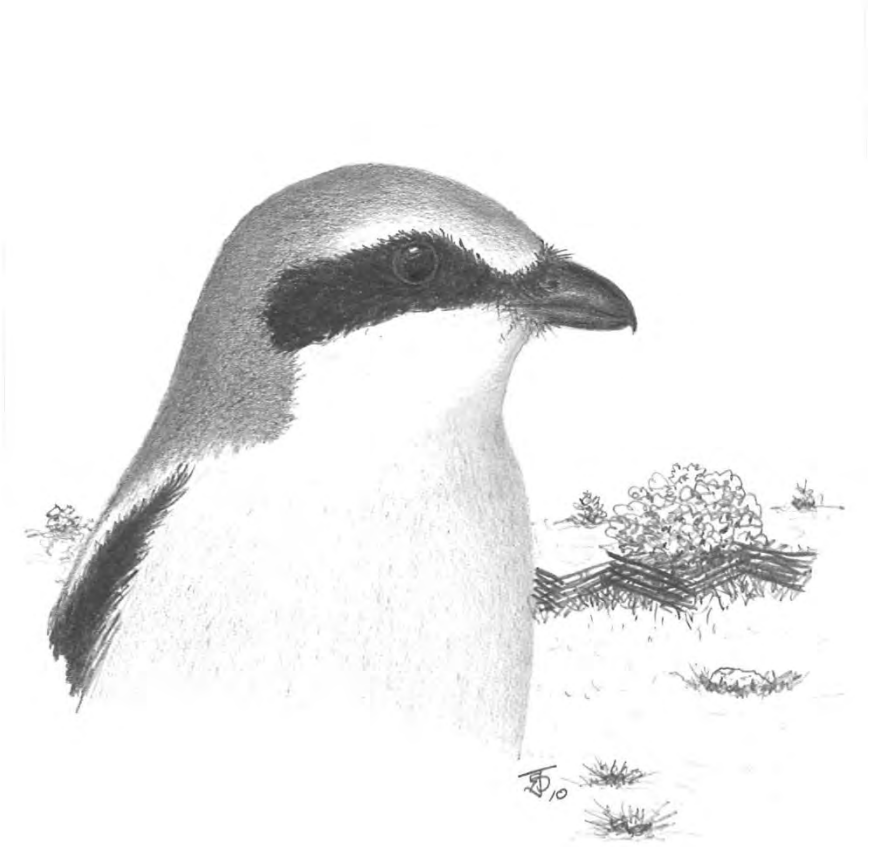
The Red-eyed Vireo is one of the most common species killed at television towers and other tall structures during migration. Between 1972 and 1982, 2,182 were killed at the Lennox chimneys near Kingston, with over 500 on 2 separate nights (Cimprich et al. 2020; Graber et al. 1985; Weir 2008).

Smith and Paton (2011) analyzed 48 years of banding data from a Rhode Island station and found that the Red-eyed Vireo migrated south significantly later in recent years. The delay in migration was attributed to climate change. In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season for 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming in the second period. The Red-eyed Vireo arrived significantly earlier during the second period but there were no significant differences in its autumn departure dates or length of the breeding season.

The Red-eyed Vireo is a common migrant in Ontario (James 1991).

Loggerhead Shrike

Lanius ludovicianus



BREEDING SEASON

Habitat Requirements

In Ontario, the primary breeding habitat for the Loggerhead Shrike is sparsely treed alvars in Carden Township and near Napanee and Smiths Falls. Formerly, when it was more abundant, it also nested in hedgerows, along roadsides, and in fields, pastures, and old orchards. Single nests were reported in a rural schoolyard, on a golf course, and in a mixed-wood swamp near some buildings (Peck and James 1987).

Habitat in the core Ontario breeding areas is different than elsewhere in its Ontario and Quebec range, and may be superior. These are limestone plains adjacent to the Canadian Shield that are flat or gently rolling and mostly open. They occur in rural areas with very low human populations and limited cultivation. Breeding sites within the core area are extensive fields of rough pasture with sparse grass on thin soils. Occupied territories near Lindsay were characterized by grazed pasture

with at least 20 2-m-tall hawthorns per 10 ha, suitable hunting perches, and a minimum of human disturbance. Nearby sites lacking one or more of these characteristics were unoccupied, and this appears to be the case across Canada. Of 167 Ontario nests, over 87% of habitat descriptions were of roadsides, farmland, hedgerows, pastures, and hawthorn meadows. Preferred ground cover in Ontario appears to be pasture, frequently with emergent stones and stone piles. Viper's bugloss is abundant in core areas and considered a good indicator of shrike habitat. Usually herbaceous hedgerows are present as are scattered shrubs such as hawthorns near Lindsay and red cedar and hawthorn near Napanee (Cadman 1985, 1990; Norris 1992).

Chabot et al. (2001b) detailed habitat in Ontario and Quebec, although there were few Quebec records. Fifty-one nests (63.8%) were in actively grazed pastures with scattered trees and shrubs, 18 (22.5%) in idle pastures, 7 (8.8%) in hayfields, 4 (5%) in old fields, and 0 in row crops. Vegetation height at nest sites ranged from 30.3 to 36.7 cm and was not significantly different at apparently suitable unoccupied sites (24.6-34.9 cm). They examined several other habitat parameters and found no significant differences among occupied and apparently suitable unoccupied sites. This suggested random habitat selection within a core breeding site except for selection of the nest tree. Habitat parameters at nest sites were: 213-364 shrubs shorter than 1 m per ha, 197-299 shrubs taller than 1 m per ha, average of 96.0-137.8 m from a road, 245.9-344.9 m to a house, and 310.0-608.6 m to the nearest source of disturbance (railway tracks, gravel pit, quarry). Within the Ontario core areas, hedgerows are scarce, although they are preferred habitat in most areas. In Quebec, 86% of nests were in hedgerows compared with 13% in Ontario. Chabot et al. (2001a) characterized habitat at Ontario core areas as unimproved pasture on limestone plain with scattered hawthorns and red cedars. Pastures were dominated by poverty grass, Canada and Kentucky bluegrass, foxtails, timothy, and sedges. Chabot et al. (2001b) found that grazers were important in maintaining habitat, with 86% of nest sites in active and idle pastures. Grazers create a mosaic of tall and short grasses that provide diverse habitats for insects: tall grasses around droppings and short grasses in grazed areas. There was no evidence that the Loggerhead Shrike actively nested near roads as has been reported elsewhere. Habitat suitability is affected by the amount of habitat around a nest site and amount of useable habitat within a core area. In the late 19th century, it was common in southern Ontario away from the core breeding areas. Habitat included roadsides in agricultural areas, hedgerows, pastures, and railway rights-of-way (McIlwraith 1894). Prior to settlement, it was probably confined to the existing core areas and prairies and savannahs in the southwestern portion of the province with

remnants eastward to Rice Lake. Most prairie and savannah habitat has since been destroyed or reduced to remnant fragments too small to support shrikes (Austen et al. 1994).

The Ontario limestone alvars are the prime breeding habitat for the Loggerhead Shrike, supporting the largest and most consistent population. This habitat is unique to the range of the eastern population. There are numerous other descriptions of shrike breeding habitat, but these tend to be either for the western population or for suboptimal habitat for the eastern population. Nonetheless, there are many similarities in habitat requirements reported from elsewhere. It prefers open areas with short vegetation such as pastures with fencerows, old orchards, mowed roadsides (particularly along gravel roads), cemeteries, golf courses, edges of agricultural fields, riparian areas, shelterbelts, and very open woodlands. In most areas, its abundance is correlated with the amount of pastureland; almost all nest sites in Illinois, New York, and Missouri were associated with pasture. In Indiana, it occurs only where Amish farmers have retained fencerows. It prefers areas of short grasses, typically 15-35 cm tall, where there are several suitable perches for hunting and an abundance of insects. Territories in the eastern states include more land in pasture and less in old fields than expected, and have greater lengths of fences, utility wires, and rights-of-way. In Kansas, it nested in habitat that may be similar to historical southwestern Ontario. It was positively associated with savannah habitat at the landscape level. Its presence was correlated with undisturbed tallgrass prairie, increasing cover of standing dead vegetation, increasing litter depth, and decreasing cover of live grasses and forbs within 10 cm of the ground. In North Carolina, preferred nest sites had low variation in ground vegetation but high variation in vegetation height, with few trees and shrubs. In western Canada, it prefers untilled prairie as well as land seeded with introduced grasses and legumes. It has also nested in isolated trees in farmyards and on rural and suburban lawns. Near Winnipeg, most nests were in areas where a mixture of mowed yards or parks, small pastures, idle grassy areas, and roadside ditches occurred in close proximity, and over half of nests were in ornamental spruce trees. In another area of Manitoba, it preferred to nest in single willows or clumps of willows or other deciduous trees. These areas contained significantly more pasture, fewer trees, and longer fencerows than random areas. In Alberta, it was more common in large blocks containing more than 100 clusters of trees and shrubs than it was in blocks containing 50 or fewer clusters (Bent 1950; Bjorge and Prescott 1996; Bohall-Wood 1987; Burton 1989, 1990; Dechant et al. 2002d; De Geus and Best 1991; Esely and Bollinger 2001; Fitch 1958; Froehly et al. 2020; Gawlik and Bildstein 1990; Hands et al. 1989a; Kirk et al. 2015; Kridelbaugh 1983; Michaels and Cully 1998; Novak 1986; Robert et al. in Gauthier and Aubry 1996; Smith and Kruse 1992; Sprunt in Bent 1950; Telfer 1992; Telfer et al. 1992; Yosef 2020).

The Loggerhead Shrike also nests in urban areas in Florida, Louisiana, South Carolina, Alabama, Georgia, and Texas. It nests in areas where mowing and other human activities create a mix of short grasses and bare ground. In a South Carolina urban area, territories were most often in less developed grassy parts of commercial or industrial parks or in intensive developments such as mall parking lots as long as there was a grassy verge nearby. These areas were located along a highway corridor. Shrikes nested most often in trees and shrubs lining or within parking lots associated with stores, businesses, or a large mall, but also in a cemetery, on college campuses, and on a golf course. These shrikes were nonmigratory and maintained their territories year round (Maddox and Hill 2024).

Most Ontario nests were in deciduous trees, shrubs, and vines (87.9%) and less frequently in conifers. Hawthorn was greatly preferred, being selected more than all other species combined (74.5% of nests). Nests were also in apple (9.2%), spruce (5.9%), cedar (5.2%), and grape vines (5.2%). Most were in crotches at the trunk of trees and shrubs but a few were on horizontal branches as far as 1.8 m from the trunk. Usually nests were placed centrally in a tree or shrub, occasionally near the top. Nests were 0.3-12 m from the ground with most 1.3-3 m up. A new nest is usually built each year, but 1 nest was used in 2 years (Peck and James 1987). In a more recent Ontario study, Chabot et al. (2001b) reported 37 nests in hawthorn, 29 in red cedar, 5 in white cedar, and 1 in buckthorn, with most nests in the Napanee Plain in red cedars. Eighty-eight percent of nest trees were isolated and 8% were in hedgerows. Hawthorns selected for nesting had significantly less canopy concealment than unused hawthorns. Selected red cedars were significantly taller than the nearest-neighbouring trees.

Throughout its range, the Loggerhead Shrike prefers to nest in thorny trees and shrubs. In some areas it prefers isolated trees and shrubs for nesting. In other areas it has a greater propensity to nest in hedgerows; this may be a function of habitat availability. Hawthorn and red cedar are preferred where available, but it may use other thorny species further south such as Osage orange, honey locust, Russian olive, plum, crabapple, or rose bushes. Other tree and shrub species it has nested in include maple, sassafras, oak, mulberry, elm, honeysuckle, spruce, pine, apple, pear, Virginia creeper, willow, poplar, Manitoba maple, chokecherry, lilac, black cherry, cottonwood, and black locust. In the southeastern United States, it regularly nests high on limbs of mature pines in pine savannahs rather than in shrubs (Askins et al. 2007). Unusual nest locations include in Russian thistle, amaranths, and a pile of old chain-link fencing. Other anthropogenic nesting locations include on a portable fence corral, on a fence, on a utility pole, on a cable in a solar farm, on the side of a building, and under a raised house. Nests have been found 0.3-15 m from the ground, but typically 1-3 or 4 m up. Since it tends to nest centrally in the nest tree or shrub, average nest heights vary significantly geographically depending on the size of suitable woody vegetation available. Average nest height in Missouri was only 0.8 m compared with 4.4 m in South Carolina. First nests are significantly lower than subsequent nests in the same season. It occasionally reuses old nests or builds on top of them, or takes materials from old nests to build a new nest. It may also build on top of other species' nests including those of Black-billed Magpie, Brown Thrasher, Northern Mockingbird, Gray Catbird, and Common Grackle (Bent 1950; Burton 1989; Davidson 1988; Esely and Bollinger 2001; Gawlik and Bildstein 1990; Gawlik et al. 1991; Graber et al. 1973; Haas and Sloane 1989; Kiliaan 1996; Kridelbaugh 1983; Miller 1931; Robert et al. n.d., Robert et al. in Gauthier and Aubry 1996; Sanders et al. 2018; Scott and Morrison 1990; Sprunt in Bent 1950; Todaro et al. 2025; Tyler 1992; Woods and Cade 1996; Yosef 1994b, 2020).

The territory includes all areas used for foraging, mating, and raising young. Despite the Loggerhead Shrike's territoriality, it often occurs in clusters rather than being evenly distributed over what appears to be suitable habitat. It maintains a much larger territory than other insectivorous birds of similar size. Territories reported in Ontario were approximately 10 ha in area, with some as small as 7.5 ha, although Chabot (in Cadman et al. 2007) suggested that Ontario territories may be as large as 50 ha. Similar-sized territories were reported from Kansas. Other territory sizes were an

average of 13.4 ha in Alberta (range 6.5-23.5 ha), an average of 8.5 ha in another Alberta study; 34 ha on a California island, average of 8.5 ha on the California mainland (range 4.4-16.0 ha), average of 4.6 ha in Missouri (range 1.0-12.1 ha), average of 7.5 ha in New York (range 5.7-9.3 ha), average of 8.35 ha in Florida (range 3-9.6 ha), and 8.9 and 25 ha in Idaho. Territory size is highly variable depending on habitat quality, presence of barriers between pairs, shrike density, and period of the nesting season. Pairs nesting in areas with sparse tree cover may have territories 2-3 times larger than birds nesting in moderately treed areas. Perch density is inversely related to territory size and birds with more available perches tend to be in better nutritional condition. In Florida, artificial perches were added to shrike territories. Initially territories averaged 10.1 ha (range 4.7-17.5 ha). After manipulation, the same territories shrank to an average of 2.3 ha, a reduction of 76.6%. Territory sizes did not change when supplemental perches were provided in California, but shrikes shifted their focal foraging sites to areas where perches were installed. In this population, home ranges of shrikes were more than 100 m apart, so there was no requirement to reduce territory size to minimize territorial conflicts. Territories may be smaller when there are barriers between neighbours such as a road or a hill that obstructs vision. Territory sizes also tend to be smaller with higher density of shrikes. In Missouri, territories were 8 ha during incubation, 3 ha during the nestling period, and 5 ha during the fledging period. After fledging, the parents cease defending the nest site and defend an area around the young. In Alberta, nests have been observed as close together as 80 m (Bjorge and Prescott 1996; Burton 1989; Cadman 1985; Davidson 1988; Dechant et al. 2002d; Fitch 1958; Hands et al. 1989a; Lymn et al. 2006; Robert et al. in Gauthier and Aubry 1996: Scott and Morrison 1990; Yosef 2020; Yosef and Grubb 1994).

Natal philopatry is very low. Highest reported rates have been from captive-bred and released birds in Ontario where 3.6% returned; in 2008, the Ontario return rate was 6.4%. In North Dakota, 2 of 243 birds (0.8%) banded as nestlings or fledglings returned to nest 3.2 and 3.8 km from their natal site. In Alberta, 3 of 249 nestlings (1.2%) were reencountered within 4 km; over 6 years 2.7% of 589 nestlings were recaptured. In southwestern Manitoba, 27 of 3,176 nestlings (0.85%) returned the year after banding and 2.3% returned over the 6-year study period. In Minnesota, 0 of 196 nestlings returned to the natal area and 1% of Indiana young returned. Adult site fidelity is also low. Females may not be faithful to a nesting territory within a breeding season, occasionally deserting a territory and switching mates. In Alberta, 38% of males and 27% of females nested within 4 km of the previous year's territory; in Manitoba 23% of adult males and 9% of adult females returned. In Indiana, 55% of male adults returned compared with 19% for females. Of birds that returned in Ontario, all returned to the same core area. Two of 9 adults (22.2%) returned to their previous territories; some females moved as far as 8-25 km. In 2002, movement of birds between the Carden and Napanee areas was confirmed. Two nestlings banded in 2001 on the Carden Plain were observed on the Napanee Plain in 2002. In 2008, virtually all Ontario adults were captured and it was determined that several previously banded birds had lost their bands. Consequently, return rates of adults were probably underestimated. In Manitoba, 7.0% of adults that raised young the previous year returned to the same territory; 2.3% of unsuccessful birds returned. Mean dispersal distance for 15 males was 0.85 km compared with 5 km for 4 females. Territories are more often reoccupied by new birds than the previous occupants. Earlier studies with unbanded birds concluded that site fidelity was high, but this is incorrect. It has been suggested that low philopatry increases

vulnerability to extirpation once regional populations are broken into isolated sites as a result of habitat fragmentation (Burton 1990; Collister and De Smet 1997; Dechant et al. 2002d; Grooms 2001; Haas 1995; Haas and Sloane 1989; Hands et al. 1989a; Kridelbaugh 1983; Pittaway and Iron 2003; Scott and Morrison 1990; Stauffer 2007; Steiner and Williams 2008; Williams and Steiner 2008; Yosef 1994a, 2020).

Limiting Factors

Eggs have been found in Ontario nests from the beginning of April until very early August with most present in the last 3 weeks of May (Peck and James 1987). The female takes 5-11 days to build the nest. After the nest is complete, another 9-18 days may elapse before any eggs are laid. Eggs are laid at the rate of 1 a day, although a day may occasionally be skipped. Incubation usually starts with the penultimate egg. The incubation period at 4 Ontario nests was 12-16 days. Over 2 years in Alberta, the mean incubation period was 16.46 and 16.75 days. Elsewhere, incubation periods of 15-20 days have been reported with the mean approximately 16 days. Hatching is asynchronous over 24-36 hours in early nests, but as long as 60-70 hours in late-season nests. Young fledge when they are 16-21 days old. Renesting usually occurs within a week after loss. In the case of second broods, the first egg of the second clutch is laid 1-3 weeks after the first brood fledges (Collister and Wilson 2007; Gawlik and Bildstein 1990; Gawlik et al. 1991; Graber et al. 1973; Haas 1995; Hands et al. 1989a; Kingery 1989; Kridelbaugh 1983; Miller 1931; Scott and Morrison 1990; S.M. Smith 1972; Tyler 1992; Woods and Cade 1996; Yosef 2020).

One or 2 broods may be raised in a year, with the incidence of double-brooding increasing southward. Two probable double broods were previously reported in Ontario. The birds were unmarked, so second broods could not be positively confirmed. The difficulty in confirming double brooding is that females may desert their first family and move elsewhere to raise a second brood with a different male. Chabot et al. (2001b) reported 1 pair double brooding in Ontario in 1991 and 3 pairs in 1992, but it was unknown if double brooding was successful. In Illinois, no instances of double brooding were known. About a third of females were thought to be double brooded in Indiana. Other reported rates of double broods are 0% in Idaho and Colorado, 10.4% in Minnesota, 8% in South Carolina, 18% in Missouri, 7.7-27% over 4 years in Oklahoma, 15% in Alabama, and 96% in Florida. Suggestions of 3 broods in the south have not been confirmed and are probably incorrect. Renesting is typical after nest loss, usually in the same territory within a few 100 metres of the first nest. One pair laid 5 clutches before it successfully raised a brood. Clutches of 4-7 eggs have been reported in Ontario, with most containing 5 or 6 eggs. Overall, clutches of 1-9 eggs have been reported, but clutches of 1-3 eggs and 8 and 9 eggs are very rare. Most clutches contain 5 or 6 eggs; about 25% of clutches are of 4 or 7 eggs. Average clutch size increases northward and there is no difference in clutch sizes between first and subsequent nests in a season (Bent 1950; Brooks and Temple 1990; Burton 1989, 1990; Cadman 1985; Gawlik and Bildstein 1990; Graber et al. 1973; Hands et al. 1989a; Kridelbaugh 1983; Miller 1931; Peck and James 1987, 1997; Pittaway 1993; Scott and Morrison 1990; Sprunt in Bent 1950; Tyler 1992; Woods and Cade 1996; Yosef 2020).

The age at first breeding is 1 year. Territories that are abandoned during a year are usually not occupied until the following year suggesting that floaters are rare. Some birds may maintain territories for 1 or 2 years without attracting a mate, also indicating there are few floaters. The

Loggerhead Shrike is typically monogamous, but polygyny occurs rarely. In Florida, there were no significant differences in territory sizes or prey fed to young among monogamous and polygynous birds, but prey delivery rate was greater by polygynous males. The greatest difference was that polygynous males fledged almost twice as many young. There were 2 strategies in polygynous matings. In the first, the second female started laying 10-12 days after young at the first female's nest hatched. The male raised the first brood and fed both females and their young. In the second strategy, the second female laid after the first brood fledged and the male provided care for her fledglings for several weeks. Females display low mate fidelity and may desert their first mate for a second mate (Cadman 1985; Collister and De Smet 1997; Dechant et al. 2002d; Scott and Morrison 1990; Yosef 1992a, 2020).

The Loggerhead Shrike feeds in open landscapes characterized by well-spaced, usually spiny trees, and shrubs in areas with short grasses or bare ground or rock. It is a sit-and-wait predator, hunting from a perch and diving at prey. About 80% of attacks occur on or near the ground and 20% in the air, with most aerial attacks directed toward small- to medium-sized insects. Hunting perches are usually small shrubs and trees as well as anthropogenic features such as fence posts and utility wires and poles. Perch heights are usually low, but highly variable depending on availability. In Florida, most perches were lower than 5.5 m. They averaged 2.1 m in California, with almost half under a metre high. In Texas, perch heights ranged from 0.9 to 7.5 m, and shrikes foraged from taller trees than expected by chance. It may hunt within 15 m of the nest, about 150 m away, or as far away as 0.9 km, reflecting perch availability rather than preference. In addition to foraging from perches, it may forage opportunistically in recently plowed fields and on mowed lawns. It may also follow hawks and visit their perches to obtain meat scraps. Small prey may be consumed on site or transported and impaled on a thorn or barbed-wire fence; larger prey is always impaled. Due to its lack of talons, it has difficulty handling large prey; impaling it facilitates tearing it apart. Impaled prey also provides a cache of food for the female. Much of the food the female feeds nestlings is prey previously impaled by the male. The female often feeds from the cache during incubation breaks. Chemically noxious prey, such as monarch butterflies, may be left hanging for about 3 days then consumed after the chemicals have degraded. Young are first successful at wedging prey in a tree at age 28-30 days and at impaling at age 33-35 days (Anderson 1976; Applegate 1977; Becker et al. 2009; Bohall-Wood 1987; Busbee 1976; Craig 1978; Davidson 1988; Gawlik and Bildstein 1990; Gawlik et al. 1991; Graber et al. 1973; Hands et al. 1989a; Morrison 1980; Scott and Morrison 1990; S.M. Smith 1972; Telfer 1992; Yosef 2020).

The Loggerhead Shrike is a highly opportunistic feeder, preying on whatever is most abundant. The diet changes seasonally and even at different times of the day. When a given prey is abundant, it may feed exclusively on it until it is depleted. Therefore, diet analyses vary considerably in their conclusions and results also vary depending on study methods. Studies that examine stomach contents and prey delivered to nestlings are most accurate. Those that rely on observations of impaled prey are biased toward larger items which are frequently atypical of the diet. Overall, invertebrates are most important in its diet, and most of these are insects. Crickets, grasshoppers (mostly short-horned), and beetles are staples with important beetles being weevils, and scarab, ground, June, carrion, click, and long-horned beetles. Earwigs, hymenopterans (ants, bees, and

wasps), and moths and butterflies are also important in the diet. Other insects it takes infrequently are preying mantises, flies, ant-lions, mayflies, dragonflies, walkingsticks, cockroaches, bugs, and cicadas. It seldom eats spiders, centipedes, millipedes, earthworms, isopods, crayfish, and snails. Although few vertebrates are consumed, they are important from a biomass perspective, especially early in the spring before insects are abundant. Most vertebrates eaten are small mammals, particularly meadow voles. Of lesser importance are salamanders, small frogs, lizards, snakes (especially the common garter snake), and small birds. It attacks birds that are small in size such as sparrows and warblers and nestlings are preferred. It has trouble carrying prey as large as adult sparrows and House Finches. It has been documented killing birds as large as cardinals and Mourning Doves, but these are atypical prey. Unusual prey items include bats, small turtles, dried-up small fish, and cattle ticks. It takes prey ranging in size from 5-mm-long insects to mammals or snakes weighing as much as 25 g. It appears to prefer prey 16-26 mm long. A laboratory study determined that it preferred mice that weighed less than 13 g and most selected were less than 8.5 g. Occasionally it feeds on carrion. Habitat quality may have a direct impact on birds' diet and condition. In Florida, birds nesting in pastures were in better condition than those in old fields, and much better than those in citrus groves (Balda 1965; Bent 1950; Burton 1989, 1990; Craig 1978; Davidson 1988; Dirck 1986; Eells 1962; Gawlik et al. 1991; Graber et al. 1973; Grubb and Yosef 1994; Ingold and Ingold 1987; Johns and Johns 2001; Johnson 1949; Knowlton and Harmston 1944; Leonard 1992; McIlwraith 1894; Moriarity and Pfannmuller 1988; Morrison 1980; Reynolds 1979; Scott and Morrison 1990; Slack 1975; S.M. Smith 1972; Sprunt in Bent 1950; Wayne 1921; Yosef 2020). Beal and McAtee (1912) examined the contents of 212 Loggerhead Shrike stomachs: 124 from the western United States and 88 from the east. The diet of western birds was composed of 2.5% vegetable matter but no vegetable matter was consumed by eastern birds. Western birds consumed 83% insects, 12% vertebrates, and 2% spiders and snails; eastern birds ate 68% insects, 28% vertebrates, and 4% spiders. The most abundant prey items consisted of grasshoppers and crickets, which comprised 43% and 39% of the stomach contents of western and eastern birds, respectively. They were eaten every month of the year and constituted nearly 70% of the diet in August and September. Beetles were second in importance of the insects consumed (16% of the diet for western birds and somewhat more for eastern birds). Most were ground and carrion beetles, but smaller beetles such as leaf beetles and weevils were also eaten. Ants and wasps constituted 11% of the diet of western birds and 3% of the diet of eastern birds. Moths and caterpillars comprised 7% of the diet of western birds and 4% of the diet of eastern birds. Bugs and flies constituted 5% of the diet, including robber flies. Small quantities of spiders, snails, and small crustaceans were also consumed. The vertebrates included mammals, birds, and reptiles, with mammals most prominent in the diet, predominantly mice but some shrews. Few birds were consumed and the reptiles were mostly lizards consumed by western birds.

Parasitism by the Brown-headed Cowbird is extremely rare and has not been documented in Ontario. The Loggerhead Shrike is a rejecter of cowbird eggs. DeGeus and Best (1991) found 3 parasitized nests in Iowa and 2 of 1,661 Manitoba nests (0.1%) were parasitized (Dechant et al. 2002d), the only known incidences. Parasitism did not appear to affect shrike productivity. In 1 nest, it is likely that a cowbird fledged.

Habitat loss and degradation are significant factors throughout the Loggerhead Shrike's range. In many areas, including Ontario, it appears to be retracting to its presettlement range. Originally, it was probably restricted to prairies, savannahs, and alvars. These habitats were not surveyed by early Ontario ornithologists who assumed it was a recent arrival as a breeding bird. Once extensive forested areas were cleared, much new habitat was created for it. Early farming practices were beneficial, such as having extensive pasturelands and fallow fields and maintaining hedgerows around small fields. As farming evolved, the amount of pasture declined and hedgerows were removed to create larger fields. Canadian regions experiencing the most severe shrike decline had a 39% decline in the amount of unimproved pasture between 1946 and 1986 compared with 12% in areas that still retain substantial populations. In Ontario, there were approximately 1.2 million ha of pastureland in 1921 compared with 0.4 million in 1986. The original forest cover that was unsuitable became prime habitat for 70-100 years then once again became unsuitable as farming practices intensified or land was converted to urban areas. Roadsides were formerly sprayed with herbicides to kill woody growth, removing potential nesting sites and hunting perches. Some areas of marginal farmland were planted to trees or allowed to revert to forest. Natural succession is a problem in one of the core Ontario breeding areas. In many states and provinces where declines are most significant, it was probably absent prior to settlement. In these areas and Ontario, populations appear to be reverting to historical distribution. Declines due in part to loss of breeding habitat are also occurring in regions where it always occurred (Burton 1993; Cade and Woods 1997; Cadman 1985, 1990; Coffin and Pfannmuller 1988; Graber et al. 1973; Hands et al. 1989a; Michaels and Cully 1998; Norris 1992; Robert and Laporte 1991; Robert et al. n.d.; Robert et al. in Gauthier and Aubry 1996; Telfer 1992; Yosef 1994a, 2020; Yosef and Grubb 1994).

Scarcity of hunting perches within otherwise suitable breeding habitat appears to be a limiting factor. When artificial perches were added to Florida territories, the size of territories was reduced by an average of 76.6%. Where perches were added, 60% of nests were successful and fledged an average of 3.1 young per nest. Control territories had a 40% success rate and an average of 1.8 fledglings per nest. Yosef and Grubb (1994) concluded that perches are very important and that much of the defended area is unusable habitat. Chabot et al. (2001b) concluded that addition of perches to the core Ontario breeding areas would be beneficial.

Much suitable breeding habitat remains unoccupied indicating that other factors are contributing to the Loggerhead Shrike's decline. Loss and degradation of wintering habitat may be a significant limiting factor. Similar habitat is preferred in winter as during the breeding season, and wintering habitat has declined substantially since the 1940s and 1950s. Since 1954, the amount of suitable habitat declined by 600,000 ha in Alabama and 480,000 ha in Georgia; between 1964 and 1987, habitat losses were 850,000 ha in Louisiana and 1.1 million ha in Mississippi. Prime habitat in Arkansas has been completely eliminated. By 1979, only 17% of native grassland in Texas had not been converted to rice cultivation and other land uses, the habitat preferred by wintering shrikes. Fire ants have invaded all the Gulf States except Texas and are found on 100 million ha of land. The ants kill young trees and shrubs, thereby eliminating many perches. They are also direct competitors for food, eating grasshoppers and other insects as well as birds. There is also competition with resident shrikes that maintain their territories year round. Migrant shrikes are often forced to use

suboptimal habitat. In Indiana, it was concluded that only resident birds still bred in the state with the migrant population having been eradicated. Declines in Minnesota were attributed to low winter survival rates; it was concluded that conservation efforts on the breeding grounds would be ineffective in maintaining populations (Brooks and Temple 1990; Burton 1990; Cade and Woods 1997; Cadman 1985, 1990; Lymn and Temple 1981; Telfer 1992; Tyler 1992; Yosef 1994a, 2020).

Kirk et al. (2015) noted that the populations in the Carden and Napanee alvars are fairly stable and suggested that there might be a minimum size of local breeding populations needed to ensure persistence in a given area. When densities are low, returning birds have a reduced probability of finding a mate and breeding.

Presence of other raptor species may affect habitat use by Loggerhead Shrikes. In Texas, Northern Harriers forced shrikes to use habitats with more escape cover. Competition from American Kestrels prevented shrikes from using the same habitat patches (Kim et al. 2003). This study was conducted in winter, but may also be relevant to the breeding season.

Hudecki et al. (2020) reported that more than 20% of nests found in Ontario and Indiana had plastic incorporated into them. In Ontario, 3 cases of fledglings becoming entangled in plastic used as nesting material were reported. Slack (1992) reported nests where young were found hanging by pieces of string that were incorporated into the nest.

Environmental contaminants appear to have had an impact on shrike populations. The sudden decline in populations started in the 1940s before farming practices intensified, and coincides with initial usage of organochlorines. In Ontario, clutch and brood sizes declined after introduction of organochlorines. It is unknown if these were direct effects or indirect effects due to reduced prey populations. Major declines in the prairie provinces corresponded with dieldrin treatment of grasshoppers, a major component of the diet. In Illinois, eggshells were significantly thinner in 1971-72 than 1875-95 and most birds contained detectable concentrations of DDE. Breeding success was still high and there was no direct evidence that DDE had an impact on shrikes. In the wintering area between 1957 and 1977, aerial spraying of dieldrin, heptachlor, and mirex was undertaken in an attempt to control fire ants. Loggerhead Shrikes accumulated 8 ppm mirex compared with 1 ppm for most other vertebrates. In the 1950s and 1960s, pesticides were responsible for the direct death of adults, but this is no longer a factor. Young shrikes fed a diet treated with 2 ppm dieldrin all died within 103 days, and this dosage could be obtained by birds feeding in dieldrin-treated fields (Anderson and Duzan 1978; Blumton et al. 1990; Busbee 1977; Cade and Woods 1997; Cadman 1985; Hands et al. 1989a; Lymn and Temple 1981; Novak 1986; Yosef 1994a, 2020). The Loggerhead Shrike has been killed by carbofuran, a substance now banned in Canada (Mineau et al. 1999). The compound Dombind® is often used as a dust suppressant along roadsides. This increases the density of invertebrates along roadsides which may attract shrikes that may subsequently be affected by dioxins, furans, and other contaminants in this chemical. There is an increasing prevalence of brominated flame retardant chemicals in the food chain, including the eggs, blood, and tissues of predatory birds. These chemicals have been demonstrated to cause reproductive failure in captive American Kestrels, a species that shares similar habitats and dietary items with the Loggerhead Shrike. It is unknown if wild populations of shrikes breeding in Ontario have been exposed to these chemicals (Kirk et al. 2015).

In most areas, the Loggerhead Shrike has high nesting success. Fledgling and adult survival rates are very low compared to most passerines, however. Mortality rates from fledging to independence have been estimated at 33-53% in different areas. Several authors noted that nesting success was high, but autumn populations were lower than expected. Overwinter mortality rates may be as high as 50% in some populations. In Minnesota, it was estimated that 5.5 young would have to be produced per pair to offset the mortality rate. This would require almost 100% nest success or consistently successful double brooding; this is highly unlikely to occur. The high mortality rate appears to be due to a combination of all other limiting factors. A population viability analysis determined that the most sensitive factors affecting populations were overwinter survival and/or low recruitment rates to the breeding population by juvenile and young adult shrikes (Anderson and Duzan 1978; Brooks and Temple 1990; Collister and De Smet 1997; Graber et al. 1973; Kirk et al. 2015; Kridelbaugh 1983; Lymn and Temple 1981; Yosef 2020).

The Loggerhead Shrike appears to be vulnerable to West Nile virus. Five birds in the captive breeding program at the Toronto zoo died from this disease (Pittaway and Iron 2003). In California, Smallwood and Nakamoto (2009) found that it declined throughout their study region except in an area where West Nile vectors were aggressively controlled. It increased in areas where mosquito control was implemented. Lindgren et al. (2009) determined that 3 dead nestlings found in a Manitoba nest had died due to the West Nile virus.

Inclement spring weather may significantly reduce nesting success. High winds may blow nests out of trees, but cold, rainy weather is more devastating. Nestlings may die of hypothermia and there may be a scarcity of food. Under adverse weather conditions, brood reduction is common due to hypothermia, starvation, and siblicide, with youngest nestlings perishing first (Etterson et al. 2007; Hands et al. 1989a; Kridelbaugh 1983; Tyler 1992; Yosef 2020). In an Alberta population, daily nest survival was positively correlated with temperature and negatively correlated with precipitation (Collister and Wilson 2007).

Due to the exposed bedrock in the core Ontario breeding areas, these sites are of high quality for aggregate extraction. New gravel pit and quarry sites have the potential to affect Loggerhead Shrike habitat (Austen et al. 1994; Cadman 1985, 1990; Norris 1992).

Its flight habit makes the Loggerhead Shrike highly vulnerable to collisions with vehicles and to predation. It tends to perch at the top of shrubs or trees then swoop very low when flying. It is frequently killed by vehicles, particularly because of its habit of hunting along roadsides. Road-kill is a significant limiting factor in Ontario and most other areas. This problem is likely to escalate because of increasing traffic volumes. The conspicuous white patches on its wings make it highly vulnerable to avian predators (Austen et al. 1994; Cadman 1990; Chabot et al. 2001b; Gawlik and Bildstein 1990; Hands et al. 1989a; Norris 1992; Yosef 1994a, 2020).

Nest predation rates may be high, particularly when the Loggerhead Shrike nests in hedgerows and other linear habitats. The domestic cat may be a significant predator, although its impacts in Ontario are unknown. The proliferation of houses along roads in the core breeding areas may result in increased predation by cats. In South Carolina, nesting success was 71.4% where cats were not observed and 53.8% where they were present. In Missouri and Florida, nests near roads and in other

linear habitats were significantly less productive than those in pastures away from roads (Austen et al. 1994; Cadman 1990; Esely and Bollinger 2001; Gawlik and Bildstein 1990; Yosef 1994b, 2020).

In the core Ontario breeding areas, light grazing by cattle improves habitat by retarding natural succession and increasing habitat heterogeneity for insects. Pittaway (1999) documented that cattle regularly cause nest failure by rubbing and pushing against nest trees, frequently shaking eggs out of the nest.

Severe winter conditions occurred on the wintering grounds from 1976 to 1979. It is thought that this may have been a significant factor in the decline of the eastern population (Yosef 1994a).

Price (2004) predicted that the range of the Loggerhead Shrike could expand in southern Ontario if the summer temperature increased. It has other significant limiting factors that an increase in temperature may not overcome.

Status

The Loggerhead Shrike population has experienced major population fluctuations in Ontario. Historically, it was either absent or, more likely, confined to prairie, savannah, and alvar habitats. After forest clearing, it became common or even abundant. With the advent of pesticides followed by modern agricultural practices and increased urbanization, it declined significantly and is listed as endangered in Ontario. Its current distribution may be very similar to historical conditions, although it may have bred in prairies and savannahs in southwestern Ontario.

The Loggerhead Shrike was first recorded in Ontario in 1860 and became common by the turn of the 20th century. In the late 1880s, one could travel a short distance in any direction from Hamilton and find 1 or 2 pairs in suitable habitat. Around 1900, it was a regular uncommon summer resident in Toronto. By 1909, it was common along the St. Lawrence River and in Muskoka District and its range included the Bruce Peninsula. It continued to expand its range northward until the 1940s, when it was fairly common on Manitoulin Island, uncommon at Sault Ste. Marie, and nesting even occurred in Rainy River District in 1937. Shortly thereafter, its range started to contract southward and numbers declined. During the first atlas, it was estimated that there were 50-100 breeding pairs in the province concentrated from Manitoulin Island to Ottawa in a band along the southern edge of the Shield. A sharp decline in numbers was noted during the first atlas and it was concluded that there were probably only about 50 pairs left by the time the atlas was completed. Numbers and the extent of the range continued to shrink until by 1990 it was mostly confined to 2 core breeding areas (the Carden Plain and the Napanee area) with scattered nesting on the Bruce Peninsula and in the Ottawa area. In the early 1990s, there were 40-50 pairs in the province, as well as several unmated birds. The population dropped to a low of 18 pairs in 1997, but subsequently recovered to about 40 pairs. Numbers were fairly stable at 30-40 pairs annually for several years in the late 1990s and early 2000s, mostly confined to the 2 core breeding areas, but also on the Bruce Peninsula as a result of releasing captive-bred birds. No significant numbers of birds have been seen recently in the Smith Falls and Rainy River areas. The population has been supplemented through a captive breeding and release program since 2000. In 2006, the breeding population declined to 18 pairs once again, and was 20 pairs in 2007 and 27 pairs in 2008 (Austen et al. 1994; Baillie and Harrington 1937; Cade and Woods 1997; Cadman 1985, 1988, 1990; Cadman in Cadman et al. 1987;

Chabot in Cadman et al. 2007; Fleming 1907; Grand 1999; Grooms 2001; Heagy 1996; James 1991; Kirk et al. 2015; McIlwraith 1894; Norris 1992; Novak 1986; Stauffer 2007; Steiner and Williams 2007, 2008; Weir 2008). The Ontario population has been bolstered by the release of approximately 100 captive-reared fledglings annually from 2006 on. By 2008, 22.2% of wild pairs confirmed in Ontario contained a released bird (Williams 2007; Williams and Steiner 2008). In 2015, there were only 11 estimated pairs in the province but this increased to 21 pairs in 2022 (Olsen 2023). In 2024, 18 wild pairs were confirmed in the province, all at the Carden Alvar and Napanee Plain. Four single birds were observed on the Bruce Peninsula and Manitoulin Island, and single birds were also documented on Pelee Island and near North Bay. A total of 14 unpaired adults was recorded (Hess 2025).

The long-term (1970-2021) population trends determined by the Breeding Bird Survey were annual decreases of 3.08% in Canada and 8.94% in Ontario. The short-term (2011-21) trends were annual decreases of 1.287% in Canada and 3.82% in Ontario. The Ontario results were of low reliability. Canadian results were highly reliable for the long term and of medium reliability for the short term (A.C. Smith et al. 2023).

The short-term objective for the Loggerhead Shrike identified in the recovery strategy is to stabilize the existing population and prevent further declines. The long-term objective is to maintain at least 20 pairs in the Carden core area, 10 in the Napanee core area, 10 within a third core area, and at least 10 pairs elsewhere within the province for a total of 60 pairs (Kirk et al. 2015).

POSTFLEDGING PERIOD

Fledglings remain in the nest tree or dense foliage near it for 2-4 days after leaving the nest. They may then disperse as far as 7 km from the nest, but remain dependent on the adults for another 3-4 weeks, and considerably longer further south (Yosef 2020).

Twenty juvenile birds remained at the Carden site for several days before dispersing. Individuals were tracked to Beaverton, Duclos Point on Lake Simcoe, Virginia Corners (east of Toronto), and Hamilton (Williams and Steiner 2008).

MIGRATION

Northern birds are migratory, including those from Ontario; southern birds are resident. Most birds north of latitude 40°N migrate because the Loggerhead Shrike tends to avoid areas that have 10-30 days of snow cover in a year. Ontario birds winter approximately 900 km due south of the breeding grounds. During migration, birds move singly and during the day; it is unknown if nocturnal migration occurs. Migration is leisurely and birds may stay and feed in an area for a few days before moving another short distance (Burnside 1987; Miller 1931; Yosef 2020).

In Missouri, experienced males were the first to arrive and set up territories in spring. In Ontario, the Loggerhead Shrike arrives in late March or early April, very rarely by late February (James 1991; Kridelbaugh 1983). Autumn migration is in the first half of September, with occasional stragglers persisting into December (James 1991).

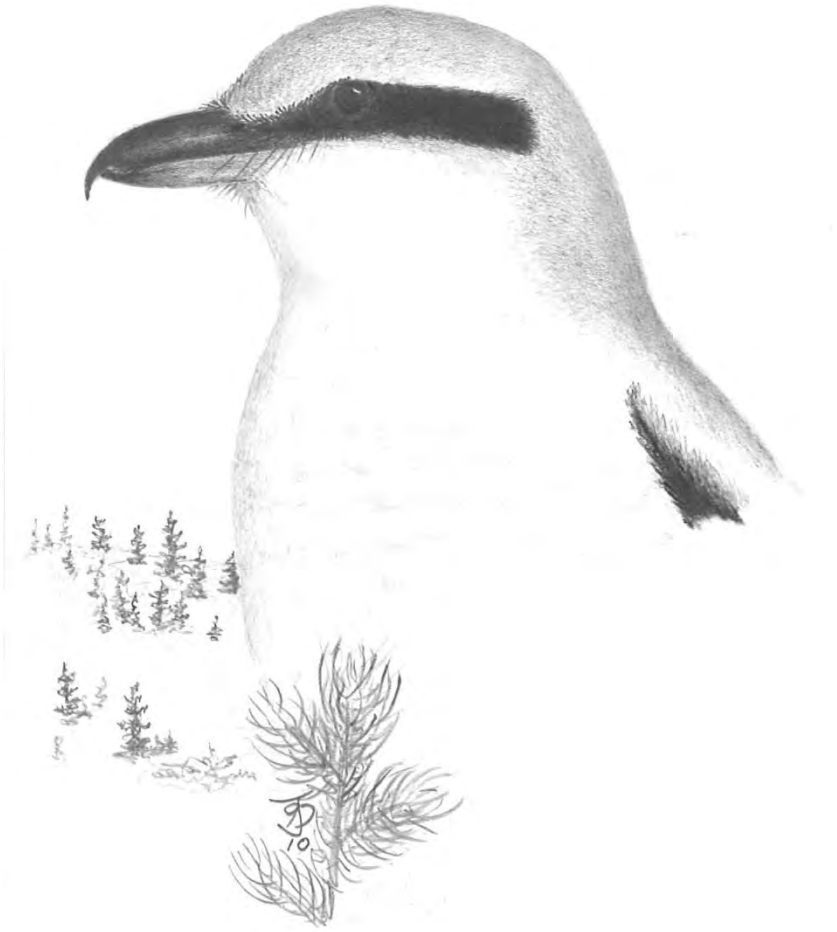
Migration habitat is very similar to breeding habitat. In British Columbia, where it is a nonbreeder, the Loggerhead Shrike prefers areas with short ground cover and frequently forages

from fence posts, telephone poles, or overhead wires. It occurs in open habitats such as beaches, brushy edges of fields, agricultural land, lakeshores with scattered shrubs, and open, mixed forests interspersed with grasslands (Campbell et al. 1997). Captive-reared juveniles inhabited pastures and hayfields as stopover sites during migration through southern Ontario (Kirk et al. 2015).

The Loggerhead Shrike is a rare migrant in Ontario (James 1991).

Northern Shrike

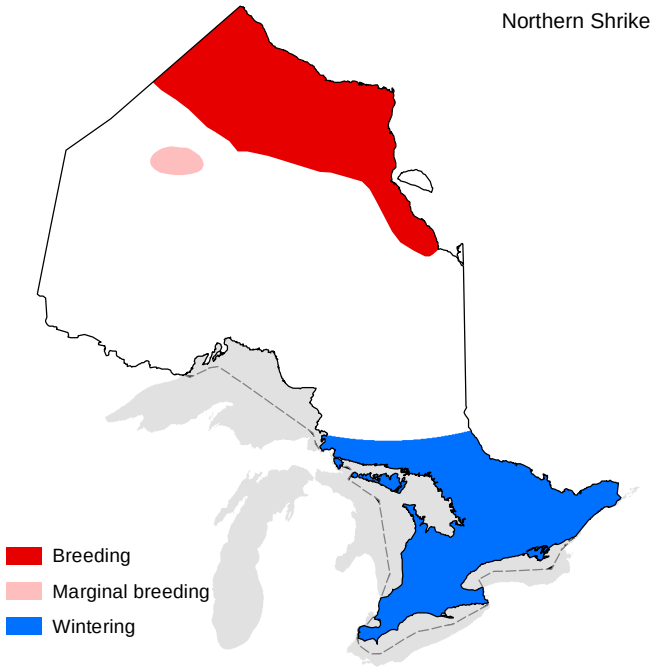
Lanius borealis



BREEDING SEASON

Habitat Requirements

The Northern Shrike breeds in the Hudson Bay Lowland and Tundra Region in Ontario, mostly in tundra habitat or large, open fens with scattered shrubs or trees. The first confirmed breeding record was in a large sedge fen with scattered tamarack and dwarf birch (Cadman in Cadman et al. 1987; James 1981; Peck and James 1987). Sutherland (in Cadman et al. 2007) described its preferred breeding habitat as sparsely treed open muskeg, spruce-lichen woodland patches within open peatlands, extensive regenerating burns, and willow and alder riparian thickets. In northeastern Manitoba and northwestern Ontario, McLaren and McLaren (1981) observed it in coniferous forests with understorey and in coniferous shrub habitats. In boreal Canada, Erskine (1977) described it as characteristic of tundra habitat.



In Alaska, breeding habitat includes tundra and coniferous forest, but continuous stands of conifers are avoided. The Northern Shrike nests either on the edge of coniferous forests or in open-canopied forests with a strong preference for forest edge. Other habitats it uses include spruce-birch forests near openings such as rivers, lakes, burned areas, muskegs, or black spruce bogs. It prefers semi-open landscapes and shrub-like vegetation, so it may nest in clumps of willows 1.3-5 m tall north of the treeline (Cade 1967).

No nests have been found in Ontario and few have been described from North America. The Northern Shrike nests both in coniferous and deciduous trees as well as in shrubs. In the southern part of its range and south of the treeline, it typically nests in spruce trees, but may nest in poplars and willows. Dense spruce trees appear to be preferred where available, and nests are well concealed, usually on a branch near the trunk. It possibly also nests in witches'-brooms and old Canada Jay nests. Old nests are rarely reused, with a new lining provided for the cup. Nests are often in the same tree or shrub as previously, but not always in consecutive years. Nests have been reported 1-10 m from ground, with most 2-4 m up (Bent 1950; Campbell et al. 1997; Paruk et al. 2020).

The Northern Shrike is territorial, but limited information on territory size is available. In Alaska, the closest nesting pairs were 1.6 km apart and other shrikes were attacked if they came within 1 km. This suggests the territory size may be in the order of 300 ha; 3 Alaska territories were approximately 145 ha in size. Most hunting is done within an area of 130-260 ha, so this is probably representative of the core territory size. Nesting birds are widely spaced and may not remain within a defined territory. Birds have been observed regularly flying as far as 3.2 km from the nest, so home ranges may be at least as large as 32 km² (Cade 1967). In Alaska, nearest-neighbour distance between nests averaged 2,333 m (range 700-4,230 m). In another area of Alaska, nests were 2-8 km apart, with high variations in numbers and density year to year. Males apparently do not defend their territory year round in North America (Paruk et al. 2020).

No information is available on natal site philopatry. Adult site fidelity appears low to moderate. In Alaska, a male nested 1.2 km from his previous nest site. Of 12 nesting areas examined 7 years, 1 was used 5 times, 3 4 times, 4 twice, and 4 once. Also in Alaska, 9 of 21 willow stands were used for nesting 19 times in a 5-year period. Although the Northern Shrike is somewhat migratory in North America, some individuals overwinter in the breeding range (Cade 1967).

Limiting Factors

Although no data are available, it is likely that most clutches in Ontario occur in June (Peck and James 1987). In Labrador, a replacement nest took 7 days to build. Most often, eggs are laid at the rate of 1 a day. The onset of incubation has been recorded twice: once after laying of the second egg, and once after laying of the seventh and last egg. Size of nestlings in Alaska nests suggested incubation began with laying of the first egg (1 case), second egg (4 cases), third egg (6 cases), and seventh egg (1 case). The incubation period is 17-21 days, and hatching is asynchronous over a 3-4-day period. Young fledge when they are 18-20 days old, but may leave the nest at 15 days if disturbed (Cade 1967; Paruk et al. 2020).

A single brood is raised annually, but renesting may occur if the first clutch is lost. No information on Ontario clutch sizes is available, but fledgling numbers have been documented. Four juveniles were observed on the Sutton Ridges, 5 at North Point north of Moosonee, and a female collected near Moosonee had 6 enlarged ova. Overall, clutch sizes of 2-9 eggs have been reported. Clutches with fewer than 4 eggs are probably incomplete. Clutches of 4-6 eggs are probably typical, but most clutches in Alaska contained 8 eggs and some 9-egg clutches occurred. There may be significant differences in clutch sizes between eastern and western populations, but insufficient data are available (Bent 1950; Cade 1967; James 1981; Manning 1981; Paruk et al. 2020; Schueler et al. 1974).

The age at first breeding is 1 year. Most birds are monogamous and it is probable that extra-pair copulations occur (Paruk et al. 2020).

The Northern Shrike prefers to hunt by perching atop one of the tallest trees in its territory. It prefers perches 3-10 m high a minimum of 25 m apart, but perch height is dependent upon the trees and shrubs that are available. It has extremely acute vision; it can see a bumble bee 100 m away, a mouse at 200 m, and another shrike at 1 km. An area of about 130 ha around the nest is used regularly for hunting, but birds occasionally range out to cover an area of about 260 ha. One was observed killing a longspur and flying 400 m with it to the nest. Once prey is observed from a perch, the shrike flies off in pursuit. Insects are snapped up in the beak in mid-air. It may pursue birds in the air for several hundred metres, but is seldom successful in capturing them in flight. It has been documented catching swallows and bats in mid-air. The feet are usually used to capture birds but occasionally they are struck by the beak. To kill rodents, it jumps and dances around the prey then strikes it with the beak. It usually kills vertebrates by severing the vertebrae in the neck with the beak. It has other hunting techniques that are used infrequently and usually with low success. It may move quickly on the ground or among shrubs and trees in an attempt to flush prey. Sometimes it hovers over a spot where prey has been seen and attacks if it is observed again. Rarely, it hunts in large sweeps 900 m back and forth, flying as high as 60-100 m. In Alaska, immature birds have been observed hunting cooperatively. Two young worked together to flush American Tree Sparrows from dense cover into the open, where they were pursued. Cooperative hunting may improve success of inexperienced birds. Once captured, it carries all vertebrates and most large invertebrates to a tree or shrub and impales them on a thorn or sharp twig or hangs them in the fork of a branch. During the breeding season, larders of impaled prey may be maintained, but not always. In Alaska, prey was hung at heights from ground level to 3.6 m, mostly 1-2.3 m from ground. Larders may attract foxes

and other predators, so are usually 40-200 m from the nest. When larders are maintained, the female may feed from them during breaks and take food back to nestlings (Cade 1967; Yosef 1994a).

When adults first arrive in April or May in Alaska, they eat mostly adult passerines and occasional voles. Once the snow begins to melt, more voles are exposed, and they make up the bulk of the diet. By late May, bumble bees emerge and they dominate and are critical to the diet. After the peak courtship of passerines is over in mid-June, the number of birds in the diet decreases rapidly; at the same time, young voles appear and become important prey. In the first week of July, fledglings of other bird species become important in the adult but not juvenile diet. In autumn, both adults and juveniles feed mostly on migrating birds. There were very few species in the diet: 4 species of birds (Savannah Sparrow, Lapland Longspur, Snow Bunting, and Redpoll), 4 species of mammals (voles and shrews), and only 6 invertebrate taxa (spiders, bumble bees, wasps, grasshoppers, ground beetles, and other beetles). Over a 1-year period, birds constituted 21% of the total weight of food eaten, young voles 22%, adult voles 52%, bumble bees 3.5%, and other insects less than 1%. Further south in northern British Columbia and Labrador, the diet is more varied. In addition to the species consumed in Alaska, it has eaten young ptarmigan, shorebirds, Downy Woodpeckers, Horned Larks, young Canada Jays, Black-capped Chickadees, Golden-crowned Kinglets, American Robins, Bohemian Waxwings, Yellow-rumped Warblers, White-crowned Sparrows, Fox Sparrows, Dark-eyed Juncos, Red and White-winged crossbills, Evening Grosbeaks, Pine Grosbeaks, red-backed voles, and meadow voles. Near Churchill, it fed on young shorebirds and longspurs captured in a nearby fen. It rarely attacks larger birds such as Mallards, Sharp-tailed Grouse, and ptarmigan. Other invertebrates consumed include caterpillars, ants, and millipedes (Bent 1950; Cade 1967; Campbell et al. 1997; Paruk et al. 2020). It is likely that Ontario breeding birds prey on most of the above species when they are available.

Food may be a significant limiting factor on the breeding grounds. In Alaska, shrikes eradicated the entire population of bumble bees and wasps in their territory, eliminated all nesting birds within 200 m of the shrike nest, and removed about 14% of the vole population. The last 2 hatchlings often die before fledging, probably because they do not get enough food. In cold, wet weather when prey is scarce, adults may cannibalize young just to stay alive (Cade 1967; Yosef 1994a).

In Wisconsin, 2 Northern Shrikes had mean feather mercury concentrations of 7.7 µg and 9.1 µg per gram. Mercury concentrations higher than 7 µg per gram may cause a 40% reduction in nesting success. Spiders have been found to have high concentrations of mercury, so it is possible that a diet high in spiders could have caused these elevated concentrations (Paruk et al. 2020).

Status

McIlwraith (1894) concluded that the Northern Shrike probably bred in the northern portion of the province. Schueler et al. (1974) provided the first breeding evidence when they collected a female with enlarged ova near Moosonee on 26 May 1972. Other sightings or specimens have been taken from Moose Factory, Winisk, Severn River, Severn House, York Factory, Akimiski Island, and the Twin Islands, and it was reported to be fairly common on the west side of Hudson Bay (Manning 1952, 1981; Schueler et al. 1974). Breeding was confirmed on 12 July 1981 when a pair was observed feeding recently fledged young at the Sutton Ridges (James 1981). Although not reported until later, Manning (1981) saw a group of 5 young at North Point, just north of Moosonee on 23 June 1975.

During the first atlas, breeding was confirmed near the Fawn River in 1983 and near the Sachigo River in 1984. Cadman (in Cadman et al. 1987) concluded that the Northern Shrike was widespread in the Hudson Bay Lowland, but at low densities. McLaren and McLaren (1981) estimated it bred at densities of 1 or less than 1 pair per km² in the Hudson Bay Lowland. James (1991) considered it a rare breeder in the Hudson Bay Lowland south and east to Moosonee.

The second atlas indicated no change in the breeding distribution or abundance of the Northern Shrike. A shift in the areas where breeding evidence was obtained between atlases was probably due to changes in coverage rather than an actual distributional change. No nests were found during the second atlas but breeding was confirmed along the Winisk River north of Peawanuk and near Shegogau Creek, 30 km north of Moosonee (Sutherland in Cadman et al. 2007).

POSTFLEDGING PERIOD

Young remain in the nest tree or one nearby for a few days after leaving the nest, staying quiet and still for the first week except when adults bring food. They gradually become more active and move away from the nest tree. The brood remains together in a loose group for more than 30 days, and the adults split the brood and continue to feed them during this period (Paruk et al. 2020).

Fledglings begin feeding themselves by attacking small arthropods while they search on the ground. These include ground beetles, flies, mosquitoes, and spiders. By 7-10 days out of the nest, they hunt from perches and begin to capture juvenile voles and shrews. By 20 days out of the nest, they are capable of wedging and impaling prey in trees and begin attacking insects and small birds in the air. They soon start to feed on bumble bees, wasps, and grasshoppers. At the end of the summer, they start taking mice and switch to birds a little later (Paruk et al. 2020).

Groups of independent juveniles may occur away from the nesting areas from July to early September. These are probably siblings and they may migrate together (Paruk et al. 2020).

MIGRATION

The Northern Shrike is an irregular, short-distance migrant, with movements occurring only during the day. It probably follows major river valleys out of the Boreal Forest Region and has been observed following ridge lines, coursing just above the treetops. Some years, most birds stay on or near the breeding grounds; other years there are large southward emigrations. During invasions, 2-5 times as many individuals migrate than in non-cyclic years. From 1900 to approximately 1950, it migrated in regular cycles, but the frequency of abundance became random thereafter. Peaks in numbers occurred approximately every 4 years in the first half of the 20th century, usually coinciding with Snowy Owl and arctic fox abundance. Prior to 1893, the interval between peaks was usually 3 years. By the 1940s, owl and shrike emigrations began to diverge, indicating that the reasons for the 2 species migrating were not the same. By the 1970s, there was no consistent pattern to emigrations, although they still occur. In Ontario, numbers counted on Christmas Bird Counts (CBC) peaked at intervals of 3-7 years with an average of 4 years until the 1970s. In Toronto in the 1930s, peaks occurred at intervals of 3-6 years, usually 4 or 5. Reasons for emigration are unclear, but they may be tied to low vole abundance on the breeding grounds. When there is a year of unusually high survival of fledglings during low vole abundance, there may be insufficient prey and many individuals may

be forced south (Cade 1967; Davis 1937, 1949, 1960a, 1974; Davis and Morrison 1988; Freedman and Riley 1980; Graber et al. 1973; Miller 1931; Paruk et al. 2020; Root 1988; Speirs 1939).

In southern Ontario, the Northern Shrike usually arrives in mid- to late October and leaves in mid- to late March, or early April in Algonquin Park (Curry 2006; Mills 1981; Tozer 2012).

Habitat used during migration is similar to that of the breeding season. The Northern Shrike may also occur on rural residential lots and in urban parks where there is a concentration of small birds or other suitable prey.

In Ottawa, a bird banded on 9 November 1985 was retrapped on 13 April 1986 suggesting that this shrike may exhibit site fidelity during migration (Rimmer and Darmstadt 1996).

The Northern Shrike is a rare migrant in Ontario (James 1991).

WINTER

The Northern Shrike prefers open habitats in winter, including grasslands, pastures, old fields, clear-cuts, burns, fencerows in agricultural areas, treed roadsides, shrublands, margins of wetlands and streams, and edges of sparse forests. It may be attracted to rural residential areas where bird feeders offer potential prey (Campbell et al. 1997; Hernández 1995; McIlwraith 1894; Weir 2008). In Idaho, shrike territories contained 4 habitat types: shrubland, grassland, agricultural land, and mesic habitat. Grasslands were used significantly more than expected. Each territory included 2 or 3 types of linear habitat such as rimrocks, roads, and riparian areas. Territories contained significantly greater lengths of roads and riparian corridors than occurred in general (Atkinson 1993). In Minnesota, 81% of shrikes were observed in wetlands with the remainder in upland areas including grasslands and woodlands. Of birds observed in wetlands, 38% were in thicket swamps and 31% each in marshes and mixed thicket swamps and marshes (Lee et al. 1992).

Shrikes used night roosts in their territories and stayed at individual roosts several times, although not necessarily on successive nights. All roosts were in deciduous trees or shrubs, particularly willow. Perches were on twigs an average of 1.5 m from ground, halfway between the trunk and edge of the canopy, regardless of tree height. All twigs used were surrounded by many stems that may have provided shelter from the wind. Roosts may also be used during day to escape from predators (Atkinson 1993).

Shrikes that move south for the winter maintain territories that may be occupied and defended for 4 months. In Idaho, territories averaged 216 ha, with core areas slightly larger than 50 ha. Territories were widely spaced and separated by an average of 1.4 territory diameters (Atkinson 1993). In Minnesota, home ranges in extensive areas of grassland and suitable habitat were about 1.25 km^2, and twice as large in less than ideal habitat (Lee et al. 1992). In northern Wisconsin, winter territories averaged 554.7 ha (range 289-889 ha) in a colder winter and 53.0 ha (range 18-93 ha) in the following winter, which was warmer (Paruk et al. 2020).

Limited data suggest that some birds may exhibit site fidelity to wintering areas. The information is based on band recoveries that are typically reported as 10' blocks. A bird recovered in the same block may have occurred at the same site as previously, or as far away as 37 km. Of 17 birds recovered the following year, 71% were in the same block. One Ontario bird was recovered in the adjacent

block (Rimmer and Darmstadt 1996). The study demonstrated that birds may return to the same general wintering area. To date, there is no evidence that individual birds home to the same wintering sites. In Idaho, the same winter territories were occupied each year, but no banded birds returned to the same territory. Further studies in Idaho revealed that some individuals used the same area for as many as 6 winters (Paruk et al. 2020). When a bird died, its territory was soon reoccupied, suggesting high demand for good quality habitat (Atkinson 1993). Paruk et al. (2020) stated that some winter territories were occupied traditionally, but it is unknown if the same birds were involved. Some territories are used frequently, but not every winter. Apparently some birds switch territories over the winter, depending on weather, food availability, and opportunity to acquire a better territory if 1 bird disappears. Some birds do not establish territories and wander throughout the winter.

In winter, the primary hunting technique is still sitting on a perch watching for prey. Due to limited food resources, the Northern Shrike uses additional methods in winter. It may be more successful and determined in aerial pursuit of birds. It may chase small birds in air until they tire and are overcome. In Ontario, it has been seen scavenging a recently killed red squirrel and eating a bat that may have either been captured or was carrion. It has been documented eating carrion and suet in winter (Bent 1950; DiLabio 1996; James and Harrison 1987; Pittaway et al. 1992; Stronks and Stronks 2020). In Utah, A. Smith (1991) observed that the same impaling sites may be reused.

The winter diet is about one third small mammals with birds comprising most of the food. In the south, meadow voles are preferred, but the Northern Shrike may alos consume white-footed, house, and deer mice. House Sparrows, juncos, and tree sparrows are staples of the winter diet. Other birds present in Ontario in winter that it may eat are Downy Woodpecker, Hairy Woodpecker, Rock Pigeon, Mourning Dove, Canada Jay, Blue Jay, Horned Lark, Black-capped Chickadee, Tufted Titmouse, kinglets, waxwings, European Starling, Snow Bunting, Lapland Longspur, Northern Cardinal, Pine Siskin, Redpoll, crossbills, Pine Grosbeak, Evening Grosbeak, and American Goldfinch (Atkinson and Cade 1993; Bent 1950; Cade 1967; Paruk et al. 2020; Graber et al. 1973; Kinch 2006; Paruk et al. 2020; Weir 2008). Where they are available, the Northern Shrike may feed on invertebrates, including caterpillars, orthopteran nymphs, beetles (especially ground beetles), ants, wasps, bees, flies, and spiders (Paruk et al. 2020).

Cade (1967) concluded that winter food might be the main limiting factor to Northern Shrikes in Alaska. Nesting success was very high, yet populations remained low. In winter, no insects are available, small mammals are protected by snow cover, and small bird populations are low.

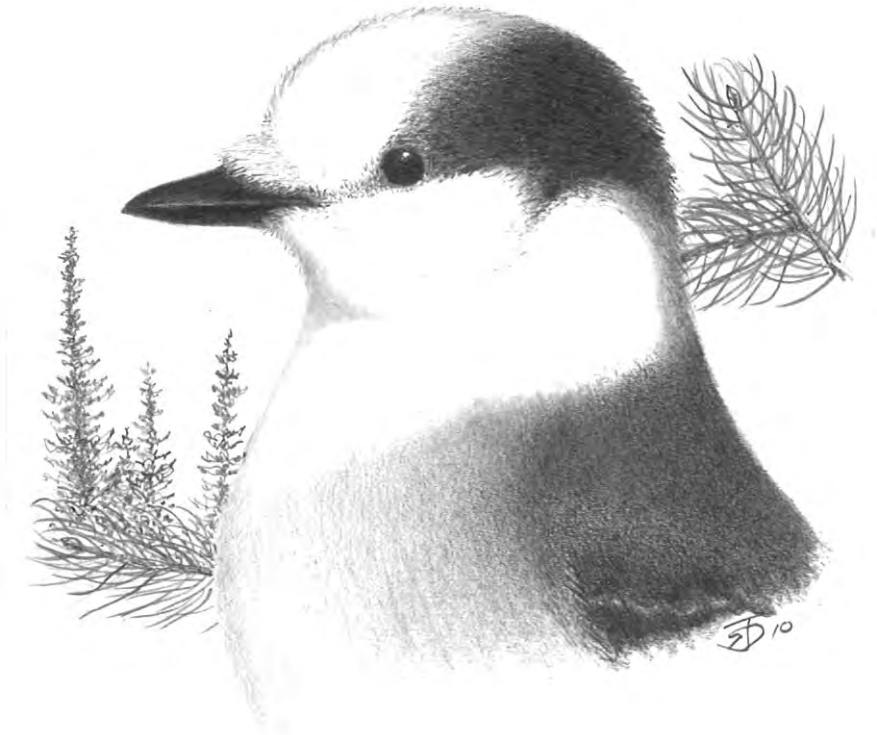
There may have been a reduction in the amount of suitable wintering habitat for the Northern Shrike. Forest regeneration, urbanization, and intensive agriculture have reduced the amount of early successional habitat (Paruk et al. 2020).

Historically, the Northern Shrike was frequently destroyed because it fed on birds and impaled its prey; it was known as the butcher bird. In the 1870s, the City of Boston hired people to shoot them to protect House Sparrows and 50 were shot in 1 year. In the 1920s, most bird banders killed them instead of banding and releasing them (Bent 1950; Davis 1937). Human destruction is no longer a significant problem.

The Northern Shrike is rare in winter (James 1991). Freedman and Riley (1980) suggested it had increased in abundance on CBCs since 1952, but this may have been an artifact of better coverage by observers. The CBC has no current trends for this species (National Audubon Society 2022).

Canada Jay

Perisoreus canadensis

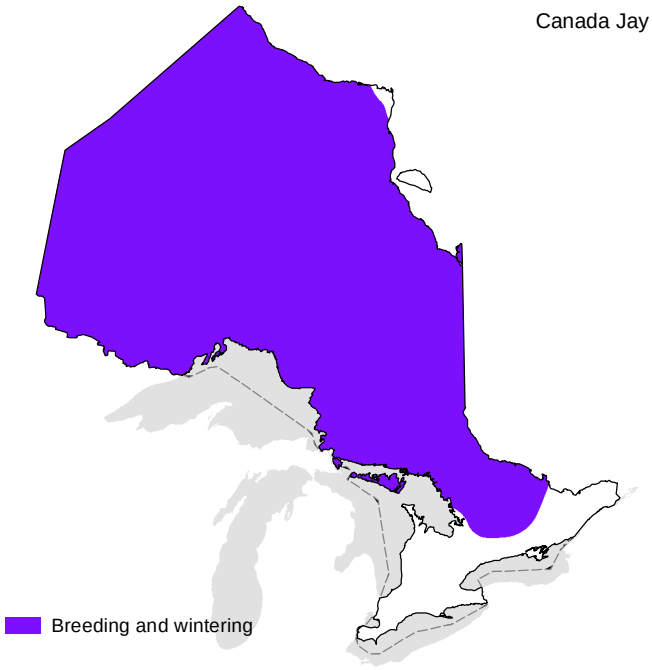


BREEDING SEASON

Habitat Requirements

In Ontario, the Canada Jay breeds most frequently in coniferous (47.3% of nests) and mixed (45.5%) woods, seldom in deciduous forests (7.3%). It commonly nests near water and in spruce bogs, but nests are almost as common in dry areas. Presence of favoured nest-tree species appears to be the dominant factor in selecting nesting habitat. It prefers open situations such as forest edges, shorelines, clearings, bogs, beaver meadows and ponds, and roadsides over dense, closed woodlands (Peck and James 1987).

In the Boreal Forest Region near Pickle Lake, the Canada Jay occurred in predominantly coniferous forests, and was representative of spruce forests (James 1980; McLaren and McLaren 1981). Near White River, it occurred most frequently in clear-cuts 18-20 years old, but was not significantly more abundant in these stands than clear-cuts 3-15 or 23-25 years old or mature stands



40-100 years old (Venier and Pearce 2005). In the Clay Belt, it was abundant in a variety of stands, including those dominated by black spruce, jack pine, and trembling aspen. It occurred over a wide moisture gradient, from very wet to dry and in sites that were poor to rich in nutrients (Welsh and Lougheed 1996).

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Canada Jay was uncommon in jack pine stands near Parry Sound and Gogama. It may not have nested in pines, but occasionally foraged in them with nesting occurring in adjacent spruce swamps (James 1979a; James and Peck 1995a). In Algonquin Park, preferred habitat is coniferous forest, particularly spruce and spruce-tamarack stands with small- to medium-sized trees. Black spruce bogs are used most consistently. Upland mixed forests of trembling aspen, white birch, balsam fir, and white spruce are inhabited, but less favoured. It may forage in pure hardwoods, but most territories contain at least 50% conifers. It avoids areas dominated by sugar maple unless they contain corridors of spruce (Rutter 1969; Strickland and Ouellet 2020). Sugar maple stands were abandoned as breeding habitat in Algonquin Park in the 1970s-90s (Strickland and Ouellet 2020). In Mer Bleue, breeding occurred in a large, open bog with small isolated clumps of black spruce and tamarack (Ouellet et al. 1976).

The Canada Jay is characteristic of the Boreal Forest Region and is strongly associated with spruce stands and spruce bogs. In Alberta, it was equally abundant in young, mature, and old-growth aspen stands, many of which contained balsam fir. In Quebec, it was equally abundant in young clear-cuts and burns and forests 120 years old. It occurs in a wide range of forest ages, from very young to mature, with a tendency to prefer older stands. Fir stands are used frequently, with lesser use of tamarack and white cedar forests. In Saskatchewan and Michigan, it also nests in jack pine stands. Although most breeding is in coniferous or mixed forests, a few occur in rural areas of British Columbia, where it prefers edges of extensive forests, avoiding dense forest. Where conifers are scarce on the prairies or in the north, it may nest among aspens and willows (Bent 1946; Campbell et al. 1997; Dawson 1979; Erskine 1977; Imbeau et al. 1999; Kirk et al. 1996; Manning and MacPherson 1952; Niemi and Pfannmuller 1979; Schieck et al. 1995; Strickland in Gauthier and Aubry 1996; Strickland and Ouellet 2020; Thompson et al. 1999). In Newfoundland, 62% of captures of Canada Jays were in areas where openings were natural features, such as peatlands, compared with 38% in areas where openings were clear-cuts (Whitaker et al. 2008). Also in Newfoundland, it was most abundant on forest edges created by roads or clear-cuts. It was less than half as abundant in forest interior as on edges, and was absent in riparian forests. Although it was absent in undisturbed

riparian forest, it occurred in low numbers in 20-50-m-wide riparian buffer strips left between aquatic habitat and clear-cuts. The forest cover was dominated by balsam fir 50-100 years old (Whitaker and Montevecchi 1997, 1999). In coniferous forests in British Columbia, it exhibited no significant distribution relationships to riparian habitat. It tended to avoid riparian habitat in winter and spring, which includes the breeding season, and to be attracted to riparian habitat in summer and autumn (Wiebe and Martin 1998).

In Algonquin Park, habitat quality is related to the proportion of coniferous trees within territories because of their superior ability to preserve cached food over deciduous trees (Strickland et al. 2011). Canada Jays have higher reproductive success on territories with more conifers. Juveniles that recruited into the study area were more likely to disperse to territories with similar abundance of conifers as on their natal area. The exception was for juveniles born in low-conifer areas, who were more likely to disperse to areas with a higher proportion of conifers. When adults dispersed, they moved to territories with higher proportions of conifers (Norris et al. 2013).

Ralston et al. (2019) surveyed for the Canada Jay in 20 plots in boreal forest habitat in New York, Vermont, Maine, Nova Scotia, and Newfoundland. It occurred at 10 of the sites, indicating broader habitat preferences than many species and an ability to use multiple boreal forest habitat types. It was associated with peatlands, black spruce, tamarack, and taller canopy cover.

The Canada Jay roosts close to the trunk of a well-foliaged spruce or balsam fir at night (Strickland and Ouellet 2020).

All nests reported to the Ontario Nest Records Scheme were in live coniferous trees: 48.4% in black spruce, 25% each in white spruce and balsam fir, and 1.6% in hemlock. Of 652 nests in Algonquin Park, 57.4% were in black spruce, 28.4% in balsam fir, and 13.5% in white spruce. Two nests were in hemlock and 1 was in a white pine. Both large and small trees were used for nesting. Most nests were against the tree trunk in crotches of lateral branches (77.8%). The remainder were 1-4.6 m from the trunk on horizontal branches. In Algonquin Park, 96% of nests were touching the tree trunk or separated from it by less than 1 nest diameter; the rest were well out on horizontal branches, usually in white spruce. Nests were 1.2-15 m from the ground, mostly 2.4-6.1 m up. The average height of nests in Algonquin Park was 6.0 m with a range of 1.6-25 m (Peck and James 1987; Strickland and Ouellet 2020).

Nests are very often at an edge, such as a bog, beaver pond or meadow, forest clearing, road, or building. Nests tend to be on the northern side of openings, 1 or 2 trees in from the edge. They are usually well concealed, but on the southern side of the tree where there is sufficient clearance to allow the late winter sun to reach the nest and give birds a free flight path. Almost all nests are in conifers, especially spruce, but western birds occasionally nest in willows and trembling aspen. Nests have been found 0-31 m from the ground, usually 1-6 m up. Snow depth may be as great as 1 m when nesting is initiated, so some nests are very close to the snow's surface. A new nest is almost always built. One pair relined a 3-year-old nest that had held eggs but not nestlings. Nests abandoned during construction or incubation are stripped of most soft materials for use in replacement nests. Nests in early phases of construction are occasionally abandoned; 1 of these was

used the following year (Bent 1946; Campbell et al. 1997; Lawrence 1947, 1968; Ouellet et al. 1976; Parmelee 1988; Rutter 1969; Strickland and Ouellet 2020; Walley 1987).

The Canada Jay defends a year-round, permanent territory. Its territory size is considerably larger than expected based on its body size. This may be due to the necessity of having sufficient food caches to ensure winter survival at a density low enough to avoid high losses due to cache predators. Average territory size was 129 ha in Algonquin Park, where territories may not be contiguous due to intervening marginal or unsuitable habitat. Other reported average territory sizes are 69 ha in La Vérendrye Park in Quebec, 65 ha in Manitoba, 23.2-41 ha in the Yukon, 27 ha on Anticosti Island, and 80 ha in another Quebec area. Birds tend to remain in core areas that are less than half the territory size (about 40-70 ha in Algonquin Park), but the entire territory is vigorously defended. Territorial boundaries remain constant year to year and successive nests are placed within 100-200 m of each other in the core area. Annual internest distance averaged 1,260 m in Algonquin Park, 890 m in La Vérendrye Park, 600 m in Alberta, and 1 km in Alaska (Desrocher 2000; Parmelee 1988; Rutter 1969; Shank 1986; Strickland 1992; Strickland and Ouellet 2020).

Occasionally juveniles breed on the natal territory, but only if both parents have disappeared. Usually they acquire a territory by moving from territory to territory until they can fill a breeding vacancy. Young have acquired territories as far as 11 km from their natal area. In Colorado, where mortality was high, dispersal was almost nonexistent because there were always unoccupied territories. Mean maximum dispersal distances were 208 m for juveniles and 265 m for adults (Ha and Lehner 1990; Strickland 1991, 1992, 2002, 2003; Strickland and Ouellet 2020; Strickland and Waite 2001).

Adult site fidelity is extremely high, with most birds spending their entire life on the same territory. Successive nests are placed in the core of the territory within 100-200 m of each other. One male occupied the same territory for 6 years despite losing 2 mates. Occasionally widowed birds move as far as 10 km to fill breeding vacancies elsewhere due to lack of replacement birds. Rarely, established birds may be displaced or switch territories. One male in Algonquin Park occupied a territory for 4 years with 2 different females, but was displaced to an adjacent marginal territory the following year. Three pairs moved into newly vacant neighbouring territories (Rutter 1969; Strickland 1992; Strickland and Ouellet 2020).

Limiting Factors

The Canada Jay is one of the earliest nesting birds. Eggs have been reported in Ontario nests from the second week of March until the first week of May, with most present from the last week of March until mid-April (Peck and James 1987). In Algonquin Park, nests are under construction from late February to early April, eggs are present mainly from late March to mid-April with extreme dates from late February to mid-May, and nestlings typically occur from mid-April to early May but may be present from mid-March to early June (Tozer 2012). In Algonquin Park, fledging dates of nestlings were from 17 April to 26 May (mean 1 May; Fuirst et al. 2024).

Both sexes build the nest, which typically takes 2-3 weeks and occasionally as long as 4 weeks; nests may rarely be built in 1 week. Several days usually elapse between nest completion and laying of the first egg. Eggs are laid at the rate of 1 a day. The mean date of the first egg at 581 Algonquin

Park nests was 23 March and also 23 March at La Vérendrye Park. Incubation begins with laying of the first egg, but effective incubation starts with laying of the last or penultimate egg; all eggs hatch on the same day. The incubation period is 16-20 days, and appears to be 18.5 days in Algonquin Park. Young leave the nest when they are 22-24 days old. Reports of young leaving the nest at age 17-20 days may have been due to regular handling of the birds (Bent 1946; Campbell et al. 1997; Lawrence 1947; Madge and Burn 1994; Ouellet et al. 1976; Peck and James 1987; Rutter 1969; Strickland and Ouellet 2020).

A single brood is raised annually. Replacement clutches may be laid if the loss occurs before 10 April; a new nest may be built and egg laying initiated within a week. In Algonquin Park, 1 pair that had access to a feeder successfully raised 4 young on the third attempt. Clutches of 1-5 eggs have been reported in Ontario, with most containing 3 eggs. The 1-egg clutch was produced by a yearling female that had moved into an unfamiliar territory and was breeding for the first time. Mean clutch sizes were 3.0 eggs in Algonquin Park and 3.2 in La Vérendrye. Elsewhere, clutches of 1-6 eggs have been documented. The normal clutch is 2-4 eggs, with 3 eggs most frequent (Bent 1946; Campbell et al. 1997; Lawrence 1947; Madge and Burn 1994; Ouellet et al. 1976; Peck and James 1987; Rutter 1969; Strickland in Gauthier and Aubry 1996; Strickland and Ouellet 2020).

Both sexes can breed when they are 1 year old, but most males do not have the opportunity until they are 2 years old. In Algonquin Park, 1-year-old males may attract a mate and breed in unoccupied, marginal habitat, but most yearling males do not breed in good, saturated habitat. Mean age of first breeders at Algonquin Park was 1.76 years for males and 1.5 years for females. Three percent of males did not breed until they were 3 years old. Nonbreeding birds, usually males, may accompany pairs during the breeding season; typically only 1 per pair. Although they are excluded from the nest area during nest building, incubation, and the nestling period, they often feed fledglings. These birds are often young of the adults from the previous year that have been unsuccessful in acquiring a territory. The Canada Jay is monogamous, and pairs remain together year round and remain mated as long as both are alive. Members of a pair are rarely apart. There are some exceptions. One Ontario male, whose mate was incubating, built a nest with another female that had moved into his territory; both nests failed. Three cases of divorce have been documented. If a mate is lost, the survivor remates (Ha and Lehner 1990; Strickland 1991, 1992, 2002, 2003; Strickland and Ouellet 2020; Waite and Strickland 1997).

The Canada Jay forages by scanning from perches. When potential prey is seen, it flies to a nearby branch, tree trunk, the ground, or shallow water before seizing it. Forest edges less than 30 m wide are prime foraging locations because it is a nest predator. In Quebec, groups of Canada Jays were closely associated with forest edges in summer. This association occurred regardless of the amount of forest within their home range, which varied from 20-94%. Jays with the most forest cover in their home range were more strongly associated with edge. Seventy-six percent of jay locations were less than 30 m from edge, although only 46% of forest was within 30 m of edge. Jays travelled more slowly along edges where foraging success was presumably greater than away from edges. In the Mackenzie District of the Northwest Territories, 97.4% of foraging occurred in conifers at an average height of 6.9 m. The Canada Jay may land on the backs of live moose to get engorged winter ticks, and snap up flying insects flycatcher-like. Occasionally, it tears up wasp nests to eat the

contents. It usually ignores small birds, but occasionally chases after them, usually unsuccessfully. It has extremely large saliva glands that secrete mucous. Food that is not consumed immediately is coated in mucous to create a bolus, which is then hidden. Caches are deposited singly in trees behind flakes of bark, under tufts of lichen, in coniferous foliage, or in tree forks, typically 3-15 m from the ground. Most food storage occurs in the territory, but occasionally in neighbours' territories. In Alaska, it may make more than 1,000 caches per day, but fewer are made in the south of its range. Caching is done any time when a surplus of food is acquired. These stores are essential to winter survival. In Minnesota, caching began in August and continued until early May. No caching was observed from early May until the end of July during leaf-out and the peak of insect activity. The early breeding season may be an adaptation to allow enough time to store food for the upcoming winter (Barnard 1996; Bock 1961; Desrochers 2000; Dow 1965; Greenberg et al. 1999; Ibarzabal and Desrochers 2004; Lawrence 1968; Rogers 2005; Rutter 1969; Strickland 2003; Strickland and Ouellet 2020; Tozer and Allen 2004; Waite 1988).

The Canada Jay is an opportunistic omnivore, but feeds extensively on insects during the breeding season, especially lepidopterans. Grasshoppers may form a considerable portion of the diet. Food brought to nestlings is a dark, viscous paste coated with saliva. It is mostly arthropods. The stomach of 1 nestling contained remains of 75 spiders and insects including larvae of geometer and owlet moths, flies (flower, crane, and horse flies), and beetles (weevils and predaceous diving and ground beetles). Aquatic invertebrates or those inhabiting damp soils were most frequent in nestlings' diets. Nestlings may be fed from caches as emergency food during late winter snowstorms. Of 67 stomachs of fledglings and adults, 31% contained fur or bone from small mammals (shrews and red-backed voles), 76% contained berry seeds, and 82% contained arthropods. In Algonquin Park, fecal samples from nestlings contained 2% vertebrates (wood frog and masked shrew), 74% arthropods, and 24% plants. Spiders and lepidopterans represented the majority of food items but the most common food items were blueberries. Twenty-eight percent of nestling food items were likely from winter caches. The most common invertebrates eaten by adults were beetles, hymenopterans, bugs, lepidopterans, flies, grasshoppers, spiders, and centipedes. In Alaska, it consumed 2.5 times more invertebrates in spring than in autumn and 5.5 times more vertebrate flesh and 2 times more berries in autumn than in spring. In Maine, 15% of food items within stomachs were spruce budworm larvae and pupae during a budworm outbreak. It takes winter ticks from infested moose and engorged ticks that have fallen off. It takes eggs and nestlings from a wide variety of species, to those as large as thrushes and grouse chicks, and there are 2 records of it killing and eating independent juvenile Magnolia Warblers. Recently fledged birds may be more important to the diet than observed. Although seldom recorded, the Canada Jay kills and consumes small rodents and this may be an important component of the diet. It also eats frogs, toads, and snakes. In Oregon, it fed on salamander larvae in small woodland pools. It has been observed attacking a wounded Green-winged Teal and a blood-stained weasel and wresting a nursing hoary bat from its roosting mother. It eats a wide variety of berries, especially those of false solomon's-seal, Canada mayflower, blueberries, elderberries, bearberry, sumac, viburnums, juneberries, and mountain-ash. Fungi and lichens are eaten and fungi are commonly stored, including slime moulds. Spruce seeds are not extracted from cones, but are eaten if found on the ground. Carrion is vital to its survival, especially when other food sources are scarce. It may eat or

store carcasses of fish, birds, bears, seals, caribou, deer, moose, and small mammals, and also consumes maggots on carcasses. There is often interspecific territoriality at large carcasses. The Canada Jay displaces the Blue Jay, but is displaced by the Common Raven. The Canada Jay is well known for taking table scraps and other food from humans. It drinks water when it is available and also eats snow. In New Brunswick, abundance of the Canada Jay was unrelated to abundance of the spruce budworm (Addison et al. 1989; Barnard 1996; Bowers and Farley 1990; Derbyshire et al. 2019; Gilmore 1996; Madge and Burn 1994; McIlwraith 1894; Mitchell 1952; Morris et al. 1958; Murray et al. 2005; Ouellet 1970; Rutter 1969; Strickland 1996; Strickland and Ouellet 2020; Sutton et al. 2024; Swift et al. 2022).

Habitat loss may be a factor at the southern extent of the range. Through natural succession, coniferous stands gradually are replaced by deciduous species, making habitat marginal or unsuitable.

Vanderwel et al. (2007, 2009) summarized studies that examined the effects of partial timber harvesting in the Boreal Forest Region on the Canada Jay with particular reference to Ontario. They reported no change in its abundance when 30%, 50%, or 70% of trees were removed. In the Boreal Forest Region of Alberta, it increased significantly compared with control plots when 50% of trees were removed from stands dominated by white spruce (Harrison et al. 2005). In Oregon, Douglas-fir forests were thinned from more than 650 trees per ha to 180 trees per ha. The Canada Jay increased after thinning and had higher populations for 7 years after thinning. By 12 years after thinning, populations were similar to pre-management conditions (Hagar et al. 2024). In Ontario, there was no difference in its abundance between burned and clear-cut stands in early successional or mid-successional forests. There was no difference in its abundance in mature and early successional stands, but it was significantly more abundant in mid-successional than mature stands (Zimmerling et al. 2017).

In Algonquin Park, survival rates of Canada Jays were consistently lower on territories adjacent to highways. Several carcasses of birds were recovered beside the highway that runs through it, indicating collisions with vehicles. During spring and summer, survival on highway territories was 4% lower than on territories distant from the highway for both adults and juveniles. During autumn and winter, mortality increased by 6% for juveniles and 2% for adults on territories adjacent to the highway. Jays exhibited no tendencies for directional dispersal away from the highway. Highways may act as an ecological trap for the Canada Jay (Norris et al. 2013).

There is evidence that the Canada Jay is declining at the southern edge of its range, possibly due to climate change. Warmer temperatures may result in degradation of the perishable food items that are used during late-winter nesting (Strickland 1992, 2014; Strickland and Ouellet 2020). In Algonquin Park, females began gaining weight 9 days prior to egg laying and the rate of weight gain was best explained by the percent coverage by conifers in the territories. The weight gain was due to consuming food that had been cached 4 or more months previously. This provides support for previous studies demonstrating that coniferous trees are better at preserving cached foods. Preservation time of food items placed on trees by researchers was longer on black spruce than on sugar maple. Food stored at Cochrane, several hundred kilometres north of Algonquin Park, lasted significantly longer under the cooler temperatures experienced there (Sechley et al. 2014, 2015;

Strickland 2014). In Alaska, cached food was recovered within 4 weeks. Jays responded to a record-breaking warm spring by foraging on emerging insects rather than caches. It may be better adapted to changes in cache integrity and food availability than previously thought (Swift et al. 2022). Warmer temperatures may favour growth of deciduous trees over conifers. In the Boreal Forest Region of eastern Quebec and Labrador, the Canada Jay was associated with forest stands with relatively low temperatures (DesGranges and LeBlanc 2012).

In Newfoundland, annual survivorship of the Canada Jay was slightly lower in forested landscapes where openings were clear-cuts than in forests where openings were peatlands and other natural features (Whitaker et al. 2008).

Walker and Marzluff (2015) examined the response of the Canada Jay to factors associated with human recreation in Washington. Its probability of detection increased in forests with at least some canopy cover compared with open sites with little or no canopy. Detection rates were greater at quiet sites compared with those with at least moderate noise. The probability of an area being used increased with greater patch richness within 5 km and it was most likely to use areas with high percent forest cover within 5 km. Probability of use was greatest in trail zones and least in day-use areas compared with backcountry areas and it was 118% more likely to use areas with greater numbers of visitors. Usage increased with distance to the nearest campground. It commonly used areas where food subsidy was available and the odds of use increased with the availability of anthropogenic food. In general, it used areas with food subsidy in high-elevation forests away from most recreational infrastructure. Food availability may allow for local increases in its presence.

In Alberta, the Canada Jay was significantly more abundant at seismic lines than in adjacent forest interior. There was no difference in its abundance at pipelines and well pads than in forest interior adjacent to these features. There were no differences in its abundance near noisy compressor stations and quiet well pads (Bayne et al. 2008, 2016).

The Canada Jay is extremely vulnerable to being caught in traps set for furbearers. New baits are being devised to help alleviate this problem (Manning and MacPherson 1952; Porsild 1943; Strickland and Ouellet 2020).

Status

McIlwraith (1894) considered the Canada Jay a common resident in Muskoka District. Baillie and Harrington (1937) stated that it bred from Algonquin Park north to Severn River and Cape Henrietta Maria, and west to Kenora. James (1991) considered it an uncommon to common permanent resident in the north, becoming rare in the Canadian Shield south to Parry Sound and central Peterborough County. There are breeding records from Mer Bleue in Ottawa and southern Peterborough County, and there is a breeding population on Manitoulin Island (Ouellet et al. 1976; Peck and James 1997; Strickland in Cadman et al. 1987).

The second atlas demonstrated that there had been no change in the Canada Jay's distribution since the first atlas. Its probability of observation increased significantly province-wide, in the Boreal Forest Region, and in the Hudson Bay Lowland. There was no significant change in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, although there was considerable turnover in the squares where breeding evidence was reported. The atlas results are contrary to more detailed

studies in Algonquin Park that indicated a 60% decline in territory occupancy. Highest abundance occurred in the northern portion of the Boreal Forest Region and in the Hudson Bay Lowland (Strickland in Cadman et al. 2007).

Since the 1980s, the Canada Jay has disappeared from many formerly occupied territories in Algonquin Park and southern Quebec. This may be a reflection of the marginal deciduous habitat or unknown pressures on a species at the extreme south of its breeding range, such as climate warming (Strickland and Ouellet 2020). Forty-three territories have been surveyed annually in Algonquin Park since 1964 and only 19 (44.2%) were occupied in 2014. Some are now dominated by hardwood tree species, but many unoccupied territories still contain much coniferous cover (Strickland 2014).

Long-term (1970-2021) population trends indicated by the Breeding Bird Survey were annual decreases of 0.367% in Canada and 0.284% in Ontario. The short-term (2011-21) trends were annual decreases of 0.22% in Canada and 0.417% in Ontario. The data were of medium reliability for the short-term Canadian results; the other results were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young start climbing out on branches 1-2 days prior to fledging. They can fly 10-30 m in level or ascending flight when they leave the nest. Recently fledged birds are mostly inactive and usually huddle close together along a branch close to the trunk of a conifer. Occasionally, the group flies 50-100 m to another similar site where they huddle together again. The family begins to travel as a group 18-21 days after the young fledge (at age 42-45 days). Partial dispersal of fledglings occurs when they are 55-65 days old. Once fledglings are that old, they start to fight among themselves until one becomes dominant and expels its siblings from the territory. About two thirds of dominant siblings are male. Expelled birds may attach themselves to a pair that was unsuccessful in fledging young. Fledglings that are unsuccessful in joining a pair have very low survival potential because there is usually insufficient time to store enough food for the winter. Dominant fledglings remain with the parents until early March when they are expelled at the beginning of the breeding season. They subsist over winter chiefly on food that the adults have cached. Juveniles use the natal or adopted territory to prospect for their own territory (Strickland and Ouellet 2020). In Algonquin Park, dominant juveniles had an 80% chance of reaching adulthood compared with 47% of expelled juveniles. Dominant juveniles produced more fledglings over their lifetime than expelled juveniles (Fuirst et al. 2023).

During the postbreeding period in Algonquin Park, adults strongly preferred forest-wetland edges and exhibited a weak preference for coniferous forests. They used mixed forests and wetlands in proportion to their availability and exhibited a weak avoidance of tolerant hardwood forests. The mean home range size of 12 adults was 84 ha with a range of 35-201 ha (Fuirst et al. 2022). The mean home range of fledglings that remained on the natal territory was 48 ha with a range of 10-140 ha (Fuirst et al. 2024).

AUTUMN

The Canada Jay is essentially non-migratory, with no reports of breeding territories being vacated in winter. Nonetheless, there are occasional wanderings and major incursions to the south some years;

reasons for this are unknown. A large invasion occurred in southern Ontario the winter of 1839-40. Birds appeared in the Toronto area in 31 years from 1825 to 2022, with multiple birds observed in 21 of these years. When flights to the south occur, birds typically arrive in October through to late January and depart in March. Incursions may result in isolated breeding records far south of the normal breeding range, as occurred at Mer Bleue after the winter of 1972-73. Large numbers were seen in southern Ontario in the winter of 1905-06, and this occurred about once every 20 years thereafter (Coady 2023; Fleming 1907; Ouellet et al. 1976; Saunders 1930a; Strickland and Ouellet 2020; Weir 2008). During an autumn flight in 2010, at least 90 of 120 birds (75.0%) were hatch-year birds (Strickland and Ouellet 2020). Major flights have occurred outside of Ontario. In southern Minnesota, major flights occurred in the winters of 1929-30, 1974-75, 1976-77, 1985-86, and 1986-87 (Janssen 1987), and there was a major flight near Godbout, Quebec in September 1884 (Bent 1946). Campbell (1965) reported thousands in the Moisie Bay area of Quebec with the flight lasting from mid-August until late October, with as many as 250 per hour passing by. Flights occurred every autumn there, originating in northeastern Quebec and Labrador, moving south to the coast, then westward and finally northwestward, possibly returning to the same area. Birds may congregate along the north shore of Lake Superior from mid-September to late November. There are 2 reports of northward spring migration from mid-May to early June at Whitefish Bay on the south shore of Lake Superior (Strickland and Ouellet 2020).

During autumn, the Canada Jay is attracted to areas where humans are present and provide a potential source of food, such as ski resorts, campgrounds, bush camps, and traplines (Campbell et al. 1997). It regularly visits hunt camps in search of handouts. Fat and entrails from big game that has been shot is an important food source. Fruit, such as chokecherries, is collected and stored at this time (Rutter 1969).

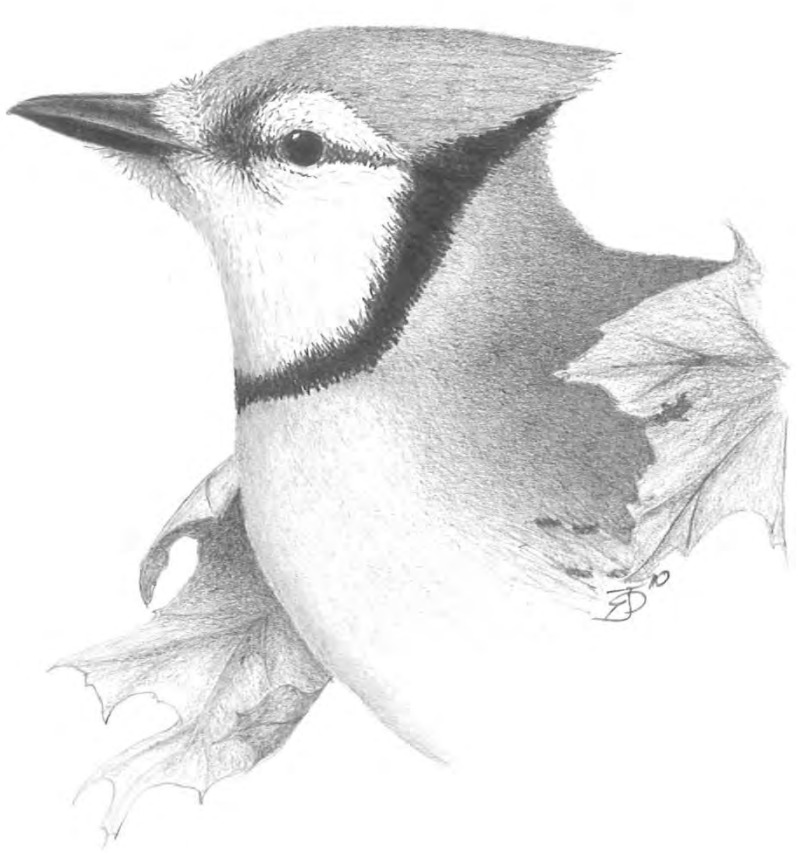
WINTER

In winter, carrion and stored food are the mainstays. In remote areas, wolf kills of deer, caribou, and moose are important to the Canada Jay as are road-kills. It readily comes to winter bird feeders and may cross 2 territories to reach them. It eats a wide variety of food at feeders and prefers suet, bread, meat scraps, cheese, baked beans, oatmeal, and peanut butter mixes. Occasionally it eats sunflower seeds, nuts, mixed seeds, and raisins. Lichens may be consumed in winter, but may be subsistence food (Bent 1946; Dow 1965; Dunn and Tessaglia-Hymes 1999; Rutter 1969; Strickland and Ouellet 2020; Whittam and Francis 2000).

Data from Project FeederWatch counts indicate that the percentage of feeders visited by Canada Jays has been declining since the peak in 1999 when 13% of feeders Canada-wide were visited (Wilcox 2006). Christmas Bird Count data indicated annual decreases in Ontario of 0.95% 1970-2021 and 2009-21 (National Audubon Society 2022).

Blue Jay

Cyanocitta cristata

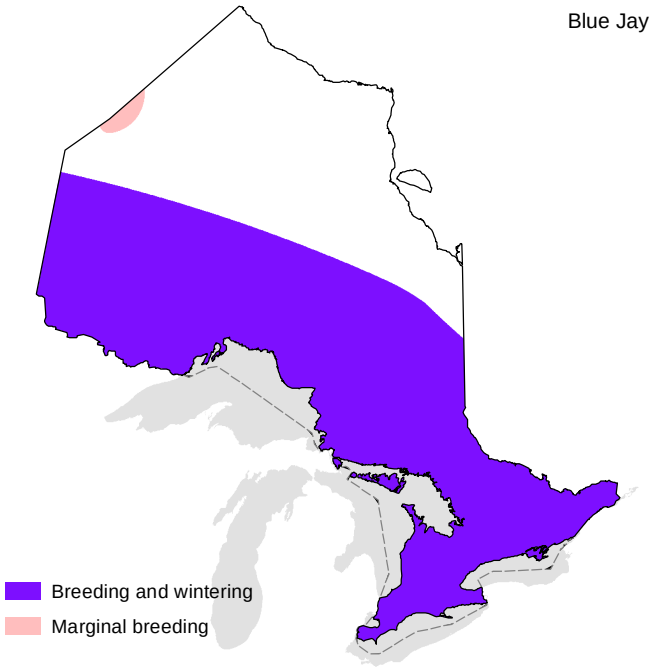


BREEDING SEASON

Habitat Requirements

Ontario Blue Jay nests were in and at edges of treed areas, with 24.7% of nests in mixed, 15.2% in deciduous, 7.4% in coniferous, and 12.4% in unspecified woodlands. Other nests were in urban and rural gardens, parks, and schoolyards (24.1%); in old fields and fencerows (10.6%); at edges of marshes, rivers, and lakes (2.8%); in orchards (2.1%); and along roadsides (0.4%). Although the Blue Jay occasionally nested in swamps, most nests were in upland areas (Peck and James 1987).

In the Boreal Forest Region, the Blue Jay nests in upland mixed forests and may occur in clear-cuts that are only 5 or 6 years old as well as in mature forest (Kendeigh 1947; Venier et al. 2009; Welsh and Fillman 1980).



In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Blue Jay commonly nests in mature and old-growth stands of white pine (Kirk et al. 2012). In jack pine stands near Gogama, it was uncommon and seen mostly in deciduous portions of mixed woods. It occasionally foraged in pines, but did not appear to nest in them. Breeding could have occurred in any mixed forest 15-20 or more years old (James and Peck 1995a). Of 5 plots of jack pine stands in Parry Sound District, it was absent in 4 and occurred at low density in an open, 5-8-m tall jack pine stand mixed with trembling aspen, white birch, white pine, and sugar maple (James 1979a). In Algonquin Park, it was absent in bogs, black spruce–white cedar woods, and pure hemlock forests. It occasionally occurred in black spruce, balsam fir–spruce, birch-poplar, and pure hardwood forests, but may not have been a breeding species. It occurred regularly in birch-poplar-fir-spruce and fir-spruce stands (Martin 1960).

In the Great Lakes–St. Lawrence Forest Region south of the Shield in Durham Region, it occurred in all forested plots, including mixed and deciduous stands, black spruce bog, upland and lowland forest, and disturbed, open stands to closed mature stands. Greater densities occurred in drier stands and in young, disturbed stands. It was a mid-succession species (Speirs and Orenstein 1975). In the Kingston area, it occurred in every square that contained trees during the atlases. It nested within most cities and towns, especially within conservation authority lands (Weir 2008). The Blue Jay is a habitat generalist and may be found in most forested areas within the Great Lakes–St. Lawrence and Carolinian forest regions, including those in urban areas.

In southern Ontario there was no difference in the Blue Jay's abundance on organic and conventional farms. Its presence was significantly associated with corridors such as roads, railways, and power line rights-of-way and the number of large, isolated trees (Kirk et al. 2011).

Habitat reported elsewhere is similar to that in Ontario. Until the early 20th century, the Blue Jay nested predominantly in forests and orchards, but numbers in residential areas are now frequently higher than in mature forests and orchards are rarely used. Although it is almost ubiquitous within its core range, it exhibits some habitat preferences. It prefers mixed to deciduous forests. Pure coniferous forests and plantations are seldom used, or it is present in these habitats in low numbers. It prefers forest edges to interior, and prefers stands with widely spaced trees. In Wisconsin, it is one of the most abundant species in pine and oak barrens, and occurs regularly at edges of moderately open barrens. It is characteristic of savannahs in that state. Most studies determined that it prefers younger forests to mature stands. Near Manitouwadge, however, it was equally abundant in young

clear-cuts, intermediate-aged stands and mature and old-growth stands. In Alberta aspen stands, it was equally abundant in stands of all ages. In Wisconsin, it was most common in pioneer stands. When it occurred in mature stands, they tended to be more open-canopied, with second-generation trees in the subcanopy. In the Pennsylvania Appalachians, it was negatively associated with old-growth forests. In forests, it selects areas with a dense understorey, or nests in undergrowth at edges of forests. After agricultural land is abandoned or forest clear-cutting occurs, it becomes established 10-20 years later once there is some shrub and sapling cover, reaches greatest abundance at 40 years then declines. It inhabits forests over the full range of moisture regimes, but greatly prefers and reaches its highest density in upland xeric stands. These forests are most likely to contain favoured mast-producing trees such as oaks, beech, and hickories. In suburban areas, best habitat occurs in areas with mature trees, especially oaks. Ornamental coniferous trees may provide suitable nest sites and lawns may be important for storing food. In New Hampshire and Maine, abundance of the Blue Jay was positively correlated with the number of coniferous trees 2-10 cm diameter at breast height. It was negatively correlated with canopy closure (Anderson and Shugart 1974; Back 1979; Beals 1960; Bielefeldt and Rosenfield 1994; Bond 1957; Campbell et al. 1997; Capen 1979; DeGraaf et al. 1998; Faanes and Andrew 1983; Graber and Graber 1963; Graber et al. 1987; Haney 1999; Hoffman 1989a; Kirk et al. 1996; Langevin and Dauphin in Gauthier and Aubry 1996; Mossman and Hoffman 1989; Mossman et al. 1991; Samson 1979; Schieck et al. 1995; Stribling et al. 1990; Suthers 1988; Temple et al. 1979; Thomas et al. 1977; Thompson and Capen 1988; Tarvin and Smith 1995; Tarvin and Woolfenden 1999; Tyler in Bent 1946; Venier et al. 2009).

In 400-m landscapes in North Dakota, the probability of occurrence of the Blue Jay increased with increasing tree cover within 100 m in landscapes with less than 30% forest cover. When the landscape was more than 30% wooded, its probability of occurrence initially increased with increasing tree cover, but levelled off and declined somewhat with high tree cover. At high levels of tree cover, it selected more edge-rich areas (Cunningham and Johnson 2016). It preferred landscapes that were 51-75% forested in North Dakota; no areas were more than 75% forested. In New York, it preferred landscapes that were 71-94% forested (Cunningham and Johnson 2019).

The Blue Jay is not an area-sensitive species and benefits from habitat fragmentation. In southern Ontario, its abundance was negatively correlated with woodlot size, amount of forest cover 100 m or more from edge, the amount of forest cover within 2 km, and the amount of regional forest cover, although only the latter parameter was significant (Austen et al. 2001). In Michigan, its abundance was negatively associated with forest size and it was not associated with any landscape variables (Crozier and Niemi 2003). Robbins (1979) concluded that it required 4 ha of forest to maintain a viable population, but Robbins et al. (1989) determined that it was most likely to occur in greatly isolated forests. In Pennsylvania, it was associated with larger woodlots but was more prevalent in fragmented landscapes (Keller and Yahner 2007). In Wisconsin, it was at least 50% more common in smaller woodlots (5-14 ha) than larger forests. Although it showed a slight preference for larger patches in xeric woods, it greatly preferred smaller woodlands in more mesic stands (Bond 1957). In Maryland and Delaware, its probability of detection in woodlands of different widths was greatest at 50 m, declining gradually to 50% at 300 m, and 33% at 800 m (Keller et al. 1993). In South Carolina, its probability of occurrence was 39% in 0.5-ha forests and 76% in 10-ha forests surrounded

by pine forests, and 53% in 0.5-ha forests and 86% in 10-ha forests surrounded by field and shrub habitats (Kilgo et al. 1997). In fragmented North Dakota aspen woodlands, its abundance was correlated with forest size. Probability of detection was 15% in 1-ha woodlots, 20% in 10-ha woodlots, 38% in 100-ha forests, and 52% in 1,000-ha forests. It did occur in very small woodlots (Grant and Berkey 1999). In Saskatchewan, it was randomly distributed within fragmented landscapes and its presence was not correlated with forest type or amount of cover within 5 km (Hobson and Bayne 2000). Stauffer and Best (1980) observed it in riparian strips as narrow as 15 m, and concluded that it would be unaffected if vegetation were reduced to a narrow riparian area.

In Tennessee, the core areas of Blue Jay territories adjacent to an open corridor appeared to be shifted toward the edge but territory density was not significantly higher near the edge than in forest interior. Territories tended to line up in rows parallel to the edge of the corridor (Kroodsma 1984). K.G. Smith et al. (2020) concluded that it was associated more with woodland edges than deep forest.

Most Ontario nests were in live trees and shrubs. Eight were in dead trees; 4 were on a building rafter, a sunporch beam, a shelf under a house eave, and a shelter on the side of a house; 1 was in dead tree roots under an overhanging earthen bank. Coniferous trees were slightly more preferred for nest sites (58%) than deciduous trees, shrubs, and vines. Species most frequently selected were white cedar (58 nests); pines, mostly white pine (53 nests); hawthorns (53 nests); spruces (37 nests); hemlock (19 nests); and maples (19 nests). Nests were more often in small than large trees, and more often near the top than middle and lower portions of the tree. Nests occurred in crotches (56.7%) and on horizontal branches and more were near or against the trunk (78.2%) than away from it. Distances from the trunk for 13 nests were 0.2-6 m, mostly 1.2-3 m. Six nests were between 2 adjacent tree trunks. Most nests are freshly built, but one was used 2 successive years, one was built on an old nest, and one was built on a squirrel drey. Nest height ranged from 0.9 to 20 m, with most 2.4-4.6 m up (Peck and James 1987).

In the east, the Blue Jay appears to prefer conifers for nesting, but in Iowa 94% of nests were in deciduous species. A high proportion of deciduous species were also reported from Illinois: 18.4% of nests were in oaks, 11.6% in hawthorn, 10.8% in apple, 9.6% in Osage orange, 9.2% in Manitoba maple, 4.8% each in cedar and pine, 4.4% each in Norway and blue spruce and elms, 3.6% in willows, 2.4% each in black cherry and chokecherry, 2.0% in grape, 1.6% each in ash, honey locust, and hackberry, 1.2% each in poplar, cottonwood, and honeysuckle, 0.8% in mulberry, and 0.4% each in hickory, lilac, and sycamore. Other species it has nested in include black locust, beech, grey alder, black alder, pitch pine, flowering dogwood, and a variety of fruit trees. Nests may be on or in buildings or other human-made structures, such as cross-members on hydro poles and transformers. Some of these nests are highly exposed and in areas of high human activity. Nests were 1 m to more than 30 m from the ground, but most are 3-8 m up. One yearling female used a nest that her parents had abandoned earlier. There are some records of long-term use of nests, with one in North Carolina used 4 consecutive years; another was used 5 consecutive years, left idle for a year, then used again. It was unknown if the same birds were reusing the nests. One pair appropriated a newly constructed robin nest (Brackbill 1950a; Duyck and McNair 1990; Fitch 1958; Graber et al. 1987; Kilham 1956; Langevin and Dauphin in Gauthier and Aubry 1996; Laskey 1958a;

K.G. Smith et al. 2020; Stauffer and Best 1980; Tarvin and Garvin 2002; Tarvin and Smith 1995; Tyler in Bent 1946).

The Blue Jay does not maintain exclusive territories and may be gregarious even during the breeding season. Occasionally neighbouring males or pairs may engage in contests similar to cock fights. Aggression is usually between adults at the same nesting stage, so that adults with nestlings may tolerate adults with fledglings entering the territory and even landing in the same tree. There is no defence of consistent boundaries. Mated pairs may form flocks and move through their neighbourhood and band together to attack predators. When territorial defence occurs, it is usually within 60 m of the nest. Territory size in Quebec was estimated at 2.61 ha. In Maine spruce forest, territory size was estimated at 4.0 ha. Home range size varies seasonally and home ranges of pairs greatly overlap. In Florida, home ranges were 0.54-6.1 ha. In Kansas, a female often flew 350 m from the nest to join other Blue Jays and food for fledglings was brought from distances of 130-275 m. The home range for this female may have been in the order of 9 to more than 30 ha (Fitch 1958; Graber et al. 1987; Langevin and Dauphin in Gauthier and Aubry 1996; Laskey 1958a; McIlwraith 1894; Morse 1977; K.G. Smith et al. 2020).

In Tennessee, 3 yearlings of a brood from the previous year returned. One of these, a female, fledged 4 young, and one of them returned the next 2 years. Another nest produced 2 fledglings, both of which returned the following year (Laskey 1958a). These data suggest that natal philopatry is fairly high, but no other information is available. In Illinois, 34 of 594 birds (5.7%) banded over 32 years returned, but the age of birds when they were banded was not specified (Graber et al. 1987). Laskey (1958a) and K.G. Smith et al. (2020) determined that most adults remained in the same area year to year in Tennessee and Florida. Adult site fidelity rates are unknown for northern populations that may be partially migratory, although the Tennessee population was mostly migratory.

Limiting Factors

Eggs have been found in Ontario nests from mid-April to mid-July, with most present in the last half of May (Peck and James 1987). In Algonquin Park, nests are under construction from early May to early June, eggs are present from early May to early June, nestlings occur from mid-June to early July, and dependent fledglings have been observed from late June to early August (Tozer 2012).

Nest construction may take as long as 26 days, but 8 or 9 days is typical. It may be some time after nest completion before eggs are laid. One egg is laid per day and daytime incubation appears to begin with laying of the penultimate egg. The incubation period of 10 Ontario nests was 13-18 days. Some of the short incubation periods and variability of incubation periods may be due to incubation starting before the clutch is complete. Elsewhere, the incubation period has been reported as typically 17 or 18 days, with extremes of 15-18 days. Young may leave the nest when they are 15-21 days old, but typically at age 17-21 days. In Illinois, the time for a successful nesting from nest building to fledging was estimated at 48 days for a 5-egg clutch (Graber et al. 1987; Laine 1981; Laskey 1958a; Madge and Burn 1994; Peck and James 1987; K.G. Smith et al. 2020; Tyler in Bent 1946).

One or 2 broods may be raised annually, and there are records of 2 broods in Ontario. The Blue Jay appears to be more productive in suburban and urban habitat, where it is most likely to raise 2

broods. One brood appears more typical in natural habitats. Third broods have been reported in Florida and Tennessee, but the Florida record is uncertain. The Tennessee record was unusual in that young fledged prematurely in the second nest due to disturbance and the young were taken into captivity. The adults may have perceived this as a failed nest with the third nest a renesting attempt. Renesting after a loss is common and may continue into July. Clutches of 2-6 eggs have been reported in Ontario, with most having 4 or 5 eggs; 5-egg clutches are most frequent. Throughout its range, clutches of 2-7 eggs have been reported, typically 4-6 in northern populations and 3 or 4 in the south. Seven-egg clutches are rare (Graber et al. 1987; Laskey 1958a; Madge and Burn 1994; Peck and James 1987, 1997; K.G. Smith et al. 2020; Tyler in Bent 1946).

Both sexes are capable of breeding at 1 year of age, but many do not until they are 2 years old. The proportion of each sex that breeds as yearlings varies regionally and annually. In Florida, 45% of breeding birds were yearlings in a year of high productivity but low population, but only 6% in a year of high population density. The mating system is long-term monogamy. Pairs remain together for several years and typically dissolve only when one dies. In a nonmigratory Florida population, 7% of pairs divorced (Graber et al. 1987; Laskey 1958a; K.G. Smith et al. 2020).

The Blue Jay feeds mostly in trees and shrubs and on the ground, occasionally aerially. It may hawk flying ants, cicadas, and dragonflies from the air. It takes seeds and nuts directly from the tree or shrub; acorns on trees are much preferred to those on the ground. Cached acorns are retrieved from the ground by digging with the beak. It may also raid Canada Jay caches. It has been observed trying to catch live mice, but appears fairly unsuccessful at this (K.G. Smith et al. 2020; Tyler in Bent 1946; Wourms and Wasserman 1985).

Although the Blue Jay is an opportunistic omnivore, it has definite food preferences that vary seasonally. Nestlings have been documented being fed lepidopteran pupae, but they are probably fed a wide variety of invertebrates. Beal (1897a, 1897b) examined 530 stomachs. They contained a large amount of mineral matter that averaged more than 14% of total stomach contents. The real food consisted of 24.3% animal material and 75.7% vegetable matter. The animal food was predominantly insects, with a few spiders, centipedes, millipedes, crustaceans, snails, and small vertebrates such as fish, salamanders, treefrogs, snakes, mice, and birds. Important insects were lepidopteran larvae, grasshoppers, and scarab, ground, and adult and larval click beetles. Although the Blue Jay is much maligned as a nest predator, traces of bird eggs and nestlings were found in only 6 stomachs. A wide variety of vegetable matter was eaten, but hard mast (acorns, beechnuts, chestnuts, hickory nuts, and hazelnuts) were most important and comprised 43% of the overall diet. No hard mast was found in stomachs of birds collected in July and August, but it comprised 67% of the diet from October to March. Grain was important food, especially corn which constituted 17.9% of the annual total diet. Other vegetable matter it consumed included wheat, oats, buckwheat, currants, blackberries, mulberries, blueberries, sumac, knotweed, sheep sorrel, huckleberries, black cherries, chokecherries, wild grapes, juneberries, elderberries, hawthorn fruit, and pokeweed berries. Beal et al. (1916) examined 184 stomachs collected in the southeastern United States. The diet consisted of 31.9% animal food and 68.1% vegetation. Insects comprised 26.5% of the annual diet, predominantly caterpillars and grasshoppers. Scarab beetles and June beetles were common in the diet and comprised 30% of the diet in May. It ate numerous snails, a few toads and frogs, and some

fish. Only 1 stomach contained the egg of a small bird; 13 stomachs contained hens' eggs, but these may have been taken from waste. Corn represented more than 58% of the food in August and was also commonly consumed in July and September. Mast comprised almost 46% of the annual food and was 84% of the diet in January when other food items were scarce. Other vegetable matter reported by other authors in the breeding season diet include green shoots, apples, crabapples, bladdernut blossoms, and sugar maple buds. Additional invertebrates reported in the diet include tent caterpillars and their eggs, linden looper moths, geometer moth larvae, tussock moths, cicadas, and wasp larvae. Vertebrates are a very small proportion of its diet and most of these are birds. In residential areas, nest depredation by the Blue Jay may be more frequent. In some areas, the main predator of Blue Jay nests has been other Blue Jays. It has been documented eating eggs, nestlings, and young fledglings of Rose-breasted Grosbeak, House Sparrow, Mourning Dove, Purple Martin, Northern Cardinal, Swainson's Thrush, and White-winged Crossbill. It appears to be inefficient at capturing more mature small birds and mammals. Rarely, it attacks day-flying bats; an attack on a red bat by a group of Blue Jays was interrupted by humans so the outcome was not determined. Blue Jays captured in idle lobster traps in Maine ate the flesh of other jays that had already starved to death (Atkins 1990; Clay 1959; Cline and Hatt 2011; Graber et al. 1987; Holt 1918; Johnson and Johnson 1976; Langevin and Dauphin in Gauthier and Aubry 1996; Laskey 1958a; Madge and Burn 1994; K.G. Smith et al. 2020; Steinberg and Tozer 2003; Tarvin and Smith 1995; Tozer 2012; Tyler in Bent 1946). In spring in Ontario, it has been observed feeding on icicles created by sugar maple sap (Simpson 2025). In New Brunswick, Morris et al. (1958) found no relationship between the abundance of the Blue Jay and numbers of spruce budworms. Mitchell (1952) examined the contents of 9 stomachs during a spruce budworm outbreak in Maine. By volume, they contained 0 and 2% budworm larvae and pupae.

The Blue Jay caches hard mast beginning in August, but particularly in September and October. Six birds each cached 3,000-5,000 acorns 1 autumn. While caching, 2-5 acorns or as many as 15 beechnuts are taken at once. Initially, it harvests acorns directly from trees, but later takes them from the ground once abcission has occurred. It also caches chestnuts and beaked and American hazel nuts, and occasionally egg shells, a source of calcium. Oak species that it caches acorns from include white, bur, chinquapin, Hill's, black, pin, and red, and it may prefer smaller nuts from beech and pin oak. It cannot subsist entirely on acorns and loses weight if it tries to do so. It was originally thought that it ate acorns infested with acorn weevil larvae to obtain protein supplements in the diet. Subsequent studies demonstrated that it selects healthy acorns and there is no evidence of consumption of acorn weevil larvae by wild birds. It may also cache unshelled peanuts taken from feeders. All caching apparently occurs within the bird's home range. It has been documented flying as far as 4 km for beechnuts and 1.9 km for acorns. It is highly selective about habitats that caching occurs in. In Iowa, most acorns were cached in woodlands, woodland clearings, and woodland edge habitats. Firebreaks and short-grass habitats were used according to availability for caching, and tall-grass areas were avoided. Use of grasslands for caching increased after they were burned and plowed areas may be used. Each nut is buried separately in the ground within a radius of 1-3 m and caches are typically covered with a leaf or pebble. It selects different areas for caching on each trip, and subsequent caching areas may be more than 100 m apart. The Blue Jay rarely caches food above

ground in tree crevices or old bird nests (Dixon et al. 1997a, 1997b; Graber et al. 1987; Henry and Franks 1987; Johnson et al. 1997; Johnson and Webb 1989; K.G. Smith et al. 2020).

Because of its habit of dispersing acorns a long distance, the Blue Jay is a keystone species for oak forest ecosystems and other species that inhabit them. The rapid postglacial dispersal of oaks has been attributed to the Blue Jay. From a single Wisconsin woodlot, approximately 150,000 beechnuts were dispersed by jays, and an estimated 5-6% of an oak crop was dispersed. It selects healthy acorns and caches them in ideal habitat for oaks, thereby enhancing probability of successful dispersal. From a total cache of several thousand nuts, about 150 oak seedlings per ha germinated and survived the first year. In a Virginia oak stand, jays removed an estimated 133,000 of 221,000 acorns (54%). Of the acorns remaining below trees in the woodlot, 43% had been eaten by jays and many of the remaining acorns had fungal or insect infestations, so that the proportion of viable acorns remaining near the trees was small. Distances between collecting trees and caches averaged 1.1 km (range 100 m to 1.9 km). Ninety-one percent of caches were in lawn or bare soil and an acorn was cached in a site unsuitable for germination only once. Most acorns taken were from pin oak; red oak and white oak were not used. White oak may not have been chosen because its acorns had already germinated beneath seed trees and red oak acorns may have been too large to swallow. In a laboratory study, the preference of Blue Jays for acorns of white oak, pin oak, black oak, and red oak, and shagbark hickory nuts was tested. They showed a clear preference for pin oak and strong avoidance of red oak acorns when alternative foods were available. White oak and black oak acorns were selected intermediately; shagbark hickory nuts were never used. Preference was negatively correlated with acorn size and the proportion of the seed consisting of a hard seed coat. When other food was unavailable, it readily took small red oak acorns. The large red oak acorns were mostly avoided but still used by some birds. In another study, acorns of bur and red oak were avoided due to their large size unless no other food was available. Pin oak was preferred over black and white oaks (Darley-Hill and Johnson 1981; Johnson and Webb 1989; Johnson et al. 1977; Moore and Swihart 2006; Richardson et al. 2013).

Cowbird parasitism of the Blue Jay is rare, with only 3 or 4 records; parasitism has not been documented in Ontario. In 25 experimentally parasitized nests, all eggs were rejected, 23 by ejecting eggs from the nest and 2 by abandoning the nest (Rothstein 1975; K.G. Smith et al. 2020). Because it is an egg rejecter, parasitism rates may be higher than reported.

Habitat loss and degradation do not appear to be problems due to the high diversity of habitats used. Extensive urbanization or deforestation may reduce or extirpate local populations (K.G. Smith et al. 2020). In many areas, the Blue Jay may be more abundant in towns than in rural areas (K.G. Smith et al. 2020). Graber et al. (1987) concluded that declines between 1907 and 1957 may have been due to conversion of edge habitats to blocks of habitat. In Pennsylvania, Rohnke and Yahner (2008) conducted bird surveys in a forest 16 years apart. In the interim, density of tall shrubs increased, but density of canopy and subcanopy trees and short shrubs declined. During this period, the Blue Jay increased by 219%. In New York, Brooks and Bonter (2010) surveyed the number of territories over a 35-year period in a field that was allowed to regenerate, a forest, and a managed Christmas tree plantation. There were significant increases in the number of territories in the

regenerating area and plantation, but no change in the forest. Although the plantation was maintained in early succession stage over the study period, the trees were allowed to grow taller.

The West Nile virus killed large numbers of Blue Jays. McCracken (2003a) predicted that its population would initially decline significantly, but that it should be able to recover. Kilpatrick et al. (2007) identified the Blue Jay as the species most compatible for accepting the virus and concluded that the virus had had significant effects on populations. The Blue Jay is a common resident in urban areas where it is most likely to encounter the vector. Evidence of range-wide population recovery was evident by 2005 (K.G. Smith et al. 2020).

It has been suggested that nest success is greatest in suburban areas due to fewer nest predators, and that nests closer to houses are more successful because humans may deter predators. This may not be the case in Ontario, where major nest predators such as raccoons, domestic cats, and gray squirrels are abundant in urban areas and have little fear of humans. Predation rates in suburban areas of Arkansas were not affected by nest-tree species or nest location within trees. Nest success was higher when the nest was in a patch containing several nest trees of the same species, size, and vine cover. This suggested that the more complex the habitat and the more similar the nest site was to the surrounding area, the less likely that predation would occur. This relationship did not hold true in Florida (Tarvin and Garvin 2002; Tarvin and Smith 1995).

Densities in forests appear to be unaffected by selective and diameter-limit logging, and densities may be higher in logged than unlogged areas. Forest thinning that retains snags results in higher densities than management that removes snags (Webb et al. 1977). Tozer et al. (2010) studied the effects of group-selection harvesting in tolerant hardwoods in Algonquin Park. Typical harvests affected about 5% of the stand area; intensive harvests affected about 20% of the stand. The Blue Jay increased significantly in response to intensive group selection in the first or second year after harvesting. Jobes et al. (2004) reported similar results for single-tree selection. The Blue Jay was significantly more abundant in stands that had been logged recently than in control stands and those that had been logged 15-20 years previously. In the Carolinian Forest Region of Ontario, its abundance was negatively associated with basal area, and it was more abundant in harvested than uncut woodlots (Holmes et al. 2004). In the Canadian Shield of Ontario, there was no difference in its abundance in early and mid-successional clear-cuts and burns in the same seral stages. It was equally abundant in early successional, mid-successional, and mature stands (Zimmerling et al. 2017). In Vermont, Blue Jay territories occurred both in clear-cuts and adjacent northern hardwood forests (Lent and Capen 1995). In Minnesota, it decreased in an area when riparian buffers were partially harvested but rebounded quickly in subsequent years. In another area in Minnesota, it responded positively to partial harvest of riparian buffer strips (Hanowski et al. 2002, 2005).

Farwell et al. (2019) examined the response of the Blue Jay to shale gas infrastructure (well pads, access roads, and pipelines) in contiguous forest in West Virginia. It was significantly less abundant close to these features than distant from them.

Schneider and Miller (2014) examined the effects of invasive shrubs on the Blue Jay in the Chicago area. It was negatively correlated with invasive shrub stem density, most likely related to

presence of common buckthorn, because it was positively correlated with abundance of nonnative honeysuckle species.

In North Carolina pine-oak forests, the Blue Jay responded favourably to fire (Rose and Simons 2016).

In New Jersey and Pennsylvania over a 15-year period, hemlock declined from representing 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The Blue Jay responded favourably to hemlock decline and increased in abundance (Toenies et al. 2018).

In North Carolina, abundance of the Blue Jay was significantly correlated with temperature, suggesting that it might benefit from climate change. This area was in the Appalachian Mountains where temperatures are lower than other areas at the same latitude (Lumpkin and Pearson 2013).

Status

The Blue Jay has always been common in Ontario. McIlwraith (1894) considered it common and Baillie and Harrington (1937) concluded that it was a fairly common summer resident north to at least southern Kenora District and the Missinabi River. They stated that it was much more common in southern Ontario, breeding commonly north to central Sudbury District and Thunder Bay. In the Kingston area, it was considered common in 1864, and it still is (Weir 2008). James (1991) considered it common in the south, becoming uncommon in the north to Red Lake and Kapuskasing.

The second atlas indicated that there had been no change in the distribution of the Blue Jay since the first atlas. It was common in the Carolinian and Great Lakes–St. Lawrence forest regions where breeding evidence was documented in almost every square. It was less abundant in the Boreal Forest Region, where it occurred only in the southern portion from about Sioux Lookout east to Fraserdale. There was no difference in its probability of observation province-wide or in any region except the Boreal Forest Region, where a significant increase was documented. It was most abundant in the southern Canadian Shield and south of the Shield in the Great Lakes–St. Lawrence Forest Region. Urban areas with mature trees, such as Toronto, Hamilton, Ottawa, and Kingston supported high densities as did the orchards in Grey County and Niagara Region (Coady in Cadman et al. 2007).

In other areas, Blue Jay populations are increasing in suburban habitats and rural woodlots, but declining in larger forest blocks (Graber et al. 1987; K.G. Smith et al. 2020). Long-term (1970-2021) population trends determined by the Breeding Bird Survey indicate annual increases of 1.06% in Canada and 0.826% in Ontario. The short-term (2011-21) trends were annual increases of 1.87% in Canada and 1.27% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

Most surveys reflect only relatively recent trends, but Graber and Graber (1963) compared populations between 1907 and 1957 in Illinois. Although the Blue Jay was still very common in the latter period, the population declined 50-80% with declines in all habitats except suburban areas.

POSTFLEDGING PERIOD

Fledglings move en together away from the nest, and are usually 25-100 m distant on the second day. Although fledglings are capable of feeding themselves at age 3 weeks, they follow the adults

for another 1 or 2 months to be fed. Some disperse as soon as they are independent; others may wait until autumn or winter (K.G. Smith et al. 2020).

MIGRATION

The nature of the Blue Jay's migration is poorly understood. Two patterns are evident: at least some birds remain year-round throughout the range, even in the extreme north; and at least some depart in autumn from all areas except Florida and the Gulf Coast. Birds that depart in autumn are replaced by those from further north, so that most winter populations are a combination of permanent residents and migrants. The distance travelled by migrants is highly variable and, in most areas, many jays are resident. The proportion of birds that migrate is probably not more than 20% even in northern portions of the range. Individuals may respond differently year to year, being resident some years and migratory in others. An adult that bred at 1 location may summer substantially south in subsequent years, or return to the same area after an absence of 1 or more years (Graber et al. 1997; Nunneley 1964; Smith 1986a; K.G. Smith et al. 2020).

The factors that trigger migration are uncertain, but may be related to food supplies. Some authors contend that most migrants are young birds that may be forced to migrate by more dominant resident adults. Most authors demonstrated that there is no difference in propensity to migrate among sexes or age classes. Fluctuations in abundance of mast may affect the likelihood of birds migrating, but studies report mixed results. Peak autumn flights in Ontario are associated with poor crops of acorns, beechnuts, and hazelnuts. No relationship between number of migrants or overwintering birds and mast production was observed in Wisconsin, a small insignificant correlation was evident in Missouri, and numbers were highly related to amount of mast in Pennsylvania and Iowa. The number of birds migrating has declined, and this has been attributed to increased numbers of bird feeders (Bock and Lepthien 1976a; Carpentier 2010; Hickey and Brittingham 1991; Johnson et al. 1997; Langevin and Dauphin in Gauthier and Aubry 1996; Overlease and Overlease 1987; Smith 1986b; Smith and Scarlett 1987; K.G. Smith et al. 2020).

At Holiday Beach, the most favourable conditions during the first and mid-portions of the autumn flight appear to involve light winds from a northerly or easterly direction, with cold or cool overnight temperatures followed by warm daytime temperatures. Persistent rain and sustained winds in excess of 15-20 km per hour greatly hinder or halt migration. Later in the season, winds from almost any direction do not appear to influence migration (Carpentier 2010).

Migration appears to be strictly diurnal. Flights usually start shortly after dawn, decrease by mid-morning, and cease by noon. During heavy flights, passage may continue until 1500-1700 hours, but with considerably fewer birds later in the day. Occasionally flights cease at noon, but resume for a while later in the afternoon. In New Jersey, 61.2% of birds passed through in the first 2 hours of daylight; morning fogs delayed flights (Graber et al. 1987; K.G. Smith et al. 2020; Yunick 1995a). Although it migrates over a broad front, the Blue Jay also follows landmarks such as rivers and shorelines. In autumn, migration is more concentrated along rivers, but cross-country flights are still evident. Spring destinations of birds are unknown in the Kingston area, but some may move along the St. Lawrence River into Quebec. During autumn, it is very obvious, travelling southwest along the lakeshore from Ivy Lea to Prince Edward Point. Although a few cross Lake Ontario at Prince Edward Point, most continue westward along the shoreline. Birds banded along the northern shore

of Lake Ontario have been recovered along Lake Erie and in Detroit, Kentucky, and Louisiana, suggesting that they move down the Mississippi Flyway. Flocks observed leaving Point Pelee in autumn flew directly over the lake to Ohio without stopping at Pelee Island. Many birds cross over at Sault Ste. Marie into Michigan and then Illinois. There is 1 record of a Blue Jay banded in Ontario in winter being recovered in Tennessee 2 winters later. There are numerous examples of birds spending the winter in geographically disparate areas in Canada and the United States, suggesting that irregular migration is a response to changes in natural food supplies (Brewer et al. 2018; Graber et al. 1987; Smith 1986a; K.G. Smith et al. 2020; Tyler in Bent 1946; Weir 1989).

Canadian banding records indicate that more than 50% of juveniles were recovered in a different state or province than where they were banded compared with 30% of adults. Hatch-year birds tended to travel further than adults. Fifty-one percent of hatch-year birds moved more than 100 km and 32% moved more than 500 km compared with 30% and 14% respectively for adults (Brewer et al. 2018).

Spring migration throughout the Blue Jay's range is concentrated from mid-April to late May, and from mid-September to late October in autumn (Graber et al. 1987; K.G. Smith et al. 2020). Autumn migration in Ontario occurs throughout September and October, with peaks from mid-September until mid-October and greatest numbers in late September and early October (Carpentier 2010; Curry 2006; Tozer 2012; Weir 2008).

Graber et al. (1987) summarized habitat preferences during migration in Illinois. Spring densities were highest in forest edge and shrub habitats, and the Blue Jay preferred upland habitat to lowlands. In autumn, densities were also greatest in forest edge and shrubs, and least in pines. In Pennsylvania, it was associated with more fragmented landscapes during spring migration and with larger woodlands in autumn (Keller and Yahner 2007). During spring migration in Minnesota and Wisconsin, it was significantly more abundant in upland than riparian forests (Kirsch et al. 2013).

James (2010) studied the behaviour of autumn-migrating Blue Jays in relation to tree cover and wind turbines near Port Burwell. Large numbers of jays moved along the shoreline of Lake Erie, but they also occurred as far inland as 2 km. Where they were forced to decide whether to fly across an untreed opening or follow treed fence lines or other vegetation, 45.8% continued to fly across the gap and 54.2% went out of their way to follow trees (n = 4,380 jays). They followed cover at other locations such as treed watercourses and wooded ravines. Birds frequently moved in a zigzag pattern that more than doubled the distance travelled during their westward migration. In areas along the shoreline where there were no gaps in tree cover, 86.3% of 8,160 jays continued to fly along a direct route. The avoidance of open areas by many jays may have been an antipredator tactic because Sharp-shinned Hawks, Cooper's Hawks, and American Kestrels were migrating at the same time. The jays did not demonstrate any avoidance reaction to the wind turbines and they appeared to have no appreciable effect on the migration of Blue Jays.

Loss et al. (2014) analyzed bird collisions with buildings throughout the United States. The Blue Jay was among the most vulnerable species for striking residences 1-3 stories tall, where it was 26.5 times more likely to suffer a collision than average. It was not on the lists of the 20 most vulnerable species for striking low-rises or high-rises.

In Pennsylvania, an invasion by the viburnum leaf beetle resulted in almost complete mortality of the southern arrowwood, formerly the third most abundant shrub. After the infestation, the number of spring migrating Blue Jays declined significantly (Smith and Hatch 2017).

The Blue Jay is common to locally abundant during migration, and more numerous in autumn. Counts indicate that there is a 2-year cycle, with lower counts in even-numbered years. There may also be a longer-term trend of 7-10 years between high and low points in the cycle (Chartier 2005; Curry 2006; Weir 2008). Numbers from Holiday Beach covering a 28-year period indicate an average of 292,126 jays per year. Most followed the Lake Erie shoreline with few deviating further south. Largest numbers occur in southwestern Ontario in autumn as birds coming from the east join those coming from the north and those in the west (Carpentier 2010).

WINTER

Winter habitat preferences are similar to those of summer, with the principal areas being forests, forest edges, shrublands, and suburban or rural areas with bird feeders. In Ohio, the Blue Jay's presence in forest fragments was correlated with an increase in edge, and its density increased with shrub cover. In forest cover, it appears to prefer lowland deciduous forests; pine forests are least favoured (Bock and Lepthien 1976a; Doherty and Grubb 2000; Graber and Graber 1963; Graber et al. 1987). In Arkansas, Kentucky, and Mississippi, it was equally abundant in row-crop fields with and without buffers of native grasses and forbs (Evans et al. 2015).

In Maryland, 2-5 birds roosted in a front yard in several small oaks that retained their leaves until spring. Branches used as perches were 1.2-6.0 m from the ground (Turner 1965).

The Blue Jay is nonterritorial in winter and tolerates large numbers of its species while feeding. There is a dominance hierarchy, with only one feeding from a perch at a feeder and being replaced when it is finished. Perches on an experimental feeder were large enough to support 4 jays, but typically only one used it at a time; when 2 were present, they were usually birds that had previously nested together. The relative rank of a jay present in successive winters does not change much (Racine and Thompson 1983; Whittam and Francis 2000).

Wintering jays form groups that share a common home range, often resting together during the day and roosting together at night. Individuals may move by themselves within this home range or with their former nesting partner, or the group may move as a unit. A winter group in Kansas consisted of 8 pairs that tended to move as a unit within a home range of approximately 55 ha. In Massachusetts, group sizes remained fairly constant over the course of each winter, and consisted of 14, 18, and 49 individuals over 3 years. This group focused its activity on 1 feeder, and members rarely, if ever, visited other feeders approximately 600 m away. Many jays were not observed every week, but reappeared later. Some appeared irregularly and were not really part of the social group. Most birds that survived rejoined the group the following year. Offspring of birds that had been part of the group often joined, and occasionally birds that had been casual visitors to the group previous years joined. Although many birds form groups around food resources, others spend the winter singly or with their former mate (Fitch 1958; Racine and Thompson 1983; K.G. Smith et al. 2020).

The Blue Jay is an opportunistic feeder in winter. In the southern portion of its range, cached mast is not eaten in winter but is eaten in spring, used in courtship feeding, or fed to incubating

females. Cached food is an important food source in the winter in the north. In Algonquin Park, it fed on insects in cocoons obtained by stripping bark off decaying trees. It may feed on dead adult and larvae bald-faced hornets taken directly from the nest, and also eats paper wasps. When food is abundant in winter, it continues to cache; it has been observed caching dead white-footed mice in snow. It occasionally consumes carrion in winter, and dog food, bread, and table scraps (Graber et al. 1987; Martin 1960; Smith 1986b; K.G. Smith et al. 2020; Tozer 2002a; Whitford 1996).

The Blue Jay is a widespread user of winter bird feeders, visiting virtually all feeders in its winter range regardless of habitat. Numbers seen at rural feeders are more than twice as high as those at urban ones, and jays are more likely to visit rural feeders all winter. Numbers are higher at northern than southern feeders, but northern populations are not higher in the north, suggesting greater dependence on feeders. At feeders, it prefers foods with shells, facilitating caching and delaying spoilage. Favourite feeder foods are striped sunflowers, unshelled peanuts, mixed seeds, black oil sunflowers, cracked or whole corn, hulled peanuts, pet food, meat scraps, baked goods, and water. Occasionally it eats millet, canary seed, hulled sunflowers, safflower, milo, wheat, peanut hearts, suet, peanut butter mixes, bird puddings, fresh or dried fruit, sugar water, and popped corn (Dunn and Tessaglia-Hymes 1999). Other foods it has taken at feeders include cracked butternuts and walnuts, and cheese (Graber et al. 1987). Horn et al. (2014) provided participants in Canada and the United States with 10 different types of seeds and 3 types of feeders. A total of 24,072 feeding observations were made for the Blue Jay. It preferred whole peanuts and platform feeders.

Based on Christmas Bird Count (CBC) data, Smith (1986a) concluded that the Blue Jay was unaffected by severe winter weather. In Pennsylvania, Overlease and Overlease (1987) found that numbers declined in severe weather and concluded that it may be vulnerable to depth and duration of snow cover, especially when accompanied by low temperatures. In Illinois, Graber and Graber (1979) did not detect an overall decline in numbers as a result of prolonged severe winter weather. There was a significant shift in habitat use, with jays moving from lowland forests to urban residential areas. They found 4 carcasses, indicating that the storm caused some direct mortality.

The Blue Jay is a common winter resident in the south and uncommon in the north to Thunder Bay (James 1991). Mills (1981) reported that it was virtually absent some winters in Muskoka and Parry Sound and abundant in others. CBC data indicate an annual population increase of 1.74% for Ontario for 1970-2021 and 2.12% for 2009-21 (National Audubon Society 2022). Winter numbers in the west, east, and northeastern parts of its range increased dramatically whereas southern densities declined. It was postulated that the overall increase in numbers and change in winter distribution patterns was due to an increase in bird feeding (Bock and Lepthien 1976a). Winter increases observed in Wisconsin, the eastern states, and Missouri were also attributed to bird feeders (Hickey and Brittingham 1991; Smith 1986a, 1986b). In Illinois, winter populations declined 30-45% between 1907 and 1957, but populations in urban residential habitat increased during this period (Graber et al. 1987).

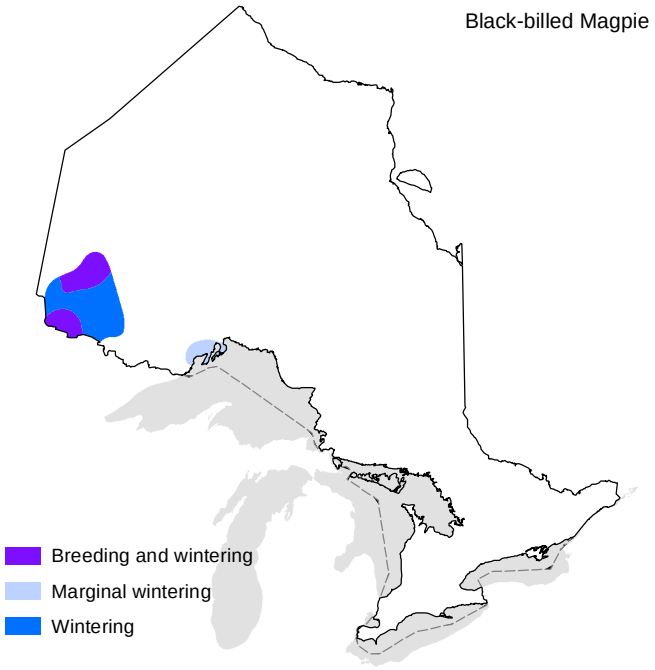
Black-billed Magpie

Pica hudsonia

BREEDING SEASON

Habitat Requirements

In Ontario, the Black-billed Magpie breeds only near Dryden, between Rainy River and Fort Frances, and at Ear Falls. Habitat in Rainy River District consists of relatively open areas dominated by agricultural lands. Most nests there were in dense shrub areas at edges of agricultural fields and marshes. Habitat near Ear Falls consisted of open woodland dominated by white birch, black spruce, and balsam fir, with scattered tall white pines. Magpies used the interface between this woodland and the headpond of a hydro generation station (Elder 1986, 2006; James 2014; Peck and James 1987, 1997).



The Black-billed Magpie is associated with open, human-altered landscapes; it avoids extensively treed areas. Habitat is characterized by linear strips of riparian vegetation and open meadows and grasslands with scattered trees and shrubs. In Kansas, magpies started nesting at a military base after habitat changed from open grassland to grassland containing savannahs of nonnative shrubs and trees. Nesting often occurs in clumps of trees and shrubs near sources of food and water, such as picnic areas and highways where road-kills are common. It also nests at forest edges and in forest clearings and old barns. It colonized the City of Edmonton in urban areas where there are many mature deciduous and coniferous trees interspersed on lawns and in gardens. Presence of water near the nest appears to be important in many areas (Andrén 1992; Bailey 2003; Buitron 1988; Campbell et al. 1997; Dhindsa and Boag 1992; Evenden 1947; Linsdale 1937; Madge and Burn 1994; Sinclair et al. 2003; Trost 2020; Winter et al. 2000). In Utah, it nested more in shelterbelts, riparian areas, and orchards than expected; monotypic hawthorn stands were used less than their availability. Underused areas had less total cover (10.1% compared with 16.6%), lower canopy closure (11.3% compared with 18.2%), and smaller patches of trees (45.1 m^2 compared with 87.4 m^2; Reese and Kadlec 1985).

In Nevada, magpies roosted together during the breeding season in tall willow clumps at the edge of a slough (Linsdale 1937). Breeding birds roost in trees within the territory, or in the nest if eggs or young are present.

Most Ontario nests were in willow trees at edges of farm fields or marshes. One was in a trembling aspen in an aspen woodlot, one was in a spruce tree, and one was in an open hay shed. Nests in trees were 2-8 m from the ground; the nest in the shed was 5 m up (James 2014; Peck and James 1987, 1997).

Many authors stated that nest-tree species are used according to availability. Others found that the magpie prefers thorny trees, or that tree or shrub structure is more important with most nests among dense growths of twigs and branches. In Edmonton, conifers were used 1.8 times their availability in urban areas and 12 times their availability in suburban areas. In British Columbia and the Yukon, most nests were in deciduous species. It has nested in Russian olive, willow, Siberian elm, Manitoba maple, hawthorn, alder, aspen, birch, cottonwood, fir, juniper, spruce, pine, elm, mountain-ash, and ash. Some magpies build nests over water where they are less accessible to snakes and humans. It frequently nests on utility poles; in Colorado several nests were supported by 3 wires well out from the poles. Occasionally it nests in barns or deserted buildings, or rarely on the

ground where there is a scarcity of trees and shrubs. One nest was on a railroad bridge under a rail and between 2 ties, and at least 1 train a day passed over it. A Wood Duck box was used in Alberta in 2 consecutive years. This appears to be the first record of a magpie nesting in a confined cavity. Nest heights of 0-19 m have been reported; most are 2-5 m up. Nest height may be influenced by the structure of available trees and by disturbance. An undisturbed population in Edmonton nested at an average height of 5.0 m compared with 9.0 m and 9.9 m by populations frequently disturbed by humans. Selection of nest height may be a compromise between exposing high nests to wind and cold and exposing lower nests to predation. Usually a new nest is built each year, but old nests are occasionally refurbished and some have been used 3-6 years. Often domes are taken from old nests and used in new ones (Buitron 1988; Campbell et al. 1997; Dhindsa et al. 1989; Erpino 1968; Linsdale 1937; Linsdale in Bent 1946; Reese and Kadlec 1985; Sinclair et al. 2003; Stauffer and Johnson 2011; Stone and Trost 1991; Trost 2020). Nests may be closely associated with raptor nests and may be in the side or bottom of raptor nests such as Ferruginous Hawk, Prairie Falcon, Bald Eagle, and Osprey. Magpies benefit by feeding on the remains of the raptor kills (Linsdale 1937).

The magpie has highly variable territorial behaviour, depending to a large degree on habitat and food availability. In Wyoming, no signs of aggression were observed and there were 6 active nests in a 0.48-ha woodlot. When it is territorial, an area around the nest is defended, but foraging may occur 300-400 m from the nest. Foraging areas are undefended and 2 or more pairs may feed side by side. Neighbouring birds do not forage near other nests. In Utah, when intruders approached within 30 m of the nest, they were chased away about half the time, but only to a distance of 40 or 50 m. Territory size was estimated at 0.5 ha. Some nests were only 10 m apart, but visually isolated. In South Dakota, nesting birds expelled intruders within 30 m of the nest, but dominated other birds in an area of 3 ha. At road-kills, the pair whose nest was closest dominated other magpies and, within a pair, the male dominated the female. In Edmonton, nests tended to be regularly spaced, with mean distances between nests ranging from 117 to 150 m over 6 years. The nearest nests were 50 m apart, but they were visually isolated. Territories ranged from 1.1 to 1.7 ha over the years (average 1.5 ha). Territories were contiguous or slightly overlapping. They were defended from before egg laying until late incubation. In many areas, nests are clustered and nesting appears to be colonial. In the Yukon, nests were usually 50-200 m apart in loose colonies; only 2 of 29 nests were isolated. In some areas, the magpie nests in clusters with groups of nests often separated by unsuitable habitat. The territorial system varies depending on food resources. When there is a sudden increase in food, nests may be clustered and territoriality abandoned. When a rich supply of food disappears, territoriality may be initiated. These responses have been observed when a steer carcass became available, fish hatcheries closed, and an abattoir was present. No information is available on home range size. In South Dakota, males regularly fed 0.5 km from the nest (Birkhead 1991; Buitron 1988; Dhindsa and Boag 1992; Erpino 1968; Knight 1988; Linsdale in Bent 1946; Reese and Kadlec 1985; Sinclair et al. 2003; Stone and Trost 1991; Trost 2020).

Natal philopatry is fairly high in dominant males. Young disperse after the breeding season, but return the following year in an attempt to inherit the territory. They typically have to wait for the parents to die or move on before the territory can be acquired. More submissive siblings and females disperse further and establish a territory if they can find a reliable source of food. In South Dakota,

only 1 male and 2 females of 126 fledglings (2.4%) returned to breed the following year and another 2 males returned the subsequent year. Two fledglings were found 6-9 km from the natal site the following year; one was found dead 200 km away. Adult site fidelity is high, with most Idaho pairs breeding in the same territory all their lives. In South Dakota, pairs nested in the same area year after year, moving an average of 280 m from the previous nest (range 0-790 m). There was no correlation between distance moved and breeding success the previous year or whether mates had changed. In Edmonton, 72% of males and 70% of females nested in the same territory as the previous year, with 69% of pairs retaining the same territory. Distance moved from the previous nest averaged 144 m (range 0-527 m). Of 8 that changed territories, 5 moved to the adjacent territory, 1 moved 2 territories away, and 2 moved 3 territories away (Birkhead 1991; Buitron 1988; Dhindsa and Boag 1992; Trost 2020; Trost and Webb 1997; Wang and Trost 2001).

Limiting Factors

Eggs are most likely to be in Ontario nests from late April until the end of May (Peck and James 1987). Well-built nests may take longer than 3 months to construct; a shoddy one may be put together within a week. In Wyoming, nests took an average of 43 days to build. Five to 7 weeks appears typical for building a nest; birds that return to territories earliest take the longest time. In Alberta, juveniles took an average of 67.3 days to complete a nest compared with 37.5 days for adults. Eleven days to 3 weeks may elapse between nest completion and initiation of egg laying. Eggs are laid at the rate of 1 a day, with occasional 1-2-day interruptions. The incubation period is difficult to ascertain as it is uncertain when it begins. Approximately 23% of time is spent incubating on the first day compared with 90-95% by day 7 of laying. Eggs hatch in about 18 days, (range 16-21 days). Hatching is asynchronous and occurs over 2-3 days in clutches larger than 6 eggs. Young fledge at age 19-32 days, but usually when they are 26-28 days old (Birkhead 1991; Buitron 1988; Campbell et al. 1997; Erpino 1968; Komers and Boag 1988; Linsdale in Bent 1946; Trost 2020; Trost and Webb 1997).

A single brood is raised annually. Renesting may occur once or rarely twice after loss of a clutch. Renesting occurs 13-16 days after loss, occasionally in the same tree but more often within the territory in a different tree an average of 90-135 m away. Some birds move out of their territory to renest. Clutches of 1-11 eggs and 13 eggs have been reported, but 5-8 eggs is the typical clutch size. Mean clutch sizes were 6.5 eggs in Utah, 6.2 in South Dakota, 6.1 in Wyoming, 7.0 in Idaho, and 6.6 in Alberta. Early nesting birds have larger clutches (6.6 eggs compared with 5.3 eggs), adult females have larger clutches than yearlings (6.3 eggs compared with 5.2 eggs), females paired with their previous mate have larger clutches than females with a new mate, pairs with an adult male have larger clutches than those with a juvenile male (6.3 eggs compared with 5.0 eggs), and first nests have larger clutches than replacement clutches (6.5 eggs compared with 5.8 eggs). Food is often limited for nestlings, so brood reduction is common due to starvation, siblicide, and possibly infanticide. Usually only 2-4 young fledge (Buitron 1988; Campbell et al. 1997; Dhindsa and Boag 1992; Dhindsa et al. 1989; Erpino 1968; Linsdale in Bent 1946; Reese and Kadlec 1985; Reynolds 1996; Trost 2020; Trost and Webb 1997).

Both sexes are capable of breeding at age 1 year, but more yearling females breed than males. Of 7 males in Alberta, 1 nested the first year, 5 at age 2 years, and 1 at age 3 years; all 4 known-age females nested their first year. In South Dakota, 9% of breeding birds were yearlings. In Utah, first-

year birds constituted 20-47% of the breeding population. Yearlings were 40% of known-age females and 47% of males. The mating system is monogamous. Some pairs mate for life and long-term fidelity is common, but divorce also occurs. In South Dakota, 8% of pairs divorced between seasons and 4% split up within a breeding season during nest building. In Edmonton, 50% of males and 62.5% of females switched mates at least once. Divorce was not related to previous reproductive success. Mate switching by males was associated with changes in territory, usually to a better breeding territory. Lost mates are frequently replaced within 24 hours, with the new mate assisting with the breeding cycle regardless of what phase it is in (Buitron 1988; Dhindsa and Boag 1992; Linsdale 1937; Reese and Kadlec 1985; Trost 2020).

The magpie is an opportunistic forager and scavenger. Most foraging occurs on the ground in the open where there is vegetation 0-20 cm tall. It tends to avoid areas of bare soil (except recently plowed fields where invertebrates are exposed) and tall vegetation. It rarely forages in trees. It often feeds near water or where the water table is high and invertebrates are near the surface. Ground litter and other potential cover for prey, including cow dung, is flipped over with the bill and feet. It has a symbiotic relationship with large ungulates such as deer, elk, moose, and domestic livestock. It frequently lands on them to feed on ectoparasites, particularly winter ticks on moose. It visits roadsides, picnic areas, and landfills for road-kills and human scraps. It often steals food from domestic animals and may singly or cooperatively kleptoparasitize gulls, Northern Shrikes, eagles, coyotes, and red foxes. It may perch close to birds of prey to feed on leftovers of their kills. It also captures small mammals. Aerial capture of bats occurs rarely and flying insects are occasionally taken. It caches food, but only for short periods of time. Most cached food is perishable and retrieved within 1 or 2 days. It caches food in the ground by creating a hole with the bill, then covering the cache with grass, or a stone, twig, or leaf. Caches are spread throughout the territory or home range, with daily caches clumped together and individual caches spaced about 13 m apart. Within a few hours, original caches are usually moved closer to the nest. Magpies appear to remember where food was cached and are capable of smelling caches, so kleptoparasitism occurs (Birkhead 1991; Buitron and Nuechterlein 1985; Genov et al. 1998; Halliday 1992; Hochachka and Scharf 1986; Linsdale in Bent 1946; Madge and Burn 1994; Sarno 1989; Sinclair et al. 2003; Trost 2020).

The magpie eats mostly ground-dwelling invertebrates, seeds, and carrion, especially insects. It is more insectivorous than any North American corvid. Both parents feed the nestlings, predominantly insects and carrion. The average length of food brought to nestlings is 7 mm; grasshoppers are important in their diet. Food delivered to nestlings differs considerably from food eaten by adults. More than 94% of nestlings' food consisted of animal matter compared with 82% for parents. Most of nestlings' food consisted of insects (18% caterpillars, 11% grasshoppers, and 11% flies). During the breeding season, ground beetles, caterpillars, grasshoppers, and carrion are important foods for adults as are insects associated with carrion. In some areas, earthworms are frequently consumed. All carrion, maggots, and other invertebrates are eaten as well as meat. Ticks and moose carcasses are critical sources of food in winter and early spring. It eats bird eggs, nestlings, and small birds. The magpie may attack small- to medium-sized mammals such as ground squirrels and cottontails. In the case of larger prey, it prefers those that are already weakened or may attack them cooperatively. It has been reported pecking into sores of livestock and eating their flesh and

subsequently killing some. It is usually initially attracted by a wound or sore, but tends to make it much larger, feeding on the flesh of the live animal. Mammals may constitute about 10% of the diet. Occasionally it kills frogs, fish, crayfish, lizards, and snakes. Near Ear Falls, fish offal was an important source of food. Some vegetable matter may be consumed, usually wild fruits in late summer or autumn, but these appear to be consumed only when animal foods are lacking (Birkhead 1991; Buitron 1988; Goulden 1975; James 2014; Knight 1988; Licht and Johnson 1992; Linsdale 1937; Trost 2020).

Food availability may be a limiting factor, especially early in the breeding season and other critical times such as winter. Food abundance may influence timing of nesting as well as success and productivity rates. Breeding populations increase where food is abundant (fish hatcheries, cattle feedlots, landfills, etc.) or crash when food becomes scarce. Populations increased 1 year when a steer carcass became available early in spring, and nesting occurred earlier. Populations and timing of breeding reverted to normal the following year. Similar results have been found where magpies were fed dog food. After a late-winter storm in Alberta, 71% of nests with access to dog food survived compared with 15% of nests without supplemental food (Hochachka and Boag 1987; Knight 1988; Trost 2020).

Presence of both adults is essential to successful breeding. From the first day of laying until young hatch, the male provides the female with all her food. If the male is lost during this period, the female abandons the nest unless a replacement male is found quickly. Males do not incubate or brood, so if the female is lost before the clutch hatches or young are close to fledging, the nest fails. If either sex dies after the young hatch, a new mate may help rear the young, then nest with the same mate the following year. Occasionally, a single parent may successfully raise fledglings if a mate is lost after the young fledge. In these cases, the bird had to greatly increase provisioning rates. Of 28 nests where males were removed in Edmonton, a replacement male assisted at 32% of nests and these nests produced as many young as nests where the pair remained intact. The nests without replacement males did not produce any young. Of 5 males and 4 females whose mates were lost in South Dakota, 2 males obtained mates within a day, 2 females had mates within a month, and the remaining 5 birds did not acquire mates that breeding season (Buitron 1988; Dunn and Hannon 1989; Reese and Kadlec 1985; Trost 2020).

Spring weather may affect nesting success, with nesting occurring earlier in warm springs and later in cold springs. Early nests produce more fledglings but these nests are also at risk from late storms. Cold or rainy weather can significantly decrease success. The risk of death of nestlings due to rain is high, and is 2 times greater if rain falls on day 1 after hatching versus day 5. Probability of nestling death on any day increases by 1.3 if it is windy. Heavy rain and snow in May in Edmonton resulted in the loss of 72% of nests (Dhindsa and Boag 1992; Erpino 1968; Gerstell and Trost 1997; Reynolds 1996).

The magpie's distribution appears to be regulated by climate, corresponding to the cold-type dry-steppe climatic region. It appears to be unable to tolerate high temperatures and humidity. Death may occur when temperatures reach 36-41°C. In the east, it does not breed where more than 61 cm of rainfall occurs annually (Linsdale in Bent 1946; Root 1988; Trost 2020; Winter et al. 2000). It may shift habitat to avoid temperature extremes. In California, summer midday temperatures at

ground level exceeded its upper critical temperature, so more time was spent on fence posts and in shade. Open ground was used more in winter, because temperatures there were warmer. The winter roost was selected to avoid heat loss (Mugaas and King 1981).

Several die-offs have occurred as a result of toxic chemicals. Organophosphates are still painted on backs of cattle to control fly larvae. Magpies are highly vulnerable to this because they routinely land on cattle to glean ectoparasites (Trost 2020).

The Black-billed Magpie is highly vulnerable to human disturbance during the nesting season. Disturbance may cause extreme reactions such as females eating their eggs or small young or moving eggs to another magpie's nest. In response to disturbance, adults reduce feeding rates resulting in brood reduction. Young may also fledge prematurely, increasing risk of predation. When populations are studied intensively over several years, the number of nesting pairs frequently declines steadily (Erpino 1968; Trost 2020). Magpies that experienced nest disturbance attempted to minimize further disturbance by placing subsequent nests higher above the ground (Dhindsa et al. 1989; Knight and Fitzner 1985).

The magpie has been widely persecuted by humans. It was considered vermin because it picked at sores on livestock and was frequently shot. Some western states and provinces paid a bounty for it in the 1920s and 1930s. In 1933, 1,033 were killed in the Okanagan Valley by 2 teams of bounty hunters and an estimated 5,000 were shot in southcentral Washington in the winter of 1920-21. Although the rate of shooting has declined, it still continues. Some western urban areas still have active eradication programs. Poison bait was widely used to kill coyotes in the west. Poison grain was put out first to kill birds so that they did not take the bait; thousands of magpies were reported killed in a single county (Bailey 2003; Campbell et al. 1997; Linsdale 1937; Reebs 1986; Trost 2020).

Status

Nesting was first confirmed in the province near Rainy River on 4 May 1980. The Black-billed Magpie continues to be a rare breeder in western Rainy River District. Prior to that, the magpie was a rare autumn and winter vagrant in the province, and it still rarely occurs east of the breeding range in these seasons (Elder 1986; James 1991; McIlwraith 1894; Peck and James 1997).

The second atlas revealed that the probability of observation of the Black-billed Magpie had increased significantly since the first atlas. Breeding evidence was obtained in 39 squares during the second atlas compared with 6 during the first. Breeding is still confined to the general area of Lake of the Woods. It appears that the Ontario population experienced a 10-fold increase since the first atlas, with an estimated population of 200-250 breeding pairs (Coady in Cadman et al. 2007). James (2014) reported a small population at Ear Falls that has probably existed since the 1980s.

Elder (2006) concluded that the magpie would not move much further east than Rainy River District in Ontario. He considered it dependent upon agricultural and anthropogenic habitat and the area to the east is predominantly forested. James (2014) noted that there was no agricultural land in the vicinity of Ear Falls, but that there was considerable open habitat that may provide suitable habitat. These include clear-cuts, wide grassy hydro corridors, bedrock outcrops in forests, and grassy openings around homes and cottages. If the magpie can adapt to these habitats and

overcome any limitations posed by summer temperatures, it may be able to extend its range eastward along the trans-Canada highway.

North American populations have fluctuated considerably. The magpie disappeared from much of its range with the demise of the bison in the 1880s and to later human persecution. Numbers started to increase in the 1910s and 1920s, and it now probably occupies all of its former range. It is unknown how present-day populations compare with presettlement populations. Long-term (1970-2021) Breeding Bird Survey results indicated an annual decrease of 0.836% in Canada and an increase of 16.7% in Ontario. Short-term (2011-21) trends were annual decreases of 1.26% in Canada and 3.31% in Ontario. Results for Canada were highly reliable; Ontario results were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings remain near the nest for 1-4 weeks after which families begin wandering widely. Groups of 2-8 families may join together in areas near food and water. Adults continue to feed fledglings until they are 6-8 weeks old (Trost 2020).

Postbreeding dispersal begins in mid-July and most movements are local. Many young birds, especially males, remain within 3.5-4 km of the natal site. Females moved further from the nest than males in Idaho (1,034 m compared with 560 m), and dominant males from a brood remain closer than their subordinate siblings. Young females may move 15-25 km from the natal nest, and there are several records of long-term dispersal. At least 40 reports were received from north-central Ontario from Sioux Lookout and Nakina south to Atikokan and Terrace Bay in 1972. Two Saskatchewan juveniles moved 580 km and 151 km southeast and a Wyoming bird moved 354 km. Large flocks rarely occur: 50 were reported in Idaho in October and 1,500 in Death Valley, California in October 1919 where it had never been seen before (Buitron 1988; Speirs 1985; Trost 2020; Trost and Webb 1997).

The magpie is less specific in its habitat requirements outside the breeding season, but is still strongly associated with human-altered landscapes. It avoids forested areas, except for roost sites, and favours open habitats. Its slow flight makes it vulnerable to raptors, so it seldom strays far from cover. Near habitation, it frequents livestock feedlots, barnyards, landfills, sewage lagoons, rural and suburban parks and gardens, and urban gardens. In natural habitats, it prefers riparian thickets, wet meadows, open forests, shrubby gullies in grassland areas, lakeshores, and beaver ponds (Campbell et al. 1997; Trost 2020).

Communal roosts are important in the nonbreeding season, and they are used traditionally. Prior to winter, their main function appears to be related to pair formation and establishment of dominance among yearlings. Even during the breeding season, breeding adults may join nonbreeders more than 1 km from the nest except during incubation and when young nestlings are being brooded. Once young have fledged, they begin following their parents to roosts, as far as 4 km from the nest. A large proportion of a local population may gather at a single roost. Roosts tend to be in dense thickets of trees or shrubs near major food sources (Buitron 1988; Campbell et al. 1997; Trost 2020). Reebs (1987) characterized 12 Alberta roosts. Two were in stands of deciduous trees and the rest were in conifers. All were sheltered in a river valley, except for one in a spruce

hedgerow in an urban area. One deciduous roost was a dense thicket of trembling aspen. The other was dense trembling aspen, white birch, and shrubs. Tree density in these roosts was 14,511 and 10,873 per ha, with average tree heights of 6.1 m and 5.9 m and average diameter at breast height of 5.2 cm and 5.9 cm. Coniferous roosts were typically tall, slim white spruce where crown coverage was more than 50%. The lower halves of trees within the stand were completely defoliated leaving dead limbs where birds could perch. Tree density in coniferous roosts was 2,200-14,900 per ha, but mostly 3,000-5,000. Birds consistently roosted on the side of trees with longer and more numerous branches. Although most birds roosted communally, some roosted singly. Within a roost, there was only 1 bird per tree, and others were prevented from roosting in adjacent trees. Roosts were typically 3-8 m from ground on branches 0.5-1.5 cm in diameter. In conifers, birds usually roosted next to the trunk on the lowest branch with needles. Some perches were used repeatedly over several nights.

Shortly after leaving the nesting area, grasshoppers are very important in the diet and the magpie may feed on them almost exclusively. Later in autumn, grain and fruit are important foods. It may eat fruits of hawthorn, mountain-ash, elderberries, dogwoods, and grapes. It follows roads and hunters to look for carcasses, and visits landfills (Birkhead 1991; Buitron 1988; Campbell et al. 1997).

AUTUMN

The magpie does not appear to be a regular migrant, and most movements may be considered dispersal or wandering. In mountainous areas, there may be seasonal elevational changes and north-south movements have been documented in some areas, including British Columbia. It is not known to migrate in the Yukon (Campbell et al. 1997; Linsdale in Bent 1946; Sinclair et al. 2003; Trost 2020).

WINTER

In winter, the Black-billed Magpie inhabits areas similar to those used during the postbreeding period, but may be more dependent on anthropogenic areas with abundant food. In western Canada, large numbers congregate near feedlots, barnyards, sewage lagoons, railway loading yards, and grain elevators. These habitats are essential to winter survival in the north. In some areas, all winter records are from landfills (Campbell et al. 1997). In Colorado, the magpie was positively correlated with the density of housing within 500 m, percent canopy cover, and percent cover by understorey vegetation. It was negatively affected by the height of understorey vegetation. Although it is known to be human-adapted, it is important to maintain some canopy cover for wintering birds (Miller et al. 2017).

The magpie selects winter roosts to provide shelter from the elements. In Alberta, deciduous roosts were abandoned a few days after permanent snow occurred on the ground. Wind speed in 1 coniferous roost was less than 10% of that in the adjacent open field. In winter, the magpie has roosted in nests and in a cattle shed, where birds rested on the backs of cattle overnight (Erpino 1968; Linsdale in Bent 1946; Reebs 1987).

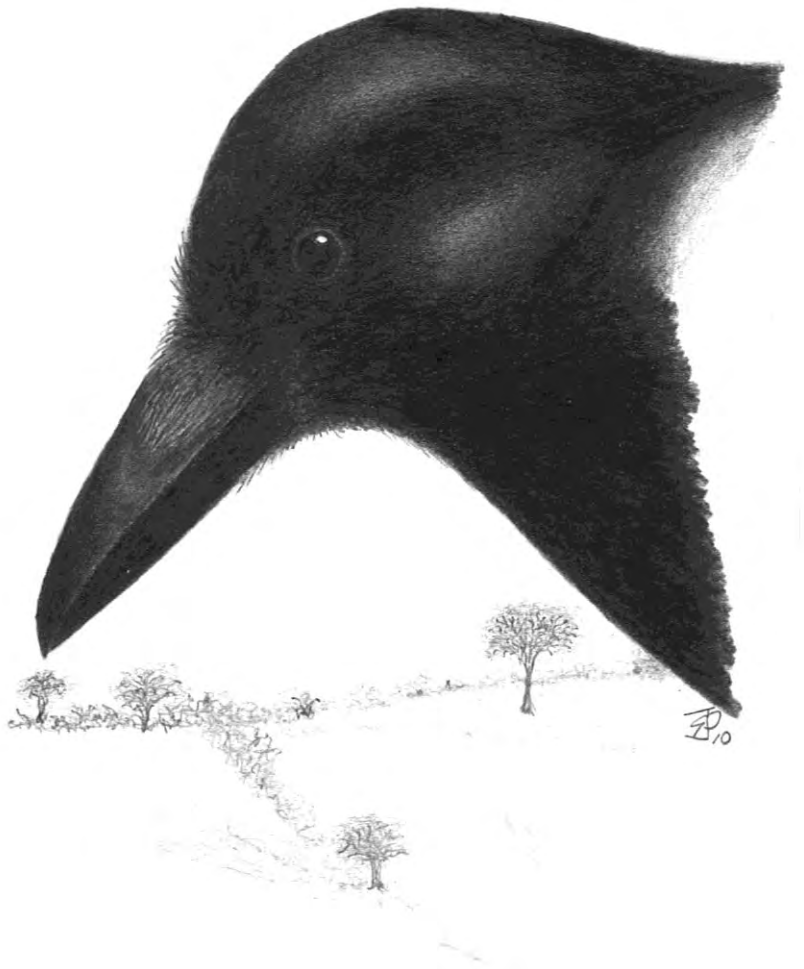
The winter diet is highly variable depending on food sources that birds elect to congregate around. In Alberta, 92% of the diet consisted of decomposed vegetation, primarily oats and wheat. Some seeds of chokecherry and pin cherry were consumed. Other food included meadow voles,

eggs, forest tent caterpillar egg masses, and garbage. Reebs and Boag (1987) concluded that waste grain, meadow voles, and garbage were the most important foods. In Colorado, the magpie is part of an avian scavenging guild that includes Bald Eagles and ravens. Because it is subordinate to these species, it often feeds in flocks at carcasses (McKinstry and Knight 1993). Linsdale (1937) concluded that grain was an important winter food, but that it was eaten out of necessity rather than preference. Grain is avoided as food in July and August when it is abundant; animal food is consumed then. Road-kills on highways are an important source of winter food (Linsdale 1937).

The magpie may visit winter bird feeders, and in Ontario it visits feeders from Rainy River District east to Thunder Bay. Preferred food at feeders is meat and suet, as well as peanuts in the shell and peanut butter mixes. It infrequently eats millet, sunflowers, cracked and whole corn, bird puddings, milo, hulled peanuts, oats, and fresh fruit (Dunn and Tessaglia-Hymes 1999).

American Crow

Corvus brachyrhynchos



BREEDING SEASON

Habitat Requirements

The American Crow breeds in almost every habitat in the province except treeless tundra, although it tends to avoid large, dense forested areas. It breeds in deciduous (18.8% of nests), mixed (10.4%), and coniferous (18.8%) woodlands, including plantations, and in unspecified woodland types (5.8%); in fencerows (13.3%); in overgrown fields or those with isolated trees (11.3%); in urban cemeteries, gardens, parks, and other residential and industrial areas (10.4%); in strips of trees along shorelines (4.6%); on islands (2.9%); in orchards (2.5%); and on treed sand dunes (1.3%; Peck and James 1987). Near Pickle Lake and Parry Sound, it was associated with forest openings near small towns, roads, railways, or buildings (James 1980; James and Peck 1995a).

In southern Ontario, the American Crow was equally abundant on organic and conventional farms. It was positively associated with spring grain, row crops, number of treatments applied to fields, farmsteads, and amount of riparian and upland woods. It was negatively associated with the number of large isolated trees, field size, number of tills, habitat heterogeneity, and road, railway, and hydro rights-of-way (Kirk et al. 2011).

In Quebec, the American Crow was much more abundant in agricultural and densely populated areas than in large forests. In heavily forested areas, it was associated mainly with water bodies, clearings, and openings created by logging and road construction (Pelletier in Gauthier and Aubrey 1996). In Illinois, Graber et al. (1987) considered it a highly generalized forest-edge species, a dominant species of black oak forest, and a common species of prairies and prairie thickets. Densities were higher in bottomland than upland forest and it shunned forest interiors. In an intensively cultivated area, 45% of nests were associated with trees in open fields, 34% were in woodlands, 14% in sparsely wooded pastures, and 7% in orchards, cemeteries, abandoned farm yards, tree plantations, and thickets. Also in Illinois, it preferred low- to medium-density habitat and avoided forested habitat. Within home ranges, there was a preference for agricultural land; high-density urban areas were avoided (Yaremych et al. 2004). In California, it was associated with urban areas and areas distant from extensive forest (Kalinowski and Johnson 2010). In British Columbia, preferred natural habitat is open to semi-open coniferous forests and adjacent grasslands, riparian woodlands, valley bottoms, and lakeshores. It is most abundant in agricultural fields among woodlands and near communities where it inhabits landfills, barnyards, parks, residential areas, orchards, railways, and road corridors. Forty-nine percent of nest sites were associated with cultivated farmland or pasture and rangeland; 12% with riparian areas; 11% with deciduous forest; 10% with urban, suburban, or industrial land; and 9% with coniferous forest (Campbell et al. 1997). In the Appalachians, it occurred in 18.2% of old-growth forests compared with 97.8% of forests statewide and 96.4% of forests on the Appalachian Plateau (Haney 1999). This crow has 2 important habitat requirements: openness for ground feeding and presence of scattered trees, woodlots, windbreaks, and forest edges for safety, loafing, nesting, and roosting. It uses a wide range of natural and human-made habitats such as logged areas, agricultural fields, cities, villages, farmland, pastures, landfills, city parks, cemeteries, golf courses, residential yards, road rights-of-way, feedlots, and shorelines. Areas of extensive grassland without trees and extensive forests are avoided. It may occur in openings in extensive forests where rivers or highways provide an access corridor (Verbeek and Caffrey 2020).

At the landscape scale, the American Crow preferred areas with 44-58% forest cover in New York (Cunningham and Johnson 2019). In Seattle, its abundance was negatively correlated with percent forest cover at the 1-km^2 scale (Marzluff et al. 2007).

In Missouri, Hayden et al. (1985) stated that the American Crow required a minimum forest size of 4.6 ha, and considered it area sensitive because it typically occurred in forests larger than its territory size. They acknowledged that the minimum forest size required in New Jersey was only 0.2 ha. Robbins et al. (1989) stated it was area sensitive in the mid-Atlantic states, with its probability of detection 100% in 10-ha forests (the smallest-sized forest for all species they considered area sensitive). Probability of detection declined to 50% in 0.2-ha woodlots. Its presence was positively associated with forest size, but negatively associated with the amount of forest cover within 2 km. In North Dakota, its probability of observation increased with forest size. Probability of occurrence was approximately 52% in 1-ha aspen groves, 80% in 10-ha stands, 90% in 100-ha stands, and 100% in 1,000-ha woodlands (Grant and Berkey 1999). Other studies found no correlation between crow presence and forest size, but confirmed that it is more likely to be present in fragmented habitat where there is a small percentage of forest cover in the landscape (Hobson and Bayne 2000; Keller and Yahner 2007; Kilgo et al. 1997). There is no evidence of it being area sensitive in Ontario. In southern Ontario, its probability of observation was negatively correlated with the amount of forest 100 m or more from edge, woodlot size, amount of forest within 2 km, and amount of regional forest cover. Only the first and last relationships were significant (Austen et al. 2001). In southern Ontario, it frequently nests in hedgerows in agricultural landscapes (Reaume 2013).

Smith (2004) examined the distribution of predators in 2 forested habitats in Michigan. The American Crow was the only species that showed a preference for forest edge over forest interior.

Communal nocturnal roosts are important to crows year round. Ontario roosts were predominantly in deciduous woodlands, often in areas subject to considerable disturbance. In Thunder Bay, a roost in a woodlot was close to high human activity including a major highway, airport, railway, and industrial and residential areas. The Chatham roost was in deciduous trees along the Thames River. The St. Catharines roost was in a willow-aspen-maple woodlot along a slope of the Niagara Escarpment in the city. This roost is used consistently, but its location shifts as much as 0.5-7.5 km along the escarpment within seasons. In Essex, a deciduous woodlot is used for roosting. In this roost, roost trees were all deciduous and included ash, elm, oak, basswood, hawthorn, maple, and hickory. Trees smaller than 3 cm diameter at breast height (DBH) and dead trees with no remaining limbs did not appear to be used for roosting. Large oaks (44-70 cm DBH) were preferred; crows settled into them first. The lowest that crows roosted was 2 m. Most Ontario crows roost in larger deciduous trees; in downtown Hamilton, some roosted in planted pines. The Niagara gorge was used historically for roosting, especially on the steep slopes between the falls and Queenston. This roost shifted to a deciduous woodlot in the mid-1920s and was subsequently abandoned. In Hamilton, crows roosted along the forested Niagara Escarpment and also near city hall in urban habitat. In British Columbia, roosts are in mature deciduous or coniferous trees distant from disturbance, typically in tall trees along rivers. New Jersey roosts were in secondary forests dominated by red maple 3-8 m tall, and were associated with superabundant food sources. In California, nesting birds roosted together in a cluster of about 40 trees within an area of high nest

density, and several nests were within the roost. Trees used for roosting were taller than random, had a greater DBH, a larger crown, and greater crown volume. During winter, ambient light levels and interior canopy temperatures were higher in roost than non-roost trees. In Illinois, roosts occurred in upland deciduous stands, particularly oaks, and in willow-cottonwood bottomland forests, plantations, hedgerows, and evergreen plantings. In New York, crows preferred to roost near water below 300 m altitude. Many other roosts are near water. Roosts tend to be traditional and may be used for decades or over a century (Campbell et al. 1997; Dobos 1985; Emlen 1940, 1942; Graber et al. 1987; Knapton and Maturi 1984; Reaume 1985, 2013; Sheppard et al. 1936; Stouffer and Caccamise 1991; Verbeek and Caffrey 2020; Weseloh 1983). Roost use varies seasonally. During the breeding season, roosts are often in the territory and near the nest. Adults, helpers, other yearlings, and fledglings may roost in the territory. Breeding males sometimes leave their territories to join the local communal roost. Numbers of roosts begin to increase in September and they are well established by mid- to late October. Maximum numbers in roosts tend to occur in late November or early December, particularly where resident birds are joined by migrants. Numbers decline again in late winter and early spring. In winter, some New Jersey birds roosted exclusively at the communal roost; others alternated between the territory and communal roost. By mid-April, most stopped using the communal roost or made individual trips to it after several nights of remaining on territory (Caccamise et al. 1997; Graber et al. 1987; Sullivan and Dinsmore 1992; Verbeek and Caffrey 2020). Foraging areas may be 7.5-80 km from the roost, with birds moving at least 34 km from the Chatham roost. Birds using the Essex roost spread over the entire county during the day, an area of about 1,925 km^2. The area used around New York roosts ranged from 130 km^2 to 1,800 km^2. Resident birds may be faithful to foraging areas within their territories. Migrants show no fidelity to foraging areas. Cooperative groups and flocks break up when returning to the roost, with individuals staging at pre-roost areas away from other members of the group. They also roost independently of each other and may attend different roosts. Pre-roosting areas are used when the birds move towards the roost in late afternoon. These tend to be fields that are bare or have very short grasses. In St. Catharines, pre-roosting occasionally occurs in trees. In California, the same fields were used day after day with similar nearby fields rarely used. Birds grouped together tightly within a field with only a small percentage of it used; locations used within the field often changed day to day. Although some foraging occurs at pre-roosts, their main function appears to be to minimize predation. Some pre-roosts were on rooftops where foraging was not possible (Caccamise et al. 1997; Dobos 1985; Emlen 1940; Graber et al. 1987; Knapton and Maturi 1984; Moore and Switzer 1998; Reaume 1985, 2013; Stouffer and Caccamise 1991; Verbeek and Caffrey 2020).

All Ontario nests were above ground, mostly in live trees or shrubs, although 3 were in dead trees, 2 were on top of dead stubs, and 1 was 15 m up in a crevice on a cliff face. Coniferous trees of 7 species supported 54.0% of nests compared with 46.0% in 16 species of deciduous trees. Tree species most frequently chosen were pines (74 nests), spruces (45), white cedar (36), oaks (24), maples (20), willows (17), and beech (16). Nests were well concealed in crotches or on horizontal limbs and most often at or near the trunk. Some nests were 0.5-6 m from the main trunk. Most were in the upper third of the supporting tree or shrub. One nest was repaired and used the following year. Nests were 0.6-26 m from ground, with most 5.5-10.7 m up. The lowest nest was on an island where only short trees were available (Peck and James 1987). In southern Ontario, rural crows favour

nesting in deciduous trees; urban crows prefer conifers (Reaume 1987a, 2013). A nest was reported on an upper ledge of the Royal Ontario Museum building, 21 m from ground. This appears to be one of very few records of crows nesting on a building. Most of these were from the prairies on abandoned buildings where there are few trees for nesting. Another nest was on a wooden ledge along a lock gate at Jones Falls (Peck 2002).

In Maine, almost all nests were in conifers; most were in deciduous species in Pennsylvania, Delaware, and New Jersey; all at Cape Cod were in conifers; it appeared to prefer oaks in Ohio; most Illinois nests were in deciduous trees and it may have preferred oaks and elms; and 50% of British Columbia nests were in deciduous species. Nest height reflects the average height of available trees. Nests are typically in the top quarter to third of trees or shrubs. Where woody vegetation is absent, the American Crow rarely nests on the ground. Nests have been reported 0-23 m from ground, but mostly 4-11 m up. A new nest is typically built each year, but old ones are occasionally used as a base, or rarely refurbished and reused. One nest was used in 3 consecutive years and another was used for at least 3 years. Nests tend to be built very near the previous year's nest and occasionally in the same tree. It has nested in old hawk nests, in cavities in trees, on hydro poles, in bulrushes above water, on top of old magpie nests, and on chimneys. In Illinois, nests in dense forests were within 36.6 m of edge. In a California walnut plantation, early nests built before leaf-out averaged 12.2 trees from edge; later nests averaged 8.8 trees from edge (Campbell et al. 1997; Chamberlain-Auger et al. 1990; Emlen 1942; Graber et al. 1987; Gross in Bent 1946; Reaume 2013; Verbeek and Caffrey 2020).

The American Crow may be nonterritorial, defend a small area around the nest or female, nest colonially, or defend large exclusive home ranges. In some cases, only core areas around nests are defended and birds feed communally in undefended areas, or foraging areas may be included in the defended area. Alternatively, territorial disputes may be intense with birds violently locking together and falling through the air. Understanding territoriality is further confounded by the fact that some nests have helpers, leading some authors to conclude that the nest site is not defended. Territories are maintained year round in Massachusetts, New Jersey, California, Oklahoma, Florida, and New York, but apparently not in Ohio or northern portions of its range (Reaume 2013; Verbeek and Caffery 2002). Nonbreeding birds may move about various territories, visit their parents, or move in with nearby groups; group sizes may change hourly to annually (Reaume 2013). Emlen (1942) described a nesting colony in California where about 60 pairs nested in a 93.7-ha walnut plantation. The spacing of nests suggested territoriality, with nests relatively uniformly distributed and averaging about 75 m apart, although 7 were only 24-27 m apart. On a California golf course, core areas averaged 1.25 ha but did not appear to be defended. Overlap of core areas occurred, especially in peripheral territories where almost complete overlap occasionally occurred; some even nested in the same tree. Neighbours regularly trespassed on other core areas, and groups from different core areas fed together without strife. When a new pair wished to establish a territory, it simply squeezed in and neighbours adjusted territories without conflict (Caffrey 1992). In Illinois, territoriality was confined to the nest tree or female, and defence of the nest appeared rare (Graber et al. 1987). Fitch (1958) concluded that crows were nonterritorial in Kansas. Kilham (1989) studied crow territoriality in Florida and New Hampshire and realized that pairs frequently had helpers. He observed 2 groups of crows in Florida that maintained distinct territories with typical territorial disputes along

boundaries. Each group had territory sizes of approximately 90 ha. One year, birds in 1 group split into 3 subgroups, all nesting in a portion of the original territory. Two subgroups had territories of 40 ha and the other's size could not be determined. These subgroups defended territorial boundaries against members of their former group. Male territorial behaviour was strongest from prior to nest building until early incubation. Females became increasingly territorial as incubation progressed. In New Hampshire, groups maintained territorial boundaries through summer and autumn, and the same boundaries were maintained for 3 years. In Massachusetts, territories were all purpose and defended year round. Mean territory size was 42.1 ha (range 9.4-104.0 ha). Mean distance from neighbouring nests was 0.86 km. Mean distance of subsequent nests in territories maintained year round averaged 0.2 km (range 0-0.6 km; Chamberlain-Auger et al. 1990). In New Jersey, birds bred cooperatively and each individual of the group maintained a small activity centre. Conflicts between neighbouring groups were infrequent and occurred primarily in early stages of breeding. Birds sometimes all left their territories to feed communally at a landfill (Caccamise et al. 1997). In Oklahoma, Knopf and Knopf (1983) observed territorial behaviour by groups of birds. In Manitoba, crows maintained non-overlapping home ranges or territories that averaged 2.6 km^2 (range 0.8-6.0 km^2). The mean foraging flight distance was 382 m (range 16-2,078 m; Sullivan and Dinsmore 1992). Overall, territory sizes have been reported as 0.72-278 ha. In urban areas of New York, crows defended territories averaging 8.7 ha (range 0.8-28.3 ha) compared with 37.7 ha (range 12.6-95.0 ha) in rural areas. Oklahoma families occupied non-overlapping to slightly overlapping territories of 50-150 ha (average 94 ha; Verbeek and Caffrey 2020). Yaramych et al. (2004) radio-tracked 45 American Crows from late spring to early autumn in Illinois. Home range averaged 9.6, 6.7, and 6.4 km^2 for hatch-year, subadult, and adult crows, respectively. In Guelph, home ranges of families averaged 15 ha with extremes of 8-20 ha (Reaume 2013). Territories or home ranges of 1-3,500 ha have been reported elsewhere. Urban birds tend to have smaller home ranges than rural birds due to greater abundance of food. In Manitoba, the average home range size during the breeding season was 260 ha. Other home range sizes include 50 ha in Florida, 67 ha in Maryland, 59 ha in Illinois, 94 ha in Oklahoma, 31 ha in suburbs and 67 ha in rural New York, 25-49 ha in New Jersey, 20 ha in Philadelphia, and 42 ha in Massachusetts with a range of 9.4-104 ha (Reaume 2013).

No information is available on natal site fidelity for migratory populations. In Illinois, homing to nesting areas was not documented, but juveniles were recovered after a year near the nesting area (Graber et al. 1987). In New York, dispersal from natal to breeding sites ranged from 0 to 60 km and averaged 3.2 km in urban areas and 3.3 km in rural areas. Of 49 crows raised in urban areas, only 2 nested in rural areas. None of the birds raised in rural areas nested in urban areas. Three urban-raised females moved to other cities to breed (Verbeek and Caffrey 2020).

In resident populations, juveniles often remain in the natal territory and become helpers at their parents' nest. In California, 75% of young known to be alive were still on the natal territory with their parents the following season. Yearlings that were not helpers often remained on the natal territory, but might join the resident nonbreeding flock or trespass on core areas of other breeding pairs. In Massachusetts, over 94% of breeding was cooperative, with offspring remaining in the family unit throughout the year. In all cases when a pair raised young unassisted, these young remained and assisted the following year. Each breeding group consisted of the breeding pair and offspring aged

1 to several years old. All surviving young remained on the natal territory and acted as helpers. In California, significantly more females (100%) remained in the natal territory to help than males (64.3%). Some remained with their adults an additional 1-3 years. In all cases, these individuals helped some years but not in others. In this population, 18% of juveniles dispersed from the natal area in autumn and either joined the nonbreeding flock or left the general area; half returned to the natal area the following spring. In the Seattle area, 27% of 56 juveniles dispersed more than 2 km from their natal territory and 32% remained within 1.5 km. Dispersing crows moved a median distance of 10.4 km (average 9.1 km, range 2.1-22.2 km). Birds that remained locally moved a median distance of 0.6 km (average 0.7 km, range 0.2-1.5 km). Twenty-three percent of urban juveniles helped their parents and 21% of suburban and rural young helped. Females were more likely to disperse, and males were more likely to be helpers (Withey and Marzluff 2005). In New Jersey, fidelity of individuals to core areas was 54-96% over 2 years and did not differ between adults and juveniles. Some birds remained in the same group and area for at least 3 years. Individuals were sometimes absent from the group for days or weeks, then returned without resistance from other group members. Although helpers feed nestlings and fledglings, feed the incubating and brooding female, and attend to nest sanitation, their presence does not improve productivity, so they are not helpful from an ecological perspective (Caccamise et al. 1997; Caffrey 1992, 1999; Chamberlain-Auger et al. 1990; Verbeek and Caffrey 2020).

In resident populations, adults maintain permanent all-purpose territories (Caffrey 1992). No information is available on adult site fidelity for migratory populations. In Ontario, it is unknown if the wintering population consists of permanent residents maintaining territories, if they are migrants from further north, or a combination of residents and migrants.

Limiting Factors

Eggs have been found in Ontario nests from the beginning of March until the third week of June, mostly in the last week of April and first week of May (Peck and James 1987). In Algonquin Park, nests are under construction from late March to late April, eggs are present from late April to early May, nestlings are present from mid- to late June, and dependent fledglings have been observed from mid-June to mid-August (Tozer 2012). In Guelph, nest building began on 10 March, the first egg was laid on 24 March, incubation began on 26 March, the first egg hatched on 13 April, the first nestlings fledged on 16 May, and the last nestlings fledged on 16 June (Reaume 2013).

Depending upon weather, nest construction may take 1-3 weeks, but duration of nest building also depends on whether there are helpers. California nests took 10-17 days to complete without helpers and 5-9 days with helpers; second nests are built in 5-10 days. In Saskatchewan, an average of 4.8 days elapsed between nest completion and clutch initiation; the interval was 6-16 days in Florida. In California, egg laying started before some nests were complete. Usually 1 egg is laid a day, or occasionally 1-2 days may be skipped before the last egg is laid. Incubation usually begins with the laying of the third egg, with eggs hatching over a 2-3-day period. The incubation period is 16-21 days, but mostly 17-19 days. Reported incubation periods of 14-33 days with an average of 23.2 days in Massachusetts are considered suspect by some authors. Young fledge when they are 24-43 days old, but mostly about 30-32 days. In Illinois, it was estimated that 53-59 days were required from the onset of nesting to fledging of young (Campbell et al. 1997; Chamberlain-Auger et al. 1990;

Emlen 1942; Graber et al. 1987; Gross in Bent 1946; Ignatiuk and Clark 1991; Kilham 1989; Reaume 2013; Verbeek and Caffrey 2020).

One brood is raised, but the American Crow is a persistent renester that may lay as many as 4 clutches in an attempt to raise young. Usually a new nest is built when renesting, but occasionally the old one is used. Clutches of 2-8 eggs have been reported in Ontario, with most containing 4 or 5 eggs. The 8-egg clutch appeared to be laid by 2 females because there were 2 groups of 4 eggs with different colour patterns. Overall, clutches of 2-10 eggs have been reported. Normal clutches contain 3-7 eggs, with 5 eggs most frequent. Average clutch sizes were 4.5 in California, 4.8 in Saskatchewan, and 4.7 in Pennsylvania and New York. Clutch size may increase northward. Brood reduction may occur due to siblicide (Campbell et al. 1997; Emlen 1942; Graber et al. 1987; Gross in Bent 1946; Ignatiuk and Clark 1991; Kilham 1986; Peck and James 1987; Verbeek and Caffrey 2020).

Although many birds breed when they are 2 years old, 25-65% may not breed until later. Some may not breed until they are 3 or more years old. Breeding may not occur every year. In California, 1 male that had bred for 3 years joined the nonbreeding flock when he was 7 years old. A widowed female that was at least 5 years old and had bred the previous year joined another pair to help (Caffrey 1992; Kilham 1989; Verbeek and Caffrey 2020).

The mating system is monogamous. Long-term pair bonding has been reported in resident populations, but it is unknown if this occurs in migratory populations. In more than 100 pairs monitored in California and Oklahoma, only 1 case of divorce was observed. Some California pairs remained together for at least 9 years. In New York, females resisted extra-pair copulations, but 19% of young within 23 of 71 broods (32%) were sired by extra-pair males. Extra-pair males included birds both within and outside the family group (Townsend 2009; Verbeek and Caffrey 2020).

The American Crow forages in open habitats and usually does not feed in forested areas. In Manitoba, it foraged often in cropland but this was the only open habitat used less than its availability. Wetlands were used for foraging slightly more than availability; other habitats were used proportionately. Some pairs made extensive use of a particular habitat; others made little use of the same habitat. Vegetation taller than the crows was not used for foraging. Foraging occurred in hayfields until vegetation was too tall, then resumed after cutting. In southern Ontario, most feeding occurred in hay or alfalfa fields (25%), on lawns (13%), and in small grain stubble (13%). Other substrates used for foraging included 9% in gravel, 9% in pastures, 6% in landfills, 5% in weedy fields, 4% in corn stubble, 3% in plowed fields, 2% in small grains 15 cm or less in height, 2% in corn of similar height, and 2% in recently planted fields that were still bare earth. Hayfields were used much more than their availability. It obtains most food by walking on the ground, but takes some fruit from trees and shrubs. It takes food from the surface of the ground or on vegetation, but may dig with its bill and turn over cow dung and other debris to find food. It may catch flying insects or pounce from a perch onto prey and occasionally captures small birds in flight. Amphibians and small fish may be captured in water. It was observed waiting for cooperatively feeding Common Mergansers to drive fish into shallow pools, where crows captured some of them. Kleptoparasitism of other birds and river otters occurs, and it may rob other birds' stores. Occasionally the crow walks on the backs of pigs and cattle and removes and eats ticks and lice from them. It may walk beside the heads of rooting pigs to obtain invertebrates. In Florida, it took salamanders in front of an

advancing line of White Ibises and occasionally kleptoparasitized them and Great Egrets. One or 2 birds occasionally shook leaves and branches in trees while the remainder of the group waited for invertebrates, frogs, and snakes to fall down. In Michigan, crows captured and ate little brown bats emerging from a mine. On 3 occasions, a crow descended into the mine shaft and returned with a bat. There are accounts of apparent cooperative hunting to kill a bat near Ottawa and a single crow capturing a little brown bat in flight. This crow often drops hard prey such as nuts and small turtles on pavement or other hard surfaces to break them open. Observations of tool use include modifying a piece of wood and using it to probe a hole for a spider, and a captive bird using a plastic cup to add water to dry mash (Caffrey 2000, 2001; Flaspohler 2017; Hernández et al. 2007; Hulse and Atkeson 1953; Kilham 1989; Lefevre 2005; Putnam 1992; Reaume 2013; Sullivan and Dinsmore 1992; Verbeek and Caffrey 2020; Walley 1993).

Short-term food caching occurs on the territory when food is abundant. Hard food, such as nuts, is typically cached in the ground by hammering it in with the bill. Caches are covered with grass or leaves. The American Crow may carry food as far as 2 km prior to caching it. Corn may be stored in the ground or in shallow water. Soft or more perishable foods may be stored in trees or in long grass where it may be covered with grass clippings; in winter suet may be stored under snow. During the breeding season in Guelph, 46% of caches were in lawns, 41% were in weedy areas, 8% were on or among used machinery, and 5% were in coniferous trees. Other food items the crow has cached include noodles, bird eggs, fish, clams, frogs, snakes, mice, young rabbits, and otter dung. The male occasionally feeds cached food to the female on the nest. Cached food may be stolen by other crows, and crows may raid the caches of woodpeckers (Conner and Williamson 1984; George and Kimmel 1977; Kilham 1989; C. Long and C.A. Long 1990; Reaume 2013; Verbeek and Caffrey 2020).

The diet of nestlings is essentially the same as that of adults, except that the relative percentages of individual food items vary. When they are very young, nestlings are fed readily digestible food such as spiders and caterpillars. By the time they fledge, the diet differs only slightly from that of the adults, and includes beetles, crustaceans, small mammals and grain. Food consumed by 778 nestlings consisted of 17.4% scarab beetles, 3.9% ground beetles, 2.6% other beetles, 14.6% grasshoppers, 2.6% bugs, 5.3% caterpillars, 1.9% miscellaneous insects, 9.7% spiders and centipedes, 1.8% crayfish, 0.7% fish and molluscs, 7.0% amphibians and reptiles, 1.6% wild birds and their eggs, 1.6% poultry and their eggs, 6.2% rodents, 2.6% other mammals, 4.0% carrion, 11.9% corn, and 4.6% miscellaneous vegetable matter (Kalmbach 1918).

Adults are opportunistic omnivores that quickly respond to insect outbreaks or other abundance of food. Earthworms may be an important food; crows in Guelph selectively fed on the anterior of common earthworms and left the remainder. In Florida, it fed on tapeworms passed by cattle and on their placenta. It may follow plows to feed on uncovered June beetle grubs, and may dig them up in lawns and pastures. In some areas, it is an important predator of waterfowl and heron eggs but in other areas these food items are rarely exploited. It commonly eats nestlings of other bird species but not at rates formerly reported. Mock Common Nighthawk nests were provided in rural and urban settings and on roofs in Wyoming. Predation rates were higher in urban areas where crows were more abundant, and all identified predators were crows. It may be contributing to the decline of urban nighthawk populations. Most mammals it attacks are mouse-sized, but there is 1

record of it killing a live eastern chipmunk. It occasionally attacks larger mammals such as young pigs, raccoons, and deer, but only if they are in a weakened state. Congregations have been observed at garter snake hibernacula, feeding on the concentration of snakes. It commonly scavenges on road-kills and other carcasses where it is subordinate to Turkey Vultures and ravens, but dominant to Blue Jays. In urban areas, this crow readily feeds on human garbage and discarded food. In Toronto, crows routinely foraged on small injured or dead passerines that had collided with windows of an office building (Bent 1946; Giles et al. 2015; Graber et al. 1987; Gross in Bent 1946; Kilham 1985a, 1989; Latta and Latta 2015; Nocera 2000; Reaume 1987b, 2013; Sullivan and Dinsmore 1992; Verbeek and Caffrey 2020; Walley 1993). Watermolen (1996) reported crows eating sand which may aid in the digestion of grains and acorns.

Kalmbach (1918) examined 2,118 stomachs throughout the American Crow's range. The adult diet consisted of 28.1% animal matter and 71.9% was vegetable material. Most (52.4%) animal food was consumed in May with a uniform decrease through June (47.0%), July (44.3%), and August, but even as late as September animals constituted about a third of the diet. Lower percentages of animals (11.0-18.4%) by month were eaten from October through April. Beetles represented 7.6% of the yearly food, including 4.3% adult and larval scarab beetles, 1.6% ground beetles, 0.6% weevils, and 1.0% miscellaneous beetles. Grasshoppers, crickets, and katydids comprised 7.3% of the diet with most taken in July, August, and September. Other animal food included 1.6% caterpillars; 0.6% bugs, including cicadas, leafhoppers, and stink and leaf-footed bugs; less than 0.5% flies; 0.7% hymenopterans; 0.5% spiders; 0.7% miscellaneous insects such as caddisflies, dragonflies, mayflies, and dobsonflies; 1.2% crustaceans, (mostly crayfish); 0.3% aquatic and terrestrial molluscs; 0.6% fish remains; 1.4% reptiles (turtles, snakes, and lizards) and amphibians (toads, frogs, and salamanders); 0.3% wild birds and their eggs, 0.6% poultry and their eggs; 1.6% small mammals (young cottontails, voles, white-footed mice, house mice, rats, shrews, moles, weasels, and bats); and 2.6% carrion. May was the month when the least (47.6%) amount of vegetation was consumed. Highest consumption occurred from October through February. Corn is a staple and constituted 38.4% of the annual diet with peak consumption from October through February. Other grain constituted 12.7% of the diet, including wheat, oats, and buckwheat in order of abundance. It may also eat cultivated plants including fleshy fruits (apples, pears, and plums), the rind and pulp of melons, the meat of nuts, frozen waste pumpkins, turnips, blackberries, mulberries, grapes, strawberries, potatoes, peanuts, beans, peas, and cherries. Wild fruit comprised 14.0% of the annual diet, with peak consumption in September and October. This was mostly mast in the forms of acorns and chestnuts, but it also ate fruits of sumac, poison ivy, greenbrier, grapes, Virginia creeper, black gum, dogwoods, wild cherries, plums, strawberries, mulberries, raspberries, juneberries, blueberries, red cedar, beech, hackberry, barberry, currants, hawthorns, and huckleberries. It occasionally eats mushrooms. Weed seeds constituted less than 0.5% of the diet and included those of knotweeds, foxtails, ragweed, amaranths, and pokeweed. In the southeastern United States, the diet was comprised of 31% animal food and 69% vegetable matter. Insects comprised almost 20% of the diet, with June beetle adults and larvae, weevils, grasshoppers, and caterpillars dominating. Crustaceans, predominantly terrestrial crayfish, were an important food item (7.4%). It also fed in aquatic habitats with molluscs, amphibians, and fish comprising 4% of the diet. Corn and wild fruits were the dominant vegetable matter in the diet. Corn constituted about 25% of the diet and about a third of the crow's food was

fruit of black gum, sumacs, pokeweed, blackberries, and greenbriers. Some grain and cultivated fruits were also taken. It caused some damage to watermelon, pea, strawberry, and peanut crops (Beal et al. 1916). Other miscellaneous vegetation that it may consume includes soybeans, squash, sunflowers, elderberries, nightshade, winterberry, and yellow flatsedge tubers (Verbeek and Caffrey 2020).

Peck and James (1987) reported a punctured Brown-headed Cowbird egg in a crow nest, but it was uncertain if the egg had been laid in the nest or carried to it by a crow. Three cases of cowbird parasitism of the crow have been reported in North America (Verbeek and Caffrey 2020), but chances of successful parasitism are nil.

The American Crow is highly vulnerable to West Nile virus and a high proportion of birds that contract it die. In 2000, 1,095 of 1,105 birds (99.1%) testing positive for the virus in Ontario were crows; 1,122 of 1,125 (99.7%) in New Jersey were crows (McCracken 2003a; Verbeek and Caffrey 2020). In 2002, more than 2,700 dead crows were found in Burlington south of the Queen Elizabeth Way (Mike Cadman, personal communication). It was scarce in urban Burlington in 2003 and less common throughout the entire Hamilton area, but appeared to make a quick rebound from this setback (Curry 2006). On the 2003 Christmas Bird Count (CBC) held in the Oakville/Mississauga area, a 90% decline in crow numbers was observed, possibly due to West Nile virus. This virus arrived in Quebec in 2002 with major fluctuations in crow numbers in 2003 and smaller fluctuations in 2004 and 2005. Thereafter, the crow population stabilized (Reaume 2013). In Illinois, 68% of 45 crows died and tested positive for West Nile virus. This crow's preferences for low- and medium-density housing habitat exposes it to the primary sector for West Nile virus, and its large home range results in it potentially spreading the virus over a large area (Yaremych et al. 2004). Kilpatrick et al. (2007) stated that significant effects on its population occurred due to the virus. In California, the crow was one of the most vulnerable species to West Nile virus (Smallwood and Nakamoto 2009; Wheeler et al. 2009). Caffrey et al. (2005) estimated that 65% of an Oklahoma crow population died as a result of West Nile virus. Reaume (2013) provided an in-depth account of the relationships between the American Crow and West Nile virus.

Humans have a long history of persecuting crows. In the 1920s and 1930s, it was common practice to dynamite roosts. From 1934 to 1939, the kill from shooting in Illinois was estimated at 300,000 and an additional 630,000 were dynamited between 1934 and 1945; 127 roosts were dynamited in Oklahoma killing 3.8 million crows. Eighty thousand were killed 1 night in Texas. Poison has also been used to control numbers. The crow was regularly shot and some provinces and states paid bounties for dead crows. In the 1940s, most nest losses occurred before foliage developed sufficiently to conceal the nest, and shooting was the major cause of loss. In Illinois, 94% of band recoveries were birds that had been shot or trapped. In the 1920s, a roost in Niagara Region was abandoned due to logging and shooting. Although the incidence of shooting has declined, crow hunting is still a popular sport. In the United States, the crow is partially protected, with hunting seasons not to exceed 124 days and they must exclude the breeding season. In Ontario and most of Canada, it is unprotected. Some Canadian towns and cities have initiated eradication programs, and controlled crow hunts have been held in Chatham. Beginning in the 1950s, crows recognized that they were safe from shooting in urban areas and started nesting in them. Urban and rural crows

exhibit different nest defence behaviours based on their relative wariness of humans. Urban crows are habituated to humans. In rural areas, crows stay outside of gun range and fly from the nest at distances that would give a human few clues in finding the nest (Bailey 2003; Campbell et al. 1997; Erskine 1998; Graber et al. 1987; Gross in Bent 1946; Houston 1977; Knight et al. 1987; Pelletier in Gauthier and Aubry 1996; Sheppard et al. 1936; Verbeek and Caffrey 2020).

Habitat changes have been mostly beneficial for crows. Clearing and fragmentation of forests, tree planting in urban centres and around homesteads, planting coniferous plantations, and tilling of agricultural land have been beneficial. Corn is planted much more frequently and over a larger proportion of southern Ontario than previously, and this is a major source of food. More roads and higher traffic volumes produce more carrion for foraging crows. In a Pennsylvania woodland where the density of tall shrubs increased over a long period, and densities of canopy and subcanopy trees and short shrubs declined, the crow population increased by 733%. In intensively farmed areas, numbers may decline (Graber et al. 1987; Rohnke and Yahner 2008; Verbeek and Caffrey 2020). Along the Michigan shoreline of Lake Superior, the crow was significantly more abundant where cottage development had occurred than in forested habitat on the other side of the road (Ford and Flaspohler 2010).

In the Carolinian Forest Region of Ontario, there were no differences in the abundance of the American Crow in unharvested forests, woodlots where standard thinning had occurred, or those in which diameter-limit cuts had been made (Holmes et al. 2004). In the Canadian Shield of Ontario there was no significant difference in its abundance in early and mid-successional clear-cuts and burns in the same seral stages. It was equally abundant in early successional, mid-successional, and mature stands (Zimmerling et al. 2017). In New York woodlands, selective logging was beneficial for crows. Crows occurred on 32% of unmanaged forests and in 42%, 53%, 78%, and 70% of forests where 25%, 50%, 75%, and 100%, respectively, of legal diameter trees were harvested (Webb et al. 1977).

The American Crow can contract rabies by feeding on rabid, dead vertebrates. It may also be infected by other crows that have the disease (Verbeek and Caffrey 2020).

Status

The American Crow is probably much more abundant now than it was before European settlement and forest clearing (Verbeek and Caffrey 2020). McIlwraith (1894) noted that it preferred cultivated areas and increased as Ontario became settled. Fleming (1907) considered it an abundant summer resident in Toronto. Baillie and Harrington (1937) concluded that it was one of the most common residents and that it bred throughout the province. It was known to breed north to southern Kenora District and range rarely north to Hudson Bay. In the Niagara area, it was formerly abundant in the breeding season, but only fairly common in 1936 due to abandonment of a major roost (Sheppard et al. 1936). It was very common in eastern Ontario in the 19th century, and numbers in the Kingston area are gradually increasing (Weir 2008). James (1991) considered it a common resident north to Kenora and Cochrane, and rare and local north to Hudson Bay.

The second atlas demonstrated that there had been little change in the distribution of the crow since the first atlas. It was found in a few more locations in the Boreal Forest Region and the Hudson

Bay Lowland, but this may have been due to better coverage. Its probability of observation increased significantly province-wide and in the Boreal Forest Region between atlases. Trends in other regions of the province were positive or stable. It was most abundant south of the Canadian Shield, including on eastern Manitoulin Island, although it was relatively scarce in Essex County where it may be limited by the low number of trees. Even Metro Toronto supported a higher density of crows than Essex. In the north, there were nodes of higher abundance around urban areas such as Kenora, Dryden, Thunder Bay, Sault Ste. Marie, and Sudbury, and in the agricultural and more open areas of Rainy River and the Clay Belt. Crows tended to be concentrated along major highways in the north, but were absent from adjacent forested areas. Highways provide a source of carrion as well as openings in the forest that are suitable for nesting (Sandilands in Cadman et al. 2007).

Graber and Graber (1963) compared Illinois crow populations in 1906-09 and 1956-58. Populations in most habitats were much higher in the earlier period than later. They concluded that breeding populations had declined by 72% and wintering populations by 71%. Habitat changes between the 2 survey periods should have been beneficial and they had no explanations for the decline. Given that the wintering population decreased significantly, this appeared to be a wide-scale decline because the Illinois winter population consists of residents as well as migrants from Ontario, Michigan, and Wisconsin.

Long-term (1970-2021) Breeding Bird Survey results indicated annual decreases of 0.569% in Canada and 0.308% in Ontario. The short-term (2011-21) trends were annual decreases of 1.65% in Canada and 2.74% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings may spend about 10 days in the canopy near the nest before coming to the ground. If they fall before then, they usually cannot get off the ground and are preyed upon. Adults feed the young for at least 2 weeks after fledging, and young may be fully independent 1 or 2 months after fledging (Verbeek and Caffrey 2020).

MIGRATION

The American Crow withdraws from the northern portion of its Ontario breeding range. It is unknown if wintering birds are residents, migrants from further north, or a combination of these. Some birds well within the resident range migrate south. In the eastern states, half of banded crows between latitudes 38°N and 43°N were residents, and Illinois birds that breed south of latitude 43°N are mostly sedentary. In Quebec, most birds migrate, although those south of latitude 51°N are considered resident (Graber et al. 1987; Pelletier in Gauthier and Aubry 1996; Verbeek and Caffrey 2020). In wintering roosts in New York and California, it was a partial migrant. Some birds migrated and others were resident. Individual birds were consistent in their migratory behaviour across years and site fidelity was high, with birds generally returning to the same wintering areas each year (Townsend et al. 2018).

Migration appears to be diurnal except for a record of a nocturnal flock flying north over Saskatchewan. The American Crow migrates in flocks of 30-200 birds, occasionally in flocks as large as 500-1,000, rarely over 2,000; some individuals migrate singly. Three birds roosted at the same communal roost along the way in each of 3 years and 3 other crows roosted in different roosts in 2

different years. Some Ontario birds migrate southwestward to Illinois, Arkansas, Tennessee and North Carolina. A crow banded in Ontario in May was recovered in Arkansas the following January (Brewer et al. 2018; Graber et al. 1987; Morrison 1995; Reaume 2013; Verbeek and Caffrey 2020).

In southern Ontario, arrival is in late February or early March, occasionally in early February, and continues into mid-April in the southern Shield. Southward migration may begin in September and peaks in mid-October; movement continues until mid-November (Curry 2006; Mills 1981; Morrison 1995; Tozer 2012; Weir 2008).

The American Crow uses similar habitat during migration as in the breeding season. Agricultural landscapes are preferred and suburban and urban areas are used. Natural habitats frequented include open woodlands and small woodlots, forest edges, treed riparian areas, and marshes. In British Columbia, large areas of coniferous forest act as a barrier to the American Crow. In Illinois, bottomland forest, forest edges, and shrubby areas were favoured in spring and autumn (Campbell et al. 1997; Graber et al. 1987). In Pennsylvania, it preferred larger woodlands during spring migration and fragmented landscapes during autumn migration (Keller and Yahner 2007).

The American Crow is a common to locally abundant migrant (James 1991). Over an 8-hour period in mid-October, Morrison (1995) estimated that 3,000 passed along Georgian Bay northwest of Parry Sound. In mid- to late October, 3,000-5,000 birds may be counted daily along the Elgin County Lake Erie shoreline and flocks of 2,000 are common inland (Lancaster et al. 2004). In 2010, more than 343,000 were counted during autumn migration at 2 raptor counting stations along Lake Erie (Woodliffe 2011).

WINTER

Root (1988) concluded that the American Crow was absent where the average minimum January temperature is below –18°C. Ontario CBC results demonstrated that most counts south of latitude 47°N recorded crows every year, except for Manitoulin Island and the southern Shield south of North Bay. North of 47°N, only the Thunder Bay CBC recorded crows annually. Central Ontario was the northern limit of early winter distribution (Weseloh 1985).

In winter, this crow is strongly associated with anthropogenic habitats and its local distribution is influenced by food abundance. Corn fields are favoured habitat until they become snow covered. Congregations may occur at landfills, cattle feedlots, and slaughterhouses, with lesser numbers at bird feeders. Roads are frequented for road-kills. In more northern areas, it may be almost completely dependent upon landfills (Campbell et al. 1997; Knapton and Maturi 1984; Pelletier in Gauthier and Aubry 1996; Reaume 1985; Weir 2008). In Pennsylvania, wintering crows were associated with larger woodlands within fragmented landscapes (Keller and Yahner 2007).

Shoemaker and Phillips (2011) observed wintering crows roosting on the ground in urban areas in Ohio. Birds roosted on the roof of a building, in nearby trees, and on parking lots that had been cleared of snow. Ground roosting may have provided shelter from the wind and heat conductance from the pavement. Reaume (2013) observed the entire crow population roosting on the ground in Essex twice. Ground-roosting appeared to be unrelated to weather conditions. Crows normally roost in trees in winter and radiate out to foraging areas in the morning along a series of flight lanes. Large increases in the number of crows using a particular flight lane may occur if a food patch is discovered

along it, such as grain spilled from a railcar or an unharvested sunflower field. Langley (2014) established artificial food plots directly in the path of flight lanes at least 10 km from a roost. The number of crows using flight lanes closest to food patches increased but numbers using adjacent flight lands remained constant or declined. Some crows flew from an adjacent flight lane to one that supported a food patch. Roosts may function as information centres with crows learning about food availability.

Some birds or groups of birds may be territorial in winter; others in the same location are not. In New Jersey, wintering crows had territories of 26-49 ha. Territories of 2 groups overlapped slightly, and territorial disputes occasionally occurred in this area. Vagrants that occasionally foraged in the same fields were tolerated by territorial birds. Territoriality is nonexistent in roosts and densities may be as high as 3.7-5.4 crows per m^2 (Stouffer and Caccamise 1991; Verbeek and Caffrey 2020).

Graber et al. (1987) analyzed 1,214 pellets and 718 stomachs of crows wintering in Illinois. Corn comprised 94.7% of pellet and 93.1% of stomach contents. Other vegetation it ate included seeds of smooth sumac, poison ivy, hemp, hackberry, linden, and giant ragweed, and sedge tubers. Grit comprised 20.5% of the volume of pellets and stomachs. Small mammals constituted 1.4-3.0% of the diet, with deer mice most frequent followed by voles and shrews. Miscellaneous food items included insects, crayfish, and snail shells. Near Essex, crows often pecked at bases of cornstalks. Gizzards of 17 of 18 crows contained European corn borer larvae. At least 4% of all cornstalks within 25 km of the roost had been perforated by crows and over 85% within 2 km were perforated. Crow predation resulted in a 50% reduction in the number of larvae that successfully overwintered. The corn borer was an important winter food. Other items crows had eaten included large quantities of fish, unidentified meat, corn kernels, and garbage (Quiring and Timmins 1988). The crow may feed on the fruit of sumac in winter in southern Ontario (Reaume 2013).

This crow is readily attracted to carrion, and supplemental feeding by placing out carcasses increases local wintering populations. When a large carcass is found within the territory of a group, numbers in the immediate area only increase slightly (Heinrich 1988; Knight and Anderson 1990).

The American Crow frequently comes to bird feeders. Favourite foods at feeders are meat scraps, cracked and whole corn, peanuts in the shell, pet food, baked goods, and popped corn. Less frequently, it eats mixed seeds, canary seed, millet, sunflowers, milo, hulled peanuts or hearts, suet, bird puddings, fresh or dried fruit, and oats (Dunn and Tessaglia-Hymes 1999). At a southern Ontario feeder, a crow attacked and killed an American Goldfinch that was snow bathing. The crow flew with it to a nearby tree and completely consumed it within 8 minutes (Sandilands 1992).

Reaume (2013) reported that numerous crows died at the Essex roost due to an ice-storm. Hailstorms have killed roosting crows at other locations. It is vulnerable to severe weather events because large concentrations of birds occur in small areas.

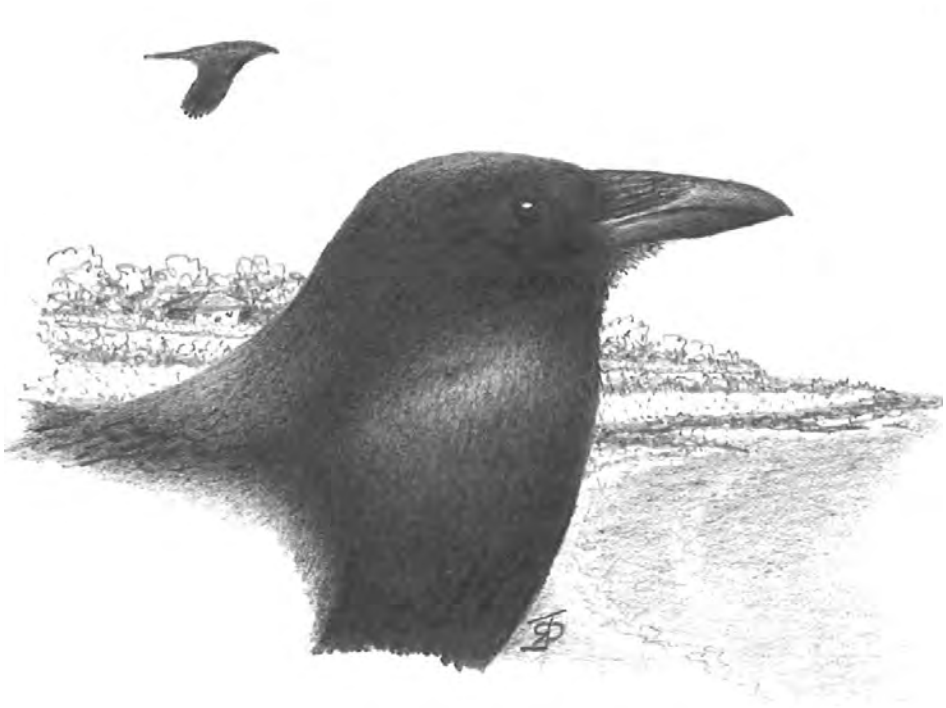
The American Crow was formerly rare to uncommon during winter in southern Ontario. McIlwraith (1894) stated that most left for winter, but that it suddenly reappeared if a carcass became available, suggesting it typically avoided areas near human habitation. Fleming (1907) reported that only a few overwintered near Toronto. In the 19th century, a few remained all winter along the St. Lawrence River and still only a few overwinter in the Kingston area (Weir 2008). In the Hamilton area,

crows were scarce during winter in the 1950s, but thousands have been present since the early 1980s (Curry 2006). Weseloh (1985) reviewed results from 77 Ontario CBCs from 1975 to 1983. Highest concentrations were in Thunder Bay, Essex, south Lambton, in a strip around Lake Ontario in Niagara, and in Toronto. There were also large numbers in the rest of southwestern Ontario, excluding the Bruce Peninsula, and in eastern Ontario off the Shield. Freedman and Riley (1980) examined CBC trends in southern Ontario from 1929 to 1977. Peak numbers occurred 1929-35 and 1964-77, with low numbers in between. They thought numbers recorded might reflect changes in roost sites. Sheppard et al. (1936) confirmed that roost locations affected local abundance. They considered it abundant in the Niagara area until a roost was abandoned, after which few were seen in winter. Woodliffe (2011) summarized more recent CBC counts. Between 1986 and 1990, there was an average of 7.8 crows counted per party-hour in all counts reporting the species. The average increased to 31 between 1999 and 2004 but dropped to 16 from 2005 to 2010. The reasons for the decline were uncertain. Many Ontario CBCs recorded their highest numbers in the 2000s. Trends determined by CBC data indicate annual increases in Ontario of 5.75% 1970-2021 and 0.43% 2009-21 (National Audubon Society 2022). James (1991) considered the crow a common to locally abundant winter resident in the Carolinian Forest Region, rare to locally uncommon elsewhere in the south and in the north at Thunder Bay, and occasional and rare elsewhere in the north to Atikokan and Moosonee.

There are several large winter roosts in the province. Weseloh (1983) estimated 50,000-75,000 crows at the Essex roost; Quiring and Timmins (1988) stated that numbers had swelled there to 90,000, with a peak of 96,669 (Woodliffe 2011). Reaume (2013) monitored this roost and determined that crows using it spread throughout Essex County during the day, an area of about 1,900 km^2. The St. Catharines roost was estimated at 6,000-7,000 crows (Knapton and Maturi 1984). At the Hamilton roost, 4,200-5,000 crows have been documented (Curry 2006); Reaume (1985) estimated 3,500-4,000 at the Chatham roost. The Chatham roost now surpasses the Essex roost for numbers with an all-time high of 159,860 reported on the 2000 CBC. This count does not record all the birds. A bird control company hired to discourage crows from roosting in the city estimated that there may be 250,000-500,000 crows present between late October and mid-November when there is a mix of migrants and birds intending to overwinter (Woodliffe 2011). At Thunder Bay, about 500 crows congregate in the roost. Weseloh (1985) reported a substantial roost of undetermined size near Port Hope–Cobourg. Reaume (2013) reported a winter roost of about 50,000 crows in the southeastern end of Woodstock. Ontario supports the largest crow roosts in Canada, but some roosts in Oklahoma and Kansas support as many as 6,000,000 wintering crows (Reaume 2013).

Fish Crow

Corvus ossifragus



BREEDING SEASON

Habitat Requirements

A single pair of Fish Crows nested in Mississauga in 2018. The habitat consisted of suburban residential and park areas, all close to the shoreline of Lake Ontario (Fazio 2019).

The Fish Crow breeds predominantly in coastal areas along beaches, marshes, and estuaries and into adjacent pine woods and riverine forests. It is usually found near water, including large rivers and lakes as well as saltwater areas. It often nests in heronries which may be in swamps. Islands in saltwater marshes that are forested with red cedar and pitch pine are favoured in some locations. Into the early 20th century, it was strictly coastal and occurred along major rivers upstream to the extent of tidewater influence. It has since adapted to inhabit more inland areas, including agricultural lands, urban and suburban residential areas, and commercial areas. It breeds in farmland as far as 160 km inland in Pennsylvania and Maryland, but occurs less in agricultural lands than the American Crow. It is now common in urban areas, although urban nesting was known as early as the 19th century. In upstate New York, it prefers urban parks, golf courses, and wooded residential areas over rural or heavily forested areas. It also nests in wooded cemeteries (Bent 1946; McGowan 2020).

The Ontario pair built 3 nests before successfully fledging young. One was in a spruce and the final nest was in the tallest white pine in the area (Fazio 2019). The Fish Crow typically nests in trees and occasionally in shrubs; there is 1 record of it nesting on a building. The nest is frequently in the uppermost crotch of a tree. It nests in both deciduous and coniferous species, showing a slight preference for conifers, especially pines. It has nested in junipers, red cedar, black oak, holly trees, beech, gum, sycamore, wild cherry, and maples. One nest was in the tallest shrub within a Green Heron colony. Nests were 1.7-45.7 m from the ground, with the highest nests in large sycamores. Average nest height tends to be 5-10 m above ground and is dependent upon the size of the nest tree. Nests are not used again in subsequent years but new nests may be built in the same tree even when the old one is still present. Several nests may be started before one is completed and used (Bent 1946; McGowan 2020).

Fish Crow nests may be close to each other and it has been suggested that it forms small colonies (Bent 1946; Madge and Burn 1994). It does not have multiple nests in the same tree or in adjacent trees, so it is not truly colonial. Nests may be clumped in areas where suitable nest sites are limited. Two pairs with nests approximately 100 m apart in a small woodlot simultaneously defended the woodlot from passing conspecifics. The nest and area around it are defended chiefly by the male. No information is available on the area that is defended around the nest. Chases of other Fish Crows are frequent. The area immediately around the nest is defended from the American Crow, but the 2 species may nest within 50 m of each other. Adults may forage 0.5 km or further from the nest, so the home range is a minimum of 79 ha but is probably much larger (McGowan 2020).

No information is available on natal philopatry or adult site fidelity rates. Young from previous years do not appear to return to their natal area but no studies have been done to test this theory. It is uncertain whether the Fish Crow is a true migrant. Even if it is a resident in much of its range, it may move to different habitats during the nonbreeding seasons and not necessarily return to the same breeding location (McGowan 2020).

Limiting Factors

No information is available on how long it takes to build the nest, whether time elapses between completion of the nest and egg laying, the egg-laying rate, or when incubation begins. Construction of the first Ontario nest was initiated on 23 April, but it was abandoned 3 days later. A second nest was initiated and quickly abandoned and the third and final nest was initiated on 1 May. The

incubation period is 16-19 days, mostly 18-19 days. The nestling period is approximately 5 weeks. Young in 5 Florida nests fledged at ages of 32-40 days; young fledged from the Ontario nest on 13 July. Young may fly from the nest and return before finally leaving (Bent 1946; Fazio 2019; Madge and Burn 1994; McGowan 2020).

The Fish Crow raises a single brood in a season but renests if nest loss occurs early in the season. The Ontario pair built 3 nests but these did not appear to represent replacement nests because it is unlikely that any eggs were laid in the first 2 nests. This appeared to be more typical of the species' habit of starting several nests before completing one to raise a brood. Clutches of 2-6 eggs have been reported, with most containing 4 or 5 eggs. Mean clutch sizes of 4.5 and 4.6 eggs have been reported. The clutch size of the Ontario nest was unknown, but 2 young fledged from it. The number of young produced is typically lower than the average clutch size, indicating that brood reduction is common (Bent 1946; Fazio 2019; Madge and Burn 1994; McGowan 2020).

The age at first breeding is unknown, but the Fish Crow probably does not breed until it is 2 or more years old. The mating system is monogamous. The duration of the pair bond is unknown but is likely to be long term. A third bird often attends nests, occasionally during nest building, and it may feed the nestlings. These appear to be adults rather than yearlings and are probably unrelated nonbreeders. These birds are probably not true helpers and the pair spends much time driving them away. The third bird is probably trying to establish a bond with the female and may attempt to copulate with her while she is incubating (McGowan 2020).

The Fish Crow is an omnivore that uses a variety of foraging techniques. It frequently robs heron nests of eggs and young nestlings, and it may breed in or congregate in heronries where they may significantly affect heron populations. It takes eggs and nestlings of a wide variety of waterbirds and passerines. It often feeds on the seashore and in marshes and other water bodies, wading in shallow water. It patrols low over water to pick up floating items such as dead fish and has been reported catching small fish and lizards from the surface of the water with its feet. It is an important predator of turtle eggs, digging them up and eating them. It often forages on the ground, on the edge of water, and in trees for bird nests. In urban areas, it frequents dumpsters, parking lots, and landfills in search of waste and offal. It spends less time on the ground foraging than the American Crow, but may follow plows in fields to pick up grubs and other arthropods. It may land on the backs of cattle to prey on ticks. It kleptoparasitizes other Fish Crows, American Crows, gulls, ibises, and Ospreys to obtain prey. The Fish Crow hops from a perch to catch terrestrial insects, picks small spiders from their webs, and sallies from the ground or an elevated perch to catch flying insects. It scavenges migratory birds killed at communication towers. It may spread its bill tips to open balls of dirt and dig in dirt or litter with a sideways swipe of the bill (Bent 1946; Madge and Burn 1994; McGowan 2020).

The Fish Crow has perches where it regularly brings food to eat (Bent 1946; McGowan 2020). It frequently stores food for later use, often at the perch. Caches may be in grass, Spanish moss, or tree bark. Those in grass may be covered by another object such as a leaf. Caches near the nest are used by both pair members to feed the nestlings (McGowan 2020).

The male feeds the female while she is incubating; the female may also leave the nest to obtain her own food. At the Ontario nest, the male brought the female Mourning Dove eggs and nestlings of House Sparrows, Baltimore Orioles, Red-winged Blackbirds, and Common Grackles (Fazio 2019). Adults may dunk food in water before giving it to the nestlings, or take water directly to them. Food supplied to nestlings in 1 area included chicken bones, young swallows and Blue Jays, bread, and other refuse (McGowan 2020).

In the core of the Fish Crow's range, adults specialize on preying on eggs and nestlings of colonial waterbirds such as herons, cormorants, gulls, and terns. It eats eggs and nestlings of a wide variety of birds including shorebirds, rails, chickens, ibises, waterfowl, pigeons, grackles, Blue Jays, Northern Mockingbirds, Brown Thrashers, House Sparrows, and Red-winged Blackbirds. It may be a locally important predator on turtle eggs. On beaches and in salt marshes, it consumes small crabs, shrimps, crayfish, dead and live fish, amphibians, carrion, and offal. It also eats ants and grasshoppers. It consumes a wide variety of vegetable matter, including seeds, fruits, and grain. It eats seeds of locusts, flowering dogwood, wild rice, and hackberry and fruits of pokeweed, mulberries, huckleberries, red cedar, black gum, magnolias, hollies, pawpaw, greenbrier, mistletoes, pears, oranges, tomatoes, and acorns. The grain that is consumed is mostly corn and oats and appears to be mostly waste grain. In Virginia, it inflicts considerable damage on peanut crops (Bent 1946; Madge and Burn 1994; McGowan 2020).

Habitat loss is not a significant limiting factor for the Fish Crow, particularly now that it is adapting to urban life. In South Carolina, it decreased when natural succession was allowed to proceed in abandoned farmlands, but it increased in other habitats (McGowan 2020).

The Fish Crow died in large numbers in 1999 during an outbreak of West Nile virus in New York and New Jersey but populations have rebounded. Occasionally it is struck by vehicles; young birds in their first summer are usually the victims (McGowan 2020).

The Fish Crow is highly tolerant of human activity near the nest. At the Ontario nest, it was oblivious to pedestrians, wedding parties, and trail construction. It readily abandons the nest if a human climbs up to it and may abandon nests with young as old as 2 weeks (Fazio 2019; McGowan 2020).

Hunting may be a major source of mortality and may be the most significant limiting factor. In most states, the Fish Crow is unprotected by legislation and is widely shot. Some states have closed seasons on it, but no bag limits when the season is open (McGowan 2020). Crows are not protected by a closed season in Ontario.

Status

James (1991) considered the Fish Crow a vagrant to Ontario, with 3 documented records at that time, all at Point Pelee: on 15 May 1978, 21 April 1982 (James 1983), and 20 May 1983 (James 1984a). Several occurred in the province in 2012, with 2 seen on 14 March to 29 July at Bronte, 2 from 26 March to 13 April in Guelph, 1 on 4 and 5 May at Thickson Point in Durham Region, 1 on 7 May at Turkey Point, and at least 5 at Fort Erie from 15 January to 26 February. By the end of 2012, the Ontario Bird Records Committee (OBRC) had accepted 22 records, some of which represented multiple birds (Cranford 2013). In 2014, 3 more records from Guelph, Hamilton, and Fort Erie were

accepted by the OBRC and there were many more records for which no documentation was submitted. It continued to spread into the province through the Niagara Peninsula and the west end of Lake Ontario. It was still considered very rare, with a total of 33 records accepted by the OBRC (Burrell and Charlton 2015). It is probable that some Fish Crows go undetected because of the difficulty in distinguishing them from the American Crow. In 2015, the OBRC accepted more records from Fort Erie, Waterloo, St. Catharines, Camelot in Niagara Region, Rondeau, Point Pelee, Stoney Creek, and Chatham-Kent. By then, there were 42 accepted records (Burrell and Charlton 2016). In 2018, a record of 4 birds in Mississauga was accepted by the OBRC. Burrell et al. (2019) concluded that within a decade it had gone from being a vagrant with 1 or 2 records per year to a regular and now breeding component of the Ontario avifauna. By then, there were records for every month of the year. Fazio (2019) reported that breeding behaviour was seen in Oakville in 2012 and Port Weller in 2016, but there was no evidence of successful nesting. At least 55 were seen in Niagara Falls on 4 August 2017, including a pair of recently fledged young, but it was possible that these fledglings were not produced in Ontario. A pair was seen in Mississauga calling and interacting with each other in April 2016 and this is where the first successful nesting occurred in the province. Fazio (2019) predicted that it would eventually nest in most municipalities on or near the shore of Lake Ontario and other lakes in the region.

The Fish Crow has greatly expanded its range in the last few decades and its population is increasing. In the 19th century, it occurred from southern Connecticut to Louisiana as well as up the Hudson River and casually into Massachusetts. At that time, it was strictly coastal and occurred up major rivers to the extent of tidewater influences. It expanded inland along major rivers in the late 20th century, and northward along the Atlantic Coast. It generally colonizes in a leapfrog fashion, establishing new breeding areas long distances from its previously known range, despite the presence of suitable breeding habitat in between. A population near Ithaca, New York, was established 200 km from its former breeding range. All newly established New York colonies were at least 55 km from the nearest known range limit at the time. Colonies were also established by leapfrogging in Maine and Virginia, and the Ontario nest is another example of this behaviour. The expansion of the Fish Crow's range in the United States may have followed the expansions of heron and Common Grackle colonies which are both major sources of food. The increase in its population in the core of its range may have fuelled the range expansion. Its more recent adaptation of nesting in urban areas may promote its establishment in new areas (McGowan 2020; Wells and McGowan 1991).

Results from the Breeding Bird Survey (BBS) for 1966-98 indicated that the Fish Crow increased at a rate of 1.6% annually throughout its range. Most of the increase occurred 1966-79 when it increased at a rate of 6.0% per year. It did not exhibit any significant trends 1980-96, with a modest increase of 0.8% per year (McGowan 2020). There are no BBS data for Ontario.

POSTFLEDGING PERIOD

Young can fly short distances when they fledge. Fledglings stay in trees for several weeks after leaving the nest until they are proficient at flying. They then follow their parents to the ground and begin foraging for themselves. Young remain with the adults for 1 month or more after fledging and continue to be fed until they are about 70 days old (McGowan 2020). At the Ontario nest, the

single fledgling stayed close to the female for its first week out of the nest. It was fed by the female, with the male absent most of the time. The last time the female and fledgling were seen together was 5 October (Fazio 2019).

The Fish Crow is highly gregarious during the postfledging period and other nonbreeding seasons. It may congregate in foraging flocks of hundreds of birds that include juveniles, adults that bred, and nonbreeders. These flocks are often mixed with the American Crow (Bent 1946; Madge and Burn 1994; McGowan 2020).

Communal roosts are an important habitat component in nonbreeding seasons, and some limited use of communal roosts may be made while breeding. Roosts tend to support large numbers of birds, with more than 45,000 Fish Crows reported at some roosts. It often roosts with the American Crow and also with herons and egrets. Roosts tend to be distant from the favoured foraging area. A Florida roost in pine trees was 48-64 km from the feeding areas. The Fish Crow typically roosts in trees but has been reported roosting in willows along lakeshores and in rushes in marshes. In the core of its range, it prefers to roost in isolated rural areas and on offshore islands (Bent 1946; Madge and Burn 1994; McGowan 2020).

MIGRATION

It is uncertain whether the Fish Crow is a permanent resident within its range or a short-distance migrant. Some are found year-round even in the northernmost portions of its range. Individuals may simply withdraw from areas where they nested and move to locations with a plentiful food source in winter. Seven birds banded in winter along the Louisiana coast were shot in central Arkansas in spring, suggesting that migration had taken place. All other recoveries were within 300 km of the banding site. Observations of flights of several hundred per day in autumn in New York are suggestive of migration. All movement appears to occur during the day (McGowan 2020). Longer movements may possibly represent juvenile dispersal.

WINTER

Winter habitat is similar to breeding habitat but the Fish Crow congregates near abundant food sources such as estuaries, landfills, feedlots, and shopping centres in winter. In Maine, it wintered at an inland landfill and moved to the coast for the breeding season. Overwintering at landfills near rivers or other aquatic habitats is becoming more common. It exhibits no territoriality in winter and continues to roost communally at night (Madge and Burn 1994; McGowan 2020).

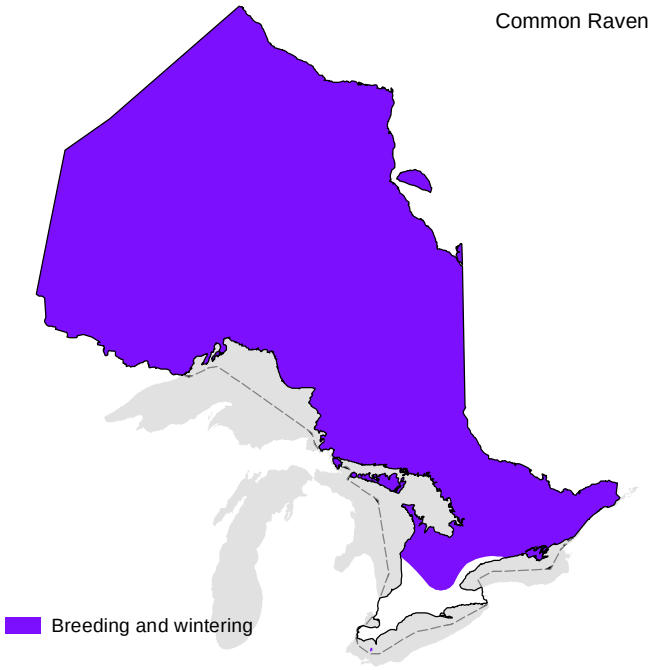
Common Raven

Corvus corax

BREEDING SEASON

Habitat Requirements

In Ontario, the Common Raven nests in forested areas, open grasslands and shrubby areas, near buildings and hydro rights-of-way, and in tundra. It prefers mixed woodlands over deciduous or coniferous forests. Most nest sites overlook vistas, even in forests, and nests are near water (Peck and James 1987). In the Gogama area, it nested in groves of mature pines and foraged in recently cut, planted, or burned forests and along roads (James and Peck 1995a). Near Kingston, it nested in the Canadian Shield and was associated with rock faces and outcroppings in mature, undisturbed forest (Weir 2008). In Ottawa, it nested in an active quarry (DiLabio and Martin 1959) and it has nested 43 m below ground level in an open-pit mine at Sudbury (Blomme in Cadman et al. 1987). It also nested in an active quarry in Halton Region (personal observation). In Ontario, it is associated with landscapes that are predominantly forested, but is becoming increasingly common in the



agricultural south. Near Elora, it apparently nested for several years in Norway spruce around a farmstead (Grant Egerdee, personal communication).

The raven prefers areas with considerable topographical relief, such as cliffs, because they provide thermals for long-distance foraging flights, and areas with cliffs, trees, or human structures that provide nest sites. In the north, it prefers wilderness and often avoids areas with human activities. Where food resources are scarce, it adapts to human presence (Boarman and Heinrich 2020). Erskine (1977) considered the raven more characteristic of coniferous than deciduous forests in the Boreal Forest Region, but it was a wide-ranging species not confined to 1 community or forest type. In Quebec, it inhabits mixed and coniferous forests, mountainous regions, tundra, seacoasts, and, more recently, urban areas. In the south, it prefers mountainous areas and extensive mixed and coniferous forest. Distribution is patchy in southwestern Quebec where the low relief, scant forest cover, and intense human activity probably discourage it from nesting (Roy and Bombardier in Gauthier and Aubry 1996). In British Columbia, 40% of nests were in forested habitat, at a 3:1 ratio of mature to second-growth forests; 36% were associated with cliffs; and 7% with industrial sites. The remaining nests were in residential areas, parks, burns, and miscellaneous habitats. Fifty-six percent of nests were in forested areas and 35% were in human-altered areas (Campbell et al. 1997). In Michigan, the raven nested in bogs treed with spruce (Parmelee 1988). In Wyoming, it nested in isolated stands or on edges of large stands (Dunk et al. 1997), but was unaffected by distance from edge in California (Brand and George 2001). In Saskatchewan, it was randomly distributed within fragmented landscapes. Forest size, amount of forest within 5 km, and forest type had no significant effect on its distribution (Hobson and Bayne 2000). In the Appalachians, it had neutral affinity to old-growth forests, occurring in them at equal frequency to other ages of forests (Haney 1999). Cities had the highest density of ravens in Wyoming where the dominant habitats were sagebrush steppe and grasslands with interspersed human settlements. All other habitats had low densities; of the linear habitats, occupancy was greater along roads than in riparian habitat. Edge habitats had the lowest level of occupancy. Ravens were consistently present in cities and along roads. Nest sites, food, and water may have been scarce outside cities (Bui et al. 2010). In open habitat in Idaho, it was significantly associated with anthropogenic features. There was a 31% decrease in its probability nesting for every 1 km increase in distance from a transmission line. Ravens were most likely to nest near edges of cover types that were associated with direct human disturbance or fire (Howe et al. 2014). Presence of suitable nest sites and adequate food supply may be more critical than habitat types. In Ontario, it is

predominantly associated with extensively forested landscapes with minimal human disturbance, but is beginning to encroach into areas with more human activity.

In Wyoming, nest sites had 51.4% cover compared with 30.4% at random sites, the basal area at nest sites was 0.79 m^2 compared with 0.52 m^2, nest sites had 3.1 snags compared with 1.9, ground cover at nest sites was 72.1% compared with 65.3%, and slope at nest sites was 16.3% compared with 12.4% at random sites (Dunk et al. 1997).

Raven roosts have not been reported in Ontario, but have been documented in several areas. They are unlikely to occur in areas of low nesting density, but even in these areas temporary roosts may be established around abundant food sources outside the breeding season. Roost characteristics are variable, with roosts reported in white pine groves, hard-stemmed bulrush marshes, on cliffs, on telephone and hydro poles and wires, on high-tension power lines, in abandoned buildings, in birch woodlands, on oil tanks, and on the ground. A large roost on new high-tension towers in Idaho occurred where birds formerly roosted on rock outcrops, scattered clumps of low trees, and smaller transmission lines. Use of roosts varies seasonally. In Massachusetts, roosts were used July through September. In Oregon, roosts formed in mid-October, with peak numbers in January and abandonment in mid-March. In Idaho, highest numbers occurred from July to September and lowest numbers were from January to March. Use of roosts for 10-15 years has been documented, but most roosts are transitional. Some are present for 2 or 3 months never to be used again; some congregations occur for only a week or single night. One area in California that had never been used previously was used by 1,500 birds for 36 nights then abandoned. Within traditional roosting areas, the roost site varies considerably and may move a few hundred metres or even kilometres in response to weather conditions, disturbance, and unknown factors. In Idaho, radio-tracking over 209 days demonstrated that some individuals remained at a single roost during this period; another changed roosts 19 times. Movement occurred between all roosts, including those 63 km apart. In some areas, pre-roosts are used. These are typically unvegetated or sparsely vegetated areas. The number of birds at roosts is usually 10 to less than 100 birds, but large roosts in excess of 2,000 occasionally occur. The primary function of roosts appears to be as an information centre for food. Strangers are readily accepted and led to food sources. Roosts used mostly in late summer are dominated by juveniles but all age classes may be present at winter roosts. At Churchill, numbers at a winter roost increased with windchill (Boarman and Heinrich 2020; Cotterman and Heinrich 1993; Engel et al. 1992; Flanagan 1993; Heinrich 1988; Stiehl 1981).

In Ontario, the raven has nested on natural and human-made substrates. These included ledges and crevices of cliffs (55.5%), trees (27.0%), bridge beams (4.8%), hydro towers (4.8%), grain elevators (3.2%), small sheds (1.6%), lumberyard incinerators (2.4%), and radar-dish girders (0.8%). Human structures that have supported nests include towers for hydro, radar, and navigation; active or abandoned buildings, silos, and grain elevators; bridges and canal locks; racetrack light platforms; and water towers. One nest was on a moving power crane. Tree nests were in living trees, both in deciduous (54.5%) and coniferous (45.5%) species. Poplars were preferred over spruce and pine. Nests were typically near the top of the tree in crotches near the tree trunk. Nests on cliffs and human-made structures faced all directions, but more frequently towards the southwest. Nests are frequently reused and the raven has used old Bald Eagle nests in the province. Some cliff nests were

abandoned Peregrine Falcon nests. Nests on cliffs were 1.8-152 m from ground, with most 12-24 m up. Tree nests were 3-30 m from ground, with most 10.5-15 m up. Nests on human-made features were 3-35 m from ground, with most 7.5-18 m up (Peck 2005a; Peck and James 1987, 1997). The 70 nests found in southern Ontario since 1980 showed more use of human structures than occurred historically. Forty-nine percent were on cliffs and rocky ledges (mostly on the Niagara Escarpment); 20% were in trees; and 31% were in or on buildings, towers, or other human-made structures (Peck 2005a). At Cape Henrietta Maria, the raven was apparently scarce due to rarity of nesting sites until the radar stations were erected in the 1950s. Subsequently, it nested on the radar screens and on a cable tower support attached to a cabin (Peck 1972). In Algonquin Park, it nested on a sawdust burner (Tozer 2012).

Throughout its range, the raven nests either on cliffs, in trees, or on human-made objects. Human substrates are usually used only in areas with limited tree growth and topographical relief. In such an area in Idaho, 73.2% of nests were on anthropogenic features; 53.0% were on electrical transmission towers. Natural nest sites included 6.2% on rock ledges and 20.6% in a variety of native and cultivated tree species. In some areas, it strongly selects cliffs despite the abundance of suitable nest trees; in other areas the reverse is true. In Virginia, only 3 of 57 nests were in trees. Individuals use the same nest-type for their life. Nestlings may become imprinted to nest substrates, possibly explaining why certain populations prefer cliffs over trees or vice versa. In Washington, canopy closure at nests was 85% and denser than surrounding areas. Seventy-four percent of nest trees were the tallest trees within the plot. Other authors noted that the raven tends to select tall trees and nest near the top of them. Nesting in tall trees or at edges probably improves accessibility. Although nests may be near treetops, they are in dense canopy; shading of the nest appears important. In British Columbia, some nests on cliffs were in trees. It appears to prefer coniferous trees for nesting, particularly in the west. It has nested in black and white spruce, balsam poplar, trembling aspen, hemlock, white pine, cottonwood, willow, white oak, and Manitoba maple (Bent 1946; Boarman and Heinrich 2020; Campbell et al. 1997; Fleming and Speich 1988; Sinclair et al. 2003; Tyrrell 1945). In Virginia, cliffs of particular rock types were used in proportion to availability; nest success was unrelated to cliff height. Nests on cliffs faced all directions, but mostly south and west, and most nest cliffs were at the end of ridges or where water formed a gap in the cliff. All nests on cliffs were sheltered by overhanging ledges of 2-600 cm, and most were sheltered by rock buttresses on 1 or both sides. Nests may be in cavities in cliffs or wedged into crevices. Mean width of nest ledges was 61.3 cm (range 41-91 cm). Cliffs were undercut below the nest ledge at 63.2% of sites and nearly vertical at 31.6%. Ledges often sloped away from the cliff; occasionally a small shrub helped hold the nest in place. The most important factors in cliff nest-site selection appeared to be a suitable ledge with an overhang above and steep rock face below. Proximity of other active nests also appeared important. Similar characteristics have been reported for cliff nests elsewhere. Cliff height appears secondary, but it seldom uses cliffs that are less than 15 m tall. In lieu of cliffs, the raven may nest in active or abandoned quarries and on steep road cuts (Bent 1946; Boarman and Heinrich 2020; Bowles and Decker 1930; Coates et al. 2014; Conner 1985; DiLabio and Martin 1989; Flanagan 1993; Harlow 1922; Hooper 1977; Hooper et al. 1975; Knight 1984; Peck and James 1987; Roy and Bombardier in Gauthier and Aubry 1996; Stiehl 1985). The raven has nested on or in a variety of human-made structures. These include windmills, abandoned and occupied buildings, barns, oil

derricks, high-tension towers, hydro poles, railway and highway bridges, grain elevators, church steeples and bell towers, billboards, communication towers, abandoned cars, a barbecue in an abandoned railway car, the top of a chimney, a window opening in an old lighthouse, and water towers. It typically nests on beams or other structures within abandoned buildings, but occasionally on a porch or other exterior structure. One nest on the beam of a railway bridge was only 60 cm below the tracks, and the adult remained on the nest while trains passed over (Booth 1996; Boarman and Heinrich 2020; Campbell et al. 1997; Bowles and Decker 1930; Coates et al. 2014; Congdon 1948; Dunk et al. 1997; Knight 1984; Kozij 1986; Kuyt 1992; White and Tanner-White 1988). The raven has nested in old Red-tailed Hawk, Golden Eagle, and Bald Eagle nests, and a nest used the previous year by a Great Horned Owl. It also nested on an island in a Great Blue Heron colony, but it was unknown if it nested in an old heron nest or one that it constructed (Bent 1946; Boarman and Heinrich 2020; Bowles and Decker 1930; Conner 1985; Flanagan 1993; Fleming and Speich 1988; Kuyt 1992; Stiehl 1985).

Territorial defence is greatest during the breeding season, but may occur at other times of the year. Birds usually defend their territory against other individuals or small groups and stay out of sight when a flock encroaches. Intruders may be chased for several kilometres or, when resources are plentiful, only a small area around the nest may be defended. Home range sizes vary greatly depending on availability of food and nest sites. Average home range was 40.5 km^2 (range 27.3-195 km^2) for 9 birds, but another 13 were so nomadic that home ranges could not be estimated, covering minimum areas averaging 1,252 km^2; some of these were nonadults. In coastal California, average home range for 12 breeders was 1.2 km^2 (range 0.3-4.4 km^2) and the average for nonbreeders was 8.2 km^2 (range 2.2-45.8 km^2). In spring, average home ranges were 19.5 km^2 for nonbreeders, 1.8 km^2 for breeding males, and 0.8 km^2 for breeding females. In Wyoming, 3 pairs had home ranges averaging 9.4 km^2. In the Yukon, birds were evenly spaced throughout the Boreal Forest Region with a pair every 50 km^2. In Washington, mean home ranges were 15.34 km^2 for males, 12.75 km^2 for females, 8.59 km^2 for adults, and 19.50 km^2 for nonbreeders. Median distances moved were 4.5 km for males, 7.6 km for females, 1.3 km for adults, and 14.5 km for nonbreeders. Mean maximum distances moved were 19.5 km for males, 17.7 km for females, 5.5 km for adults, and 42.4 km for nonbreeders. Not all birds demonstrate clear home ranges, and there may be overlap of home ranges. In Maine, nonbreeders wandered widely over more than 1,800 km^2. Mean internest distances also vary considerably and may be hundreds of kilometres in tundra or other places where nest sites are scarce. Normally, internest distances vary from 300 m to 9.6 km. In a high-density population in Wyoming, the mean internest distance was 1.6 km (range 0.5-2.45 km). In Virginia, the mean internest distance was 4.3 km and the closest nests were 2.2 km apart in 1 area. In another area of Virginia, mean internest distances were 4.8-5.1 km over 2 years, with a mean home range size of 38 km^2. At a third Virginia site, mean internest distance was 2.9 km with a mean home range size of 30.2 km^2. There are 2 reports of nesting colonies from British Columbia. There were 9 nests on a small, eroded cliff face and this site was used for several years before it was abandoned. At a second colony, 2 or 3 pairs nested for several years on a lakeshore cliff face (Boarman and Heinrich 2020; Campbell et al. 1997; Craighead and Craighead 1956; Dunk et al. 1994; Hooper 1977; Hooper et al. 1975; Linz et al. 1992; Madge and Burn 1994; Sinclair et al. 2003; Webb et al. 2012).

In Idaho, 4 of 163 nestlings (2.5%) returned to the natal area to breed. In Washington, juveniles left their natal territory between early July and late September, with a median date of 9 August. Sixteen of 22 juveniles (72.7%) did not return to their natal territory; the other 6 returned on and off for an additional 5-26 days. Following independence, 55% of juveniles returned at least once to their parents' home ranges, but only as members of large groups attracted to abundant food resources. Some pairs build 2 or 3 nests a year and alternate between nest sites. Most adults tend to nest within 0.5 km of the previous year's nest, but successive nests may be as far apart as 12 km. In Virginia, 4 of 12 pairs (33.3%) used the same nest the next year, 33.3% moved 0.01-0.8 km, 16.7% moved 0.81-1.6 km; 8.3% moved 1.61-2.4 km; and 8.3% moved 2.41-3.2 km. Another pair used the same nest in 3 years, even though there were at least 10 potential nest sites within 0.8 km. Ninety-one percent of birds nesting on hydro towers nested on the same tower or within 2 towers of the previous nest. In Washington, breeders displayed strong site fidelity, except in autumn and winter or after death of a mate, when some breeding ravens moved extensively. Two Algonquin Park nest sites were used 20 and 21 years. Some cliffs are thought to have been used for centuries, so it is thought that adults have high nest-site tenacity. Few studies have determined if the same birds were involved in long-term occupancy of nest sites. Of 10 nests reused in California, 2 were used by the same pair, 4 by 1 member of the previous year's pair, and 4 by different birds (Boarman and Heinrich 2020; Booth 1996; Congdon 1948; Flanagan 1993; Hooper 1977; Hooper et al. 1975; Peck 2005a; Roy and Bombardier in Gauthier and Aubry 1996; Webb et al. 2012). In Algonquin Park, ravens nested on 1 cliff most years from 1963 to 2000 (38 years) and a nest site on another cliff was occupied from 1970 to 1999 (Tozer 2012).

Limiting Factors

Eggs have been found in Ontario nests from the second week of March until mid-May, with most present from the last week of March until mid-April (Peck and James 1997). In Algonquin Park, nests are under construction from late February to early April, eggs are present from mid-March to mid-April, nestlings are present from early April to early June, and dependent fledglings have been observed from mid-May until mid-June (Tozer 2012).

Experienced birds start nesting 2 or 3 weeks earlier than inexperienced birds. Weather conditions may also influence timing of nesting. Nest construction took 9 days in Wyoming; Pennsylvania nests took 14-18 days to complete. In Pennsylvania, egg laying started 3-7 days after the nest was complete. Eggs are laid at the rate of 1 a day. Incubation may begin with laying of the first or second egg, or the female may just cover the eggs for the first few days and not incubate. The incubation period at 4 Ontario nests was 20-21 days. Elsewhere, incubation periods of 17-25 days have been reported. Eggs hatch asynchronously, typically a day apart. Fledging occurs at age 35-49 days (Boarman and Heinrich 2020; Bowles and Decker 1930; Campbell et al. 1997; Conner 1985; Engel et al. 1992; Flanagan 1993; Harlow 1922; Kilham 1989; Madge and Burn 1934; Peck 2005a; Stiehl 1985).

One brood is raised annually. Renesting may occur if a clutch is lost, either in the same or a new nest. Some pairs laid 3 clutches in attempts to raise young; many pairs do not renest. One Ontario pair renested in Timiskaming District in a second nest 183 m from the original nest. In Oregon, a male renested after the female and brood died. He remated and another clutch was laid in the same

nest. In Washington, a pair renested successfully after losing a brood. Replacement clutches may be laid 11-22 days after loss, and frequently contain 1 less egg than the first clutch. In Idaho, replacement clutches had significantly fewer eggs (5.6 compared with 4.9) and were not always successful. In Pennsylvania, ravens typically laid another clutch 3 weeks after the first one was collected. Clutches of 2-7 eggs have been reported in Ontario, but 2-egg clutches were incomplete. Most clutches contained 4 or 5 eggs. Most North American clutches have 3-7 eggs, with 8-egg clutches rare; most contain 4 or 5 eggs. Based on 200 nests from 6 studies, the average North American clutch is 5.3 eggs: 4.6 in Ontario, 6.0 in Oregon, 5.6 in Idaho, 5.4 in Utah, 5.4 in California, and 4.6 in Wyoming. It has been suggested that clutch size increases with latitude, with typical clutches of 6-8 eggs in the far north. In some areas, clutch size varies significantly annually; in others it is stable. Stable clutch sizes are most likely in populations with consistently abundant food resources and where late spring snowstorms rarely occur. Even where clutch size is consistent, there may be large annual variations in numbers of fledglings produced (Bent 1946; Boarman and Heinrich 2020; Bowles and Decker 1930; Congdon 1948; Dunk et al. 1997; Harlow 1922; Peck and James 1997; Stiehl 1985).

The age of first breeding is largely unknown. In Washington, 1 male bred unsuccessfully in his fourth year and successfully fledged young in his fifth year. In captivity, successful breeding occurs at 3 or 4 years of age; 2-year-olds make unsuccessful attempts. Once breeding is initiated, most birds breed annually, but older birds may occasionally skip a year. The mating system is considered monogamous, but few data are available. Pair members usually remain together year round and may mate for life. In Washington, pair bonds were broken only by the death of a mate; the survivor remated when this occurred (Boarman and Heinrich 2020; Ellis et al. 1994).

The raven forages mostly on the ground but also aerially, and uses several unusual techniques to secure food. Most feeding is on the ground on carrion and live vertebrates and invertebrates. It may follow plows and harvesting equipment in fields or dig in soil with its bill to obtain invertebrates. One pair regularly walked a shoreline to search for dead fish. Birds as large as Rock Pigeons and eiders may be struck down in midair and the raven has been observed aerially kleptoparasitizing Northern Harriers and Merlins; American Crows and Great Egrets have been kleptoparasitized on the ground. In Nevada, it kleptoparasitized a Golden Eagle nest, feeding on 9 of 30 prey items delivered to the nest during the chick-rearing period. It also scavenged a dead nestling. In some areas, the raven regularly patrols highways to search for road-kills. It has an important commensal relationship with large carnivores, following them to forage on their leftovers. Its relationship with the gray wolf is particularly important, especially in winter. It also follows polar bears, coyotes, lynx, and human hunters. It cannot open body cavities of mammals larger than raccoons, so may purposefully attract large carnivores to carcasses so they will open them up. Cooperative foraging by groups of ravens is common to capture larger or potentially dangerous prey, or to kleptoparasitize cats and dogs. Teams of ravens have killed roosting kittiwakes, a Common Loon, a young porcupine, caribou fawns, seals, and hares. A group of birds may distract dogs by pulling their tails, while another raven steals its food. Foraging at landfills is common. Some birds spend much time at landfills; others never visit them. Colonies of gulls, terns, cormorants, and other seabirds are particularly attractive to ravens, where they feed on eggs and nestlings. Depredation by ravens at some Ring-billed and Herring gull

colonies was so intense that it resulted in colony abandonment. It may follow traplines to pick at animals caught in traps. In the far north in winter, it follows dogs and eats their fresh dung. In Oregon, it dug female crabs from the sand during low tide, flipped them over, and ate the egg masses they were carrying, but did not eat the crabs (Bent 1946; Boarman and Heinrich 2020; Conner and Adkisson 1976; Flanagan 1993; Gehring 1993; Harlow et al. 1975; Heinrich 1988; Hendricks and Hendricks 2011; Hendricks and Schlang 1998; Hooper 1977; Irwin et al. 2003; James 1980; Jehl and Smith 1970; Kilham 1985b; Ling et al. 1992; Maguire 2000; Parmelee and Parmelee 1988; Porsild 1943; Proctor 1995; Roy and Bombardier in Gauthier and Aubry 1996; Simes et al. 2017). The raven is attracted by the sound of gunshots; this may signal the presence of a downed ungulate. Predator calls blown to imitate a dying rabbit or young deer also attract ravens (Frame 2010).

The raven is an opportunistic omnivore, but a high proportion of its diet is carrion, mammals, and birds and their eggs. In early spring at the beginning of the nesting season, carrion may be a significant component of the diet. It feeds on carcasses of large mammals brought down by carnivores and road-killed frogs, toads, and mammals. As spring progresses, it relies less on carrion, although it may still visit landfills and patrol roads. The diet shifts at this time and is dominated by small mammals, particularly juvenile rabbits, but also voles, mice, shrews, muskrats, flying squirrels, gray squirrels, and chipmunks. Bird eggs become important in the diet at this time. Eggs of any species except large raptors may be taken, from small and medium-sized passerines to loons, herons and egrets, waterfowl, gulls, terns, and cranes. Some populations may focus on preying on certain birds, such as waterfowl, Sandhill Cranes, and Whimbrel. Local populations may decline in years when these prey species are affected by drought or other factors. As the nesting season progresses, nestlings and adult birds replace eggs in the diet. The raven has been observed pulling flickers and American Kestrels out of nesting cavities, and it frequently catches and consumes Rock Pigeons. In late spring, summer, and early autumn, insects may be important food. In Oregon, insects were second to mammals in importance in summer, comprising 48.6% of adult and 29.4% of nestling food. The order of importance of insects was bugs, flies, hymenopterans, beetles, lepidopterans, and grasshoppers. Cicadas were the most important bugs, representing 18.7% of all food items and 56% of insects consumed. They constituted 21.1% of the nestling diet and 10.0% of the adult diet. Hymenopterans were the third most important insect group, particularly sawflies. Most flies were flesh fly larvae and pupae that may have been ingested incidentally with carrion, but some were probably picked off carrion. Other flies consumed were soldier fly larvae. Beetles were the most frequently occurring insects in the diet, but in small numbers and volumes. Darkling beetles were most frequent, but weevils and scarab, skin, ground, and carrion beetles were also consumed. In August in Oregon, large flocks gathered in cultivated fields as far as 100 km from nesting areas to feed on grasshoppers. The amount of vegetation eaten is highly variable; in most populations, it is a minor component of the diet, but plant material predominates in some areas. In Idaho, vegetation comprised 73.5% of food eaten and 69.3% was cereal grains (corn, oats, wheat, and barley). The remainder was Russian olive seeds and unidentified vegetable matter. In Ungava Bay, the raven ate large quantities of unspecified berries. It has eaten stems, leaves, and roots of various grasses and forbs, holly berries, hemlock seeds, spruce cones, and mountain-ash berries. Although it will eat almost anything given the opportunity, mammals are most important in the diet. Populations are highest where there are large mammals present whose carcasses provide occasional bonanzas of

food. These may be large ungulates such as deer, moose, elk, caribou, or livestock. A population in the Mackenzie delta initially survived mainly on hares. Other items it has eaten include clams (which it may drop on rocks to open them), lizards, snakes, turtles, skunks, fish, snails, grouse, garbage, crayfish, tadpoles and frogs, chickens, opossums, bobcats, dogs, squirrels, cats, woodchucks, rats, and bats (Alvo and Blancher 2001; Bent 1946; Boarman and Heinrich 2020; Bowles and Decker 1930; Engel and Young 1989; Flanagan 1993; Harlow et al. 1975; Jehl and Smith 1970; Kelly et al. 2005; Kilham 1989; Littlefield and Thompson 1985; Maguire 2000; Murray 1945; Nelson 1934; Porsild 1943; Simes et al. 2017; Sinclair et al. 2003; Stiehl 1985; Stiehl and Trautwein 1991). Occasionally, it attempts to prey upon porcupines. In 1 case, the raven was killed by quills (Katzner et al. 2015).

Food storing occurs, mostly in autumn and winter, but also during the nesting season when food is abundant. Birds may fly several kilometres from a carcass to store food. The more ravens that are present at a carcass, the further individuals fly to cache food. All types of items may be cached including meat, bones, pine nutlets, bread, and bird eggs and nestlings. Each cache is in a different location, generally in snow or on the ground covered with material such as leaves, sod, and soil. In New Hampshire, 1 pair cached food on the cliff where the nest was situated. Birds can remember cache sites for about 2 weeks, and they also remember where other birds have caches (Boarman and Heinrich 2020; Heinrich 1988; Kilham 1989).

The Common Raven requires water for drinking and uses a variety of natural and artificial sources of water. One bird learned how to turn on a faucet in a California campground and drink from it (Hanks et al. 2009).

Habitat loss may have contributed to the raven's initial extirpation in southern Ontario, but is no longer a problem. It is now extending its range southward, possibly due to a combination of abandonment of farmland, tree planting, greater tolerance of human activity, and decreased persecution by humans. In California where nest sites and food resources were scarce, fledging success was greater nearer anthropogenic resources such as residences, artificial wetlands, sewage lagoons, livestock feedlots, shopping malls, agricultural fields, and golf courses. In this area, it increased in abundance with increasing human disturbance of natural habitat (Webb et al. 2004).

In the Canadian Shield of Ontario, the raven was equally abundant in early successional and mid-successional stands created by fire and clear-cutting, and in early successional, mid-successional, and mature stands (Zimmerling et al. 2014). The results may be questionable because it is likely that ravens documented in early successional and possibly mid-successional stands represented foraging birds rather than breeders.

In the 19th and early 20th centuries, the raven was greatly maligned and persecuted by humans. It may be an agricultural pest, pecking at eyes of livestock, so was widely shot. It also frequently damaged hides of furbearers caught in traps. Poison baits were frequently set out throughout Canada to control wolves. Ravens commonly ate the baits and also the flesh of poisoned wolves, resulting in widespread declines in areas of remaining suitable habitat. The decline in wolf numbers also reduced numbers of carcasses for ravens to scavenge. These practices were discontinued, although there may still be isolated incidents of shooting (Bent 1946; Boarman and Heinrich 2020; Flanagan 1993; Houston 1977; MacLulich 1938). With large increases in western populations of the

raven, there are concerns about its depredation effects on species of conservation concern and on livestock. In California, raven eggs were oiled, resulting in a decrease in predation on Black-crowned Night-Heron eggs and chicks. Brussee and Coates (2018) concluded that oiling raven eggs can be a viable localized method to reduce raven predation of sensitive avian species. In Wyoming, a toxicant called DRC-1339 is widely used to treat ravens that are causing problems related to human health, livestock, and species of conservation concern. The toxicant is often injected into chicken eggs or sprayed on dog food; it causes death 1-3 days after ingestion (Peebles and Conover 2016).

The raven's range initially shrunk due to avoidance of humans. Now it is reoccupying previously inhabited areas, and has initiated nesting in cities in Saskatchewan and Quebec. In the Yukon and British Columbia, as well as many other northern areas, it is more frequent near settlements. In these areas, landfills provide essential food sources in the winter. In addition, more roads and increased traffic provide carrion. In British Columbia, it became more abundant along the Alaska highway when construction camps were active (Campbell et al. 1997; Flanagan 1993; Houston 1977; Jehl and Smith 1970; Kuyt 1992; Sinclair et al. 2003).

The reaction of nesting ravens to human activity varies. Those nesting in remote areas that have little contact with humans are more easily disturbed. Those that choose to nest in populated areas may be highly tolerant of disturbance. This relationship may be reversed if birds are persecuted in populated areas. In Ottawa, a pair nested in an active quarry where heavy machinery worked and dynamite blasting occurred (DiLabio and Martin 1989), and it has nested in other active quarries (personal observation). In Washington, Knight (1984) monitored responses of nesting ravens to humans in rangelands where human activity was rare and in agricultural areas with moderate levels of human activity. Rangeland nests were significantly further from highways (1,373 m compared with 53 m) and dwellings (2,404 m compared with 1,562 m) than those in agricultural lands. In rangeland there were several unused cliffs and abandoned buildings suggesting an avoidance of humans. In farmland, there were no cliffs or abandoned buildings, so ravens nested on human-made structures, but not necessarily close to occupied houses. Ravens nesting in agricultural land flushed at greater distances (456 m compared with 91 m). Nests in agricultural areas were subject to human persecution, with 42% of nests destroyed compared with none in rangeland. In Virginia, it nested close to human activity and probably relied on humans for a substantial portion of its food. Nest success was not related to cliff height or distance from a road or dwellings; those closer were slightly more successful. Response of individual birds was variable. One pair subjected to high activity of people frequently standing below the nest ledge and weekly checking of the nest was successful as was one on a 10-m cliff only 40 m from a road. Another nest 150 m from a popular stream for fishing failed in 3 years because the adults left the nest whenever humans were present. Hooper (1977) concluded that a few might be adversely affected by humans within 200 m of the nest, but that most would not. He determined that pedestrians should not be permitted within 200 m of the nest if visible to the birds, or within 100 m if hidden from view. Vehicles within 100 m of a nest would be acceptable, but parking areas should not be within 200 m. Walker and Marzluff (2015) studied the response of the raven to recreation and associated facilities in Mount Rainier National Park in Washington. It was most likely to use areas with frequent nearby edges but where there was a high percentage of forest cover within 5 km. It was less likely to use areas with complex or very complex

forests compared with simply structured forests. It was most likely to use areas with abundant nearby roads but its probability of use decreased with the number of human visitors. It was more likely to use areas where anthropogenic food was available despite avoiding areas heavily used by humans. It was correlated with edge, road length, and forest cover.

In Alberta, the raven was significantly less abundant along seismic lines than in adjacent forest interior and significantly more abundant along pipelines than in adjacent forest interior; it was equally abundant at well pads and in adjacent forest interior (Bayne et al. 2016).

Long winters may delay nesting by 2 weeks or more. Timing of egg laying is strongly influenced by the cumulative winter snowfall, with eggs laid later after winters with the most snow. Later nests produce fewer fledglings. Severe snowstorms may result in death of nestlings, even those that are fairly old (Boarman and Heinrich 2020; Dunk et al. 1997; Kozij 1986).

DesGranges and Morneau (2010) concluded that the raven was not very sensitive to climate change.

Status

Prior to European settlement, the raven inhabited all of Ontario. McIlwraith (1894) quoted Wilson who travelled along the shores of Lakes Erie and Ontario in the early 1800s and observed ravens daily; crows were absent to rare. By McIlwraith's time, ravens were gone in southern Ontario, but common in Muskoka District. Baillie and Harrington (1937) considered it a rare inhabitant in the north from Ottawa to Hudson Bay west to Manitoba. They assumed it nested throughout this area, but had nesting records from only 5 areas. In Algonquin Park, where it is now common, it was rare in the wilder parts of the park (MacLulich 1938). The rarity of the raven during this period in ideal habitat was probably related to intensive poisoning programs with direct impacts on ravens and indirect effects due to loss of wolves and the essential carrion they provided. It is uncertain when populations began to recover, but it was probably before the mid-20th century. It was rare in the early 1900s in Muskoka and Parry Sound, reduced from its former abundance by scavenging on poisoned wolf bait. It began to increase in this area in the 1950s, but was still scarce in the 1970s and early 1980s (Mills 1981). James et al. (1976) considered it a common permanent resident throughout the province, but rare south of Algonquin Park. In the Ottawa area, it was a rare resident in 1911 until about 1944 when it became locally extirpated; it returned as a local breeder around 1984 (DiLabio and Martin 1989). In the Kingston area, it was apparently absent in the 1850s, but occasional sightings started in the 1960s (Weir 2008). The raven was common around Niagara Falls in the early 1800s, but southern populations were extirpated by the mid-1800s. In the early 2000s, small numbers began to recolonize the Hamilton area along the Niagara Escarpment and in quarries (Curry 2006). Blomme (in Cadman et al. 1987) stated that the raven reoccupied the Bruce Peninsula in the 1970s, and the first atlas documented an eastward range extension into the Ottawa area. James (1991) considered it common in central Ontario and becoming uncommon to rare in the Hudson Bay Lowland and in southern areas such as the Bruce Peninsula and central Peterborough and Leeds counties. By 2004, it had been confirmed breeding south as far as York, Durham, and Halton regions (Hofmann 2005), and was confirmed breeding in the Rouge Park in Toronto in 2012 (Worthington 2012).

The second atlas confirmed that the raven had extended its range significantly south of the Canadian Shield since the first atlas. Although there was no change in its probability of observation province-wide, it increased significantly in the Great Lakes–St. Lawrence Forest Region, particularly south of the Shield, and in the Hudson Bay Lowland. It was most abundant in the Hudson Bay Lowland, generally decreasing southward and uncommon south of the Shield. The largest areas of high density were along the western portion of the Hudson Bay coast and in the Boreal Forest Region in northwestern Ontario (Peck in Cadman et al. 2007).

The decline with European settlement was widespread in North America. Mayfield (1988) considered the main reason for the raven's disappearance in the Lake Erie area to be the disruptive influence of humans, and replacement of it by the American Crow. The disappearance of ravens in southern Ontario was much more complicated than this. Forest clearing eliminated suitable breeding habitat and favoured the crow; replacement of the raven by crows was an effect and not a cause. Most importantly, the clearing of forests had significant impacts on large carnivores and mammals. Temporary loss of the raven in the west has been attributed to the decimation of bison and the carrion they provided (Bent 1946; Boarman and Heinrich 2020; Houston 1977). Prior to European settlement, gray wolves occurred throughout southern Ontario. With clearing, their habitat disappeared. Some of the large mammals that formerly occurred in the south also disappeared. The moose formerly ranged all along the northern shoreline of Lake Ontario, and elk were present in southern Ontario but became extirpated before 1830 (Banfield 1974). The loss of these large ungulates and their primary predator was undoubtedly a major factor in the extirpation of the raven in southern Ontario.

Long-term (1970-2021) population trends determined by the Breeding Bird Survey indicated annual increases of 2.92% in Canada and 1.94% in Ontario. The short-term (2011-21) trends were annual increases of 0.925% in Canada and 1.2% in Ontario. All results were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Some fledglings leave the nest area almost immediately to join a communal roost. Although many join the nearest roost, some joined roosts 50-60 km from the nest site in Idaho. Most fledglings remain near the nest site for 1-6 weeks; in Virginia young remained with their parents all winter. Young become independent of adults by July or August. Inexperienced late nesters may still be feeding young in August (Boarman and Heinrich 2020).

The raven is a year-round resident throughout its range. In autumn and winter, it may wander widely, especially where food resources are scarce and patchy. In the Yukon and many other areas, there are local movements into human settlements in late autumn with a return to natural habitats in early spring (Boarman and Heinrich 2020; Campbell et al. 1997; Sinclair et al. 2003).

WINTER

During winter, the raven may congregate near populated areas or remain in more remote breeding areas. All natural and anthropogenic habitats may be used in winter. Although it may be locally common at some landfills, it may frequent farm fields, feedlots and barnyards, highways, railways,

mine sites, ski resorts, bush camps, and urban and suburban areas. In the Yukon, it is most common around towns in winter (Campbell et al. 1987; Sinclair et al. 2003).

The most critical limiting factor for raven populations is presence of adequate food in winter. Although it is widely distributed, there are large areas where there is insufficient winter food to support any birds. Access to carcasses or other clumped, unpredictable food supplies is essential. Away from habitation, it is heavily dependent on wolves that provide carcasses of large animals. Highways are heavily patrolled in winter, as many ungulates are killed during this period. The raven also feeds on Pine Siskins, crossbills, and Evening Grosbeaks that were killed while eating road salt (Boarman and Heinrich 2020; Campbell et al. 1997).

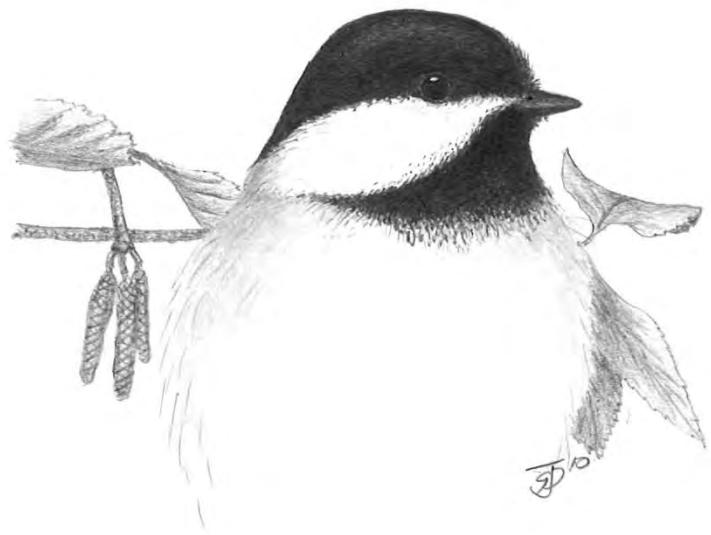
Heinrich (1988, 1994) placed carcasses out for ravens in winter in Maine and Vermont. Sheep and deer carcasses were completely consumed in 2 days; as many as 90 fed simultaneously at a carcass. There were large congregations at carcasses, but ravens were rare when no carcasses were put out for them. Resident pairs were quiet around a carcass and did not advertise its presence; they made regular and punctual visits. Nonresidents gave a yell call at carcasses that attracted large groups that attracted additional birds. Groups of birds appeared irregularly and were absent for months or years at a time. Groups were mostly subadults and juveniles (90%) and the composition of the group changed daily. Of 61 marked birds, 36 were never seen again after 6 days, 29 were seen a month later at a newly established bait, and only 1 was seen 6 weeks later at the original bait. Some showed up at baits more than 50 km away. Of 71,000 raven sightings, only 2 were of the 54 birds marked the previous winter. Some travelled at least 90 km per day to feed at known food resources; daily flights to search for food are probably even greater. Individuals did not stay at a feeding site even though the food remained abundant. Birds wander widely and may visit several roosts in succession.

Addison et al. (1989) kept moose in pens in Algonquin Park and infected them with winter ticks. Ravens visited the pen with infected moose, but ignored the other pen. They ate engorged ticks that had fallen off moose, but did not take ticks from moose. They also ate oats that had fallen from the moose feeder or were present within moose feces.

The raven is an infrequent visitor at bird feeders, possibly because few people provide its preferred food of meat scraps. Suet is readily taken, and it frequently cuts smaller pieces off and probably caches them. In the absence of meat, baked goods are preferred. Other foods infrequently eaten are mixed seeds, sunflowers, corn, cracked corn, popped corn, pet food, and peanut butter mixes (Dunn and Tessaglia-Hymes 1999; Heinrich 1999).

Black-capped Chickadee

Poecile atricapillus

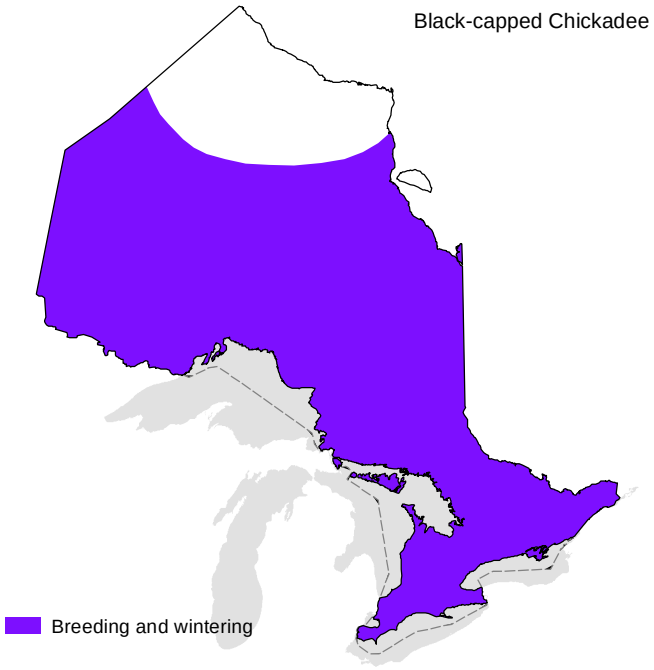


BREEDING SEASON

Habitat Requirements

In Ontario, the Black-capped Chickadee nests mostly in open forests and woodland edges (60.4% of nests), with mixed woods (37.2%) selected over deciduous (17.2%) and coniferous (6.0%) woods. It also breeds in agricultural areas, including overgrown fields and pastures, hedgerows, floodplains, and orchards (22.0% of nests); in beaver ponds, bogs, and marshes (4.0%); in park and cottage areas (2.4%); in sand-dune areas (2.0%); and burns (0.4%). Most nests were beside roads and water bodies. Breeding occurred more often in wet habitats, probably due to the greater abundance of dead trees in these areas (Peck and James 1987).

In the Boreal Forest Region, Erskine (1977) considered the Black-capped Chickadee typical of poplar and birch stands, and reported it in white pine, red pine, pitch pine, and hemlock stands in Ontario. Where their ranges overlap, the Black-capped Chickadee replaces the Boreal Chickadee in hemlock stands. Boreal Chickadees replace Black-capped Chickadees in balsam fir stands. Near White River, the Black-capped Chickadee was significantly more abundant in clear-cuts 23-25 years old than in younger clear-cuts or in mature forests (Venier and Pearce 2005). Near Hearst, Welsh and



Fillman (1980) observed it in clear-cuts in upland mixed forests 9-14 years old. Venier et al. (2009) observed it in clear-cuts, young forests, and mature and old-growth forests near Manitouwadge.

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Black-capped Chickadee is common in mature and old-growth white pine stands (Kirk et al. 2012). In jack pine stands near Gogama, it was common in the deciduous portions of mixed forests. It was absent in new-growth jack pine, present sporadically in younger stands, and present in low density in mature stands (James and Peck 1995a). In jack pine stands in Parry Sound District, it occurred in low densities in some open canopy stands with mixed deciduous trees (James 1979a). In Algonquin Park, it occurred in black spruce, black spruce–white cedar, birch-poplar, birch-poplar–balsam fir–spruce, balsam fir–spruce, immature white pine, balsam fir–spruce-hardwood, hardwood, and hemlock forests. It was most abundant in hemlock stands and was the second-most abundant species in immature white pine stands. It was absent in bogs (Martin 1960).

In the Kingston area in the Great Lakes–St. Lawrence Forest Region south of the Shield, the Black-capped Chickadee nested in urban, agricultural, and woodland habitat, but was most abundant in forested areas (Weir 2008). Near Kingston, only 1 of 27 habitat characteristics Ramsay et al. (1999) measured differed significantly between control and nest sites. There were significantly more trees with a diameter at breast height (DBH) greater than 32 cm at nest sites than control sites. In Durham Region, it occurred in a variety of deciduous and mixed stands as well as in a black spruce bog, and was present in a wide range of canopy closure, from open growth to closed canopy (Speirs and Orenstein 1975).

In southern Ontario, there was no difference in abundance of this chickadee on organic and conventional farms. It was significantly correlated with hedgerows and the amount of riparian and upland woods, and had positive but nonsignificant relations with habitat heterogeneity. It was negatively associated with road, railway, and hydro rights-of-way, but not significantly (Kirk et al. 2011).

Throughout its range, the Black-capped Chickadee nests in a variety of habitats, including urban areas, small woodlots, rural residential lots, wooded fence lines and roads, wooded riparian strips in agricultural areas, and in almost all forest types. It is a habitat generalist, with presence of a suitable nest site being the most important habitat requirement. Often the nest is in an open area, with adults foraging nearby in wooded habitat. Territories often contain 2 distinct habitats such as

second-growth and mature forest, or open areas with scattered trees and forest. Even when nesting occurs in forest, the nest tends to be in open portions. In Ohio, there were 406 trees per ha at nest sites compared with 1,472 for unused areas. Several authors concluded that it prefers to nest at forest edge. Nesting occurs in the interior, but often where tree density is low. Low tree density promotes growth of saplings and seedlings; it is associated with thickets and high density of woody understorey in wooded areas. Mixed forests are highly preferred, followed by deciduous woods; coniferous stands are used sparingly. In Saskatchewan, it occurred in almost equal density in trembling aspen, mixed, and white spruce stands. In the mid-Atlantic states, its presence was negatively correlated with mean canopy height, the number of standing dead trees larger than 3 cm diameter at breast height (DBH) per ha, density of foliage 0.3-1.0 m tall, and percent cover of forest within 2 km. Some studies concluded that it is more abundant in wetland than upland forests: others concluded the opposite. It has been reported preferring pioneer, mid-succession, and mature stands. In the Clay Belt of Ontario, it occurred in all ages of stands. In Pennsylvania, it occurred in 100% of old-growth forests, 84.2% of all forests in the state, and 97.0% of forests on the Appalachian Plateau. It was considered to have neutral old-growth affinity. In Alberta trembling aspen forests, it was equally abundant in young, mature, and old-growth stands. Some habitat ordinations have failed to put the Black-capped Chickadee into any group, indicating a true habitat generalist. Others considered it associated with an intermediate canopy and dense understorey, mature deciduous or coniferous uplands with a shrub layer, yellow birch, or small woodland openings. In Washington, it preferred the deciduous component of woodlands and was associated with a high volume of trees and shrubs and the mid-canopy level. In Vermont, its abundance was correlated with increasing successional age, high percentages of conifers, and sites with approximately the average number of dead trees. It is not significantly associated with density of snags in woodlands, possibly because it also nests in dead limbs that are not typically inventoried during these types of studies. Being a weak-billed primary excavator, it requires softer types of wood for cavity construction, explaining why poplar and birch are the most common nest-tree species (Back 1979; Beals 1960; Bond 1957; Brewer 1963a; Campbell et al. 1997; Capen 1979; Desrochers in Gauthier and Aubry 1996; Evans and Conner 1979; Graber and Graber 1963; Haney 1999; Hobson and Bayne 2000; Kirk et al. 1996; Kluyver 1961; Lent and Capen 1995; Mossman et al. 1991; Niemi and Pfannmuller 1979; Odum 1941a; Robbins et al. 1989; Rumble and Gobeille 1998; Schieck et al. 1995; Schroeder 1982a, 1990; Sedgwick and Knopf 1990; Sinclair et al. 2003; Stauffer and Best 1980; Sturman 1968a; Taylor and Taylor 1979; Temple et al. 1979; Thomas et al. 1977; Thompson and Capen 1988; Welsh 1993).

In North Dakota 400-m landscapes with less than 30% tree cover, the probability of occurrence of the Black-capped Chickadee increased significantly with tree cover within 100 m but there was no correlation between its occurrence and tree cover within landscapes with more than 30% tree cover (Cunningham and Johnson 2016). It preferred landscapes that were 51-75% forested in North Dakota and 71-98% forested in New York. There were no areas with more than 75% forest cover in North Dakota (Cunningham and Johnson 2019).

The important microhabitat requirements appear to be presence of soft wood or snags for cavity excavation and some larger trees, but in low enough density that there is a rich woody understorey. In urban areas, the important variables appear to be volume of coniferous and

deciduous trees and deciduous shrubs. In New Hampshire and Maine, its abundance was positively correlated with the number of deciduous trees 2-10 cm DBH and the number of woody stems per ha. It was negatively correlated with canopy closure and the total volume of foliage of both deciduous and coniferous trees 2-10 cm DBH (Foote et al. 2020; DeGraaf et al. 1998).

Some authors considered the Black-capped Chickadee an area-sensitive species; others found no relationship between its presence and forest size. In southern Ontario, its abundance was negatively correlated with the amount of forest 100 m or more from edge, woodland size, the amount of forest cover within 2 km, and the amount of regional forest cover, although these relationships were not significant (Austen et al. 2001). In Saskatchewan, forest size was a significant predictor of its presence, and it was more common in large forest fragments. Despite this, it was randomly distributed among forests and forest types, and within fragmented landscapes (Hobson and Bayne 2000). Keller and Yahner (2007) reported similar results in Pennsylvania. In Illinois, its presence was significantly correlated with woodlot area (Blake and Karr 1987). In North Dakota aspen stands, its presence was associated with forest size. It was predicted that it would reach 50% occurrence in woodlots 8-20 ha in size and that it would almost always be found in larger woodlands. Its probability of observation in 1-ha woodlots was 30%. It was also more likely to occur in stands with a greater proportion of trees larger than 23 cm DBH (Grant and Berkey 1999). Schroeder (1990) concluded that it did not require any minimum forest size. Robbins et al. (1989) concluded that the Black-capped Chickadee was not area sensitive. In Iowa, Stauffer and Best (1980) considered it restricted by habitat patch size based on their literature review. The minimum width of riparian strip they found it in was 15 m. They predicted that its numbers would be reduced but not eliminated if cover was reduced to a narrow strip. Foote et al. (2020) reported that it was an edge species most often found within 75 m of edge. All evidence suggests that the Black-capped Chickadee is not area sensitive in Ontario, and it also nests in non-forested habitat in the province.

During the breeding season, both adults use night roosts but do not roost together. They are often not in the same tree and may roost as far apart as 50 m. The female spends the night in the nesting cavity from the time of nest building until the nestlings are several days old. At 1 New York nest, the male roosted 20 m away among the leaves of a small maple tree. Later in the nesting season, both sexes roost on sheltered branches or in vines (Brewer 1963a; Odum 1941b, 1942).

All Ontario nests were in cavities, including those excavated by the chickadees, old woodpecker nests, and nest boxes. Nests were in standing tree stumps (61.7% of nests), trunks and branches of complete trees (19.7%), bird boxes (9.7%), wooden fence posts (6.9%), fallen tree branches and trunks (1.4%), and standing iron posts (0.6%). All nest trees were dead except for 7: 3 with dead branches, 2 with dead tops, 1 with a rotted centre, and 1 with a natural cavity. Of nests in tree stumps, 68.8% were in cavities in the side of the stump and the remainder were in a hollow exposed cavity at the top of the stump. Most nest cavities were excavated by the chickadees with lesser numbers of natural and old woodpecker cavities used. Deciduous trees were preferred for nesting; 90.1% of nests occurred in 15 species of deciduous trees compared with 9.9% of nests in 5 species of conifers. The most common nest-tree species were birches (49.7% of nests), poplars (22.4%), elms (12.1%), maples (9.1%), and white cedar (6.7%). The DBH of trees and stumps used for nesting ranged from 7.5 to 61 cm, mostly 10-18 cm. Nest height ranged from 0 to 15 m from ground, with most 0.9-3.7

m up. Two nests had cavity entrances at ground level, and in one of these the nest was 11.4 cm below ground (Peck and James 1987). Near Kingston, 35.6% of nests were in white birch; 11.1% were in sugar maple. Two thirds of nests were in dead trees. Nest trees averaged 8.7 m in height and 20.5 cm DBH. Cavity entrances averaged 5.3 m from ground (Ramsay et al. 1999). Straus et al. (2011) characterized the mean microhabitat features of 138 nests in the Carolinian Forest Region of Ontario. Average nest height was 1.7 m, DBH of nest trees averaged 12.2 cm, there were 7.1 additional cavities in the nest tree, canopy closure was 65.1%, nests averaged 166.4 m from a hard edge, 94.7% of nest trees were dead, 5.3% of nest trees were declining, 0.0% of nest trees were healthy, 5.4% of nests were in sugar maple, 18.9% were in red maple, 2.7% were in ash, 29.7% were in beech and birch, 8.1% were in fruit and nut trees, and 35.2% were in unidentified tree species.

Throughout its range, the Black-capped Chickadee nests in dead, decaying, or hollow trees and stumps. Hardness of the wood is a critical factor, as it can only excavate in soft or decaying wood. Therefore, poplars, birches, willows, cherries, and apple are often selected. In New England, gray birch is preferred, and it has also nested in beech, red oak, white oak, and basswood. Most excavated cavities are in dead tree trunks, dead or diseased branches, in rotten stumps, in knotholes, and in boles. In the Seattle area, it nested in snags that were more decayed than average and nested more in broken-top snags than expected. It is one of few species that will nest in upward-facing cavities and it shows no preference for cavity-opening orientation. It frequently nests in fallen, leaning limbs and occasionally in natural or old woodpecker cavities. Most nests are in trees with a DBH of 10-20 cm. It uses nest boxes. In urban areas, nest boxes may provide nest sites in areas where natural nesting locations are rare or absent. Artificial snags built from polyvinyl chloride tubes and filled with wood shavings are preferred to nest boxes. It has nested in a hollow steel post, and there is 1 record of it nesting in an old, unusually deep robin's nest. Nest height may range from ground level to more than 20 m but most nests are within 3.4 m of ground (Bender et al. 2016; Blewett and Marzluff 2005; Brawn et al. 1984; Brewer 1963a; Campbell et al. 1997; Cooper and Bonter 2008; Fitch 1958; Kluyver 1961; Odum 1941a, 1941b; Schroeder 1982a; Sedgwick and Knopf 1990; S.M. Smith 1967a, 1974, 1991; Stauffer and Best 1980, 1982; Tyler in Bent 1946).

Territorial defence begins in early spring when pairs start to disassociate themselves from winter flocks, usually between late March and mid-April. Most breeding territories are within the winter-flock territory. Territoriality is most intense in the 2 weeks following breakup of the winter flock. Initially the male defends an area around the female, but soon the pair defends a space. Once the female selects a nest site, territory boundaries become fixed and defence is intense until the nest is built. Territoriality wanes during egg laying and territory size shrinks at this point. The territory increases again during the nestling phase, but it is still considerably smaller than during nest building. Territoriality ceases once young leave the nest. In Utah, territories were 0.3-5.1 ha during nest building (averages 2.0 ha and 2.7 ha over 2 years), 0.2-2.1 ha during egg laying (averages 0.6 ha and 1.2 ha), 0.1-0.7 ha during incubation (averages 0.1 ha and 0.3 ha), and 0.1-1.2 ha during the nestling period (averages 0.3 ha and 0.7 ha). During the nesting cycle, the original territory may be used as a home range, but the outer limits are seldom visited as nesting progresses. Territory size varies depending on status of the male, quality of habitat, population density, and whether adjacent habitat is occupied. Dominant males have larger territories; in Utah, territories of dominant males

averaged 0.7 ha larger than beta males. Territories in wooded habitat are superior and much smaller than those in more open areas or in a mix of open and wooded habitat. If all habitat is occupied, territory sizes decrease to accommodate the additional breeding pairs. Territorial boundaries are more flexible when adjacent areas are unoccupied, and these territories may be larger. Mean territory size reported from several North American studies is 1.5 ha (means 0.07-8.8 ha). In Alberta, there was no consistent relationship between territory size and stage of breeding cycle; only 21% of territories decreased in size as the breeding season progressed. Territories averaged 7.8 and 8.8 ha over 2 years. Sizes of home ranges have been reported as 0.04-17.2 ha. In Algonquin Park, average territory size was 0.5 ha (range 0.07-1.6 ha). In birch-poplar–balsam fir–spruce stands, chickadees remained mostly in shrubs and lower branches of conifers, but ranged from the ground to treetops in fir-spruce stands. Nests are usually at the edge of the territory, and active nests have been found within 10 m of each other. Some populations may have nonbreeding floaters that have home ranges that cover 3-5 nesting territories (Brewer 1963a; Butts 1931a; Fitch 1958; Hill and Lein 1989; Martin 1960; Odum 1941a; Schroeder 1982a; S.M. Smith 1967a, 1974, 1976, 1989, 1991; Stefanski 1967). Near Quebec City, there was no aggregation of territories and singing males were more evenly distributed than by chance. There was no tendency toward colonial nesting (Bourque and Desrochers 2006).

Natal site fidelity is low. Fledglings disperse rapidly from their parents' territory and form flocks that may travel widely until they join wintering flocks. These birds may establish their first breeding territory in the vicinity of the winter territory, or move again in spring before breeding. In British Columbia, most young left the study area by September, and only one returned to breed over 2 years. In Wisconsin, most of 88 nestlings disappeared from the study area immediately after family breakup. Fourteen of these were subsequently found in winter, 12 0.5-2.4 km from the natal nest, 1 at 5.5 km, and another 11.2 km from the nest. Distances from natal sites to first breeding sites were 0.4, 0.8, 0.9, 1.3, 1.8, and 11 km (median 1.1 km). Adult site fidelity is very high. Most chickadees remain near their initial breeding site the rest of their lives (Butts 1931a; Foote et al. 2020; Odum 1942; S.M. Smith 1967a, 1991; Weise and Meyer 1979).

Limiting Factors

Eggs have been reported in Ontario nests from the last week of April until the third week of July, mostly in the last half of May (Peck and James 1987, 1997). In Algonquin Park, nests are under construction from mid-April to mid-June, eggs occur from late May to late June, nestlings are present from late May to mid-July, and dependent fledglings have been documented from late June until late July (Tozer 2012).

Usually 5-14 days elapse after pair formation before initiation of cavity excavation, with longer periods for early pairs. The female may several cavities before selecting one for nesting. Two cavities may be fully excavated before one is chosen. Cavity excavation takes 4-10 days. The female builds the nest in 2-4 days. There is often a delay of 1-2 days between completion of nest construction and egg laying; occasionally there is no delay. One egg is laid a day, but occasionally a day is skipped. Incubation usually starts with laying of the penultimate egg, or earlier in replacement or second clutches. Incubation periods of 11-17 days have been reported in Ontario, with most eggs hatching in 12 or 13 days. Overall, incubation periods of 11-20 days have been documented, with 12-13 days

typical. All eggs in a clutch usually hatch on the same day. Most young fledge when they are 16 days old, with a range of 16-20 days (Fitch 1958; Foote et al. 2020; Holleback 1974; Kluyver 1961; MacKenzie 1996; Odum 1941a, 1941b; Peck and James 1997; S.M. Smith 1991; Tyler in Bent 1946; Weise and Meyer 1979).

Usually 1 brood is raised, but occasionally 2 broods are raised. Three double broods have been reported from Ontario. True double broods are rare and possibly more frequent in low-density populations. Second clutches are started well before the first brood has dispersed and may be initiated within a few days of the young leaving the first nest. Renesting occurs if loss does not occur too late in the breeding season. Replacement nests are often 100-300 m from the original nest but occasionally nearby or even in the same nest if nest sites are scarce. Replacement clutches may be initiated 4-11 days after loss. Clutches of 3-11 eggs have been reported in Ontario, with 6 and 7 eggs most frequent. In southwestern Ontario, the mean size of 29 clutches was 5.59 eggs. Clutches of 1-13 eggs have been reported in North America, with 80% of clutches having 6-8 eggs. In British Columbia, 66% of clutches had 5-7 eggs. Overall average clutch size is 6.64 eggs. Northern clutches tend to be larger, older females tend to have larger clutches, and nests later in the season have smaller clutches. The clutch size is usually larger and eggs are laid earlier if an old nesting cavity is used (Butts 1931a; Campbell et al. 1997; Clemmons 1994; Foote et al. 2020; Kluyver 1961; Odum 1941a, 1941b; Peck and James 1997; S.M. Smith 1967a, 1991; Straus et al. 2011; Tyler in Bent 1946).

Most birds first breed when they are 1 year old. Those that do not are the lowest ranking in the winter flock and are unable to find a mate or defend a territory. These birds remain as floaters within the breeding population. Some are chased by dominant birds and may end up as far as 20 km away. Some floaters manage to breed their first year by filling in when a pair loses one of its members. Those that are unsuccessful in gaining a territory the first year join the winter flock again. They rejoin with a higher status than the previous winter and are usually successful in obtaining a mate and territory their second year. Some individuals do not breed until they are 3 years old. There are typically no more than 1 or 2 nonbreeding floaters in a subpopulation; many years there are none. There are frequently no floaters present to replace lost mates, but 1 female raised 2 broods 2 years in a row with 4 different mates (Butts 1931a; Desrochers et al. 1988; Foote et al. 2020; Odum 1941b; S.M. Smith 1967a, 1989, 1991).

Almost all Black-capped Chickadees are monogamous and maintain a life-long pair-bond. Polygyny occasionally occurs, usually when 2 females construct nests within a male's territory. When this occurs, the territory is divided in half by the females. One case of polyandry was reported from Alberta, when a mated male bred with the female of a pair in an adjacent territory. Two other cases of polyandry have been documented, including one in Ontario; in all cases, the neighbouring male had lost his mate (Clemmons 1994; Dixon 1986; Odum 1941a; Otter et al. 1994; S.M. Smith 1967b, 1991; Waterman et al. 1989). In Massachusetts, 15 cases of divorce occurred over 10 years but 84% of pairs remained intact. Near Kingston, divorce occurred in 13 of 144 partnerships (9.0%) over 8 years. Divorce may rarely be related to unsuccessful nesting, but is almost always related to social climbing. Most divorces are initiated by females, and the potential for this starts early in the breeding season. Near Kingston, nest-site selection was influenced by the range and status of the neighbouring male, and not by habitat, prey abundance, or previous nesting experience. Females

that are mated to a low-ranked male often nest within 10-15 m of the territory boundary of a superior male. Females actively sought extra-pair copulations from adjacent dominant males and 37.5% of nests had extra-pair young. Extra-pair young account for 9-17% of nestlings and occur in 29-38% of nests. Females that divorced were significantly more likely to have mixed paternity broods prior to divorce, and all moved up on the social scale. Divorce may also occur when a dominant male loses his mate. Females mated with a lower-ranking male may leave him to mate with the alpha male. All males that divorced were elevated from beta to alpha males (Foote et al. 2020; Otter et al. 1994; Ramsay et al. 1999, 2001; S.M. Smith 1974, 1988, 1991, 1992).

The Black-capped Chickadee forages predominantly on dead, damaged, or curled leaves; on twig tips; or on tree boles. In New Hampshire, it was the only species that hung upside down to uncurl leaves to pluck prey from a leaf, or uncurl a leaf rolled by a caterpillar or spider. Prey-capturing techniques were 57.0% gleaning, 28.7% hanging, 8.8% hovering, 3.5% probing, and 2.4% hawking. Of attacks on arthropods, 58.0% were on bark and 38.2% were on leaves. In Ontario, 48.3% of foraging occurred while hanging upside down; 66% of foraging occurred in deciduous species and 34% in conifers. In Ohio, 45% of feeding was below 3 m and 75% was below 10 m; plant use depended primarily on availability. It hovers near sap at woodpecker borings where it may feed on insects attracted to or trapped in the sap. In Washington, 70% of foraging was done by hanging. In early spring, it fed more often on buds and catkins than later in the season. Most foraging occurred in hardwoods, but it also fed in conifers. This chickadee fed from trunk and branch bark 73% of the time in hardwoods and 81% in conifers. Foraging occurred mostly in the subcanopy of trees, the area occupied by branches with little to no living foliage. In British Columbia, it preferred to forage within 1.5 m of the ground (Brewer 1963a; Greenberg et al. 1999; Odum 1942; Robinson and Holmes 1982; Schroeder 1982a; Sturman 1968b). During the breeding season in central Ontario, it foraged at heights of 2-13 m compared with 5-14 m in autumn. These differences were minor and nonsignificant. Foraging techniques were top-gleaning, clinging, and probing. During the breeding season, top-gleaning was the prevalent foraging method, with clinging and probing becoming more common later in the breeding season and in autumn. Early in the breeding season, all tree species were used for foraging, particularly white birch. In mid-season, foraging was concentrated in early successional hardwoods, including white birch. In autumn, greater use was made of conifers but white birch continued to be important (Mills 2007). In savannahs and oak woodlands in Illinois, it foraged throughout the foliage layers, but 63% of foraging occurred in the lower canopy (11-15 m) and canopy layers (above 16 m). In savannahs, it exhibited no preference for tree species while foraging. In closed-canopy forests, it foraged in oaks more than expected based on availability and in sugar maple and red elm less than expected (Grundel and Pavlovic 2007b).

Males bring food to females early in the nesting season to keep their energy up during the egg-laying, incubation, and brooding periods. Of 65 food items brought to nestlings in Massachusetts, 13 were large caterpillars weighing 200-300 mg, 22 were small caterpillars averaging 120 mg, 11 were spiders, 6 were termites, 6 were small unidentified larvae, 4 were small red larvae, 1 was a white butterfly or moth, 1 was a pupa, and 1 was a fly. Caterpillars and sawflies were the main items fed to nestlings; caterpillars smaller than 8 mm were rarely brought to young. Chickadees in Massachusetts concentrated where caterpillars were most abundant, but had a marked preference for clumps of

red and white pine. Most remained almost entirely in red pine until the end of June but occasionally forayed into oaks. In Michigan, young were fed predominantly spruce budworm and spring cankerworm caterpillars. During the breeding season, chickadees feed mostly on invertebrates and most frequently on caterpillars and spiders. In New Hampshire, food items consisted of 75.9% caterpillars, 13.8% spiders, 6.9% beetles, and 3.4% adult lepidopterans. The most important caterpillars were those of prominent, geometer, and sphinx moths. It occasionally eats hairy caterpillars such as gypsy moth and eastern and forest tent caterpillars. The Black-capped Chickadee has been observed probing in cattail heads in Ontario, presumably foraging on cattail borer moth larvae. It eats a wide variety of other insects such as beetles, true bugs, sawflies, ants, honey bees, and other lepidopterans, as well as small snails, slugs, and centipedes. Cicadas may be avidly consumed when they are abundant. It has been observed pecking bird eggs in Ontario and partially drinking the contents. In early spring, it regularly drinks sap from sugar maples and eats sap icicles. As the breeding season progresses, It eats some seeds and fruit, especially those of common and giant ragweed, staghorn sumac, blackberries, honeysuckles, and blueberries (Brewer 1963a; Dance et al. 2012; Dobos 1986; Foote et al. 2020; Kluyver 1961; Odum 1941b, 1942; Picman and Belles-Isles 1988a; Pribil and Picman 1994; Robinson and Holmes 1982; Simpson 2025; S.M. Smith 1991; Tyler in Bent 1946). It eats spruce budworms even when they are present in low density, but populations do not increase with increasing budworm numbers (Crawford and Jennings 1989; Venier et al. 2009; Morris et al. 1958). In Maine during a spruce budworm outbreak, its diet was composed of 44% and 37% spruce budworm larvae and pupae in 2 years (Mitchell 1952).

The Black-capped Chickadee is rarely parasitized by the Brown-headed Cowbird. Some authors stated that only 7 incidences of parasitism have been documented. There is 1 record of chickadees successfully rearing both cowbird and chickadee fledglings (Campbell et al. 1997; Lowther 1985, 1997; S.M. Smith 1991; Tyler in Bent 1946). The highest reported rate of parasitism appears to be in Ontario; 6 of 247 nests (2.4%) were parasitized (Peck and James 1997).

The Northern House Wren competes with the Black-capped Chickadee for nest sites. In addition to taking over nests, wrens frequently break or remove chickadee eggs. In Massachusetts, 20% of chickadee clutches were destroyed by wrens (Brewer 1963a; Kluyver 1961). The Tufted Titmouse may outcompete this chickadee, especially when titmice expand their populations. One chickadee population declined significantly when titmice became established; chickadees experienced a reduction in survival rates and numbers of recruits. This effect lasted only 1 year and there was no long-term effect on population size. After the population stabilized, there was still a significant decrease in survival rate but a significant increase in recruits. The population remained stable, but was comprised of a higher proportion of juveniles (Dhondt 1989). In Connecticut, there was evidence of lower average long-term survival rates, especially in winter, following establishment by the Tufted Titmouse (Loery et al. 1997).

Habitat loss and degradation do not appear to be significant limiting factors for the Black-capped Chickadee. It is predominantly an edge species, so forest fragmentation may be beneficial, providing more edge habitat for nesting. Excessive forest clearing may be detrimental. It is absent from portions of Essex County where forest cover has been significantly reduced.

It has been suggested that managed woodlots where dead trees are removed are less suitable for nesting, but this may not be the case because chickadees frequently nest in dead limbs of live trees. In the Boreal Forest Region with particular reference to Ontario, the abundance of the Black-capped Chickadee was unaffected when 30%, 50%, or 70% of trees were removed. In the North Bay area, there were no significant differences in its reproductive success in healthy sugar maple forests and those that were declining due to acid precipitation. The only difference was that chickadees in the healthy forest spent more time foraging in the canopy. Birds at the declining site spent equal time foraging in the upper and mid-canopies. Lower foraging at the declining site may have been a response to canopy dieback and lower quantity of food resources in the upper canopy. In the Carolinian Forest Region of Ontario, there were no differences in its density in control woodlots or those that had been logged. Clear-cutting removes habitat in the short term, but may be beneficial in the long term due to regeneration by birch and poplar. In Pennsylvania, there were no significant differences in its numbers in clear-cuts where snags were removed or retained. In Vermont, it nested in clear-cuts as well as adjacent uncut forest. In British Columbia, chickadees breeding in forest regenerating after clear-cutting had significantly lower breeding success than those nesting in adjacent mature, mixed-wood forest. Canopy height was significantly associated with nest success, and was significantly lower in clear-cut areas. Good quality nest sites and breeding territories may have been more limited in disturbed habitat. In New York clear-cuts, it was in a guild of species that was positively correlated with the total leaf area 0-7 m from the ground. The species in this guild attained their highest abundance 7-10 years after cutting. In New York, it was unaffected when 0%, 25%, 50%, 75%, and 100% of merchantable timber was removed from stands. This silvicultural technique left the smaller diameter trees that are preferred for nesting by the Black-capped Chickadee. No significant effects due to partial harvest were observed in the Boreal Forest Region of Alberta. In Minnesota, it responded positively to partial timber harvesting, but was not significantly more abundant in cut than uncut forests (Desrochers in Gauthier and Aubry 1996; Foote et al. 2020; Fort and Otter 2004; Lent and Capen 1995; Hanowski et al. 2003, 2005; Harrison et al. 2005; Holmes et al. 2004; Keller et al. 2003; Mahony et al. 1997; Straus et al. 2011; Stribling et al. 1990; Vanderwel et al. 2009; Webb et al. 1977). In the Canadian Shield of Ontario, it was equally abundant in early successional clear-cuts and burns, but was significantly less abundant in mid-successional clear-cuts than in mid-successional burns. It was significantly less abundant in early successional than mature stands but equally abundant in mid-successional and mature stands (Zimmerling et al. 2017).

Blewett and Marzluff (2005) studied the effects of urban sprawl on the Black-capped Chickadee in the Seattle area. Higher densities were associated with high interspersion of habitats at the landscape scale. There was no difference in breeding densities in urban forests and more extensive forests. In Colorado, it was more abundant in undeveloped landscapes than in areas with low or high density of homes. Abundance was negatively correlated with distance to houses, suggesting sensitivity to humans (Foote et al. 2020).

After forestry applications of fenitrothion, songbirds may experience 50-60% brain cholinesterase E depression. The 50% level is loosely associated with a variety of physiological effects and mortality in many species. Chickadees were able to remember their food caches at this level of contamination, but their physical abilities were visibly impaired (Mineau et al. 1994).

In response to anthropogenic noise, the Black-capped Chickadee sang its notes at higher frequencies when ambient noise levels were higher. Anthropogenic noise did not affect its abundance or health. It is well adapted to noise and its abundance was not correlated with noise levels (Bayne et al. 2008; LaZerte 2014; Proppe et al. 2012, 2013). In New York, Damsky and Gall (2017) played Tufted Titmouse mobbing calls and mobbing calls accompanied by anthropogenic noise, including traffic with occasional airplane and lawnmower noises. The addition of noise resulted in an approximately 80% decrease in the number of chickadees approaching the speakers; there was no effect on feeding behaviour. The decrease in response to the mobbing call as a result of noise was considered a concern. These calls are given in response to a threatening stimulus. If birds are slow to respond to the warnings, they may be unable to take advantage of them.

In Edmonton, this chickadee was equally abundant near roads and in undisturbed habitats. There were no differences in hematological measures of stress or physical condition of birds residing near or distant from roads. Proppe et al. (2013) concluded that roads did not affect its abundance, health, or physical condition. Bayne et al. (2016) compared its abundance near energy sector disturbances and adjacent forest interior. It was more abundant near pipelines and well pads than in adjacent forest interior. There was no difference in its abundance in forest interior and near seismic lines.

In Minnesota, blowdown of spruce-fir forest resulted in an 80% decline in canopy cover and a 100% increase in shrub cover. The Black-capped Chickadee bred in the control plots but was only a visitor to blowdown areas (Burris and Haney 2005).

In New Jersey and Pennsylvania over a 15-year period, hemlock declined from representing 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The Black-capped Chickadee responded favourably to hemlock decline and increased (Toenies et al. 2018).

In New York, Brooks and Bonter (2010) surveyed territories over 35 years in a field that had been allowed to regenerate, in forest, and in a managed Christmas tree plantation. Over this time, the number of Black-capped Chickadee territories in regenerating areas increased significantly. There was no change in numbers in forest habitat; it was absent in the Christmas tree plantation.

Cold spring weather does not appear to be a significant limiting factor. In Massachusetts, cold weather delayed clutch initiation, but did not affect clutch size (Kluyver 1961). Severe spring storms may cause death of fledglings (Smith 1967a).

In southwestern Ontario, daily survival rates were negatively correlated with nest height, canopy closure, tree DBH, and arthropod biomass. Areas with lower canopy closure tend to develop dense sapling layers which may provide nest concealment (Straus et al. 2011). In New York, the most important factor influencing nest success from predators was thickness of the cavity wall, with less predation of thicker-walled cavities. Lower rates of predation were associated with harder wood at the nest site and larger tree circumference at the nest. Nest height did not affect success (Christman and Dhondt 1997).

Price (2004) predicted that the range of the Black-capped Chickadee could contract in southern Ontario if the average summer temperature increased by 2°C.

Status

The Black-capped Chickadee has always been a common breeding bird in Ontario. McIlwraith (1894) concluded that it was distributed throughout the province. Baillie and Harrington (1937) considered it a fairly common breeding species from the southern border north to Fort Albany and west to Lake of the Woods, and probably northward along the Manitoba border. Historical populations did not vary significantly from present in Elgin County (Lancaster et al. 2004) and the Kingston region (Weir 2008), and probably throughout the province. James (1991) considered it a common permanent resident north to Big Trout Lake and Moosonee, and rare to Little Sachigo Lake and Attawapiskat.

The second atlas revealed that the probability of observation of the Black-capped Chickadee had not changed significantly province-wide, although the trend was positive. Significant increases occurred in the Carolinian and Boreal forest regions. The increase in the Carolinian Forest Region was mostly in Essex County, but it was also observed in several new squares in adjacent Chatham-Kent and Lambton. It was most abundant in the Great Lakes–St. Lawrence Forest Region, although it was notably less abundant west of a line between the western base of the Bruce Peninsula to about the Cambridge area. It was relatively uncommon in the Carolinian and Boreal forest regions and in the southern portion of the Hudson Bay Lowland (Cheskey in Cadman et al. 2007).

Long-term (1970-2021) population trends determined by the Breeding Bird Survey were annual increases of 0.78% in Canada and 2.05% in Ontario. Short-term (2011-21) trends were annual decreases of 0.49% in Canada and 0.466% in Ontario. The long-term results for Canada were of medium reliability; the other estimates were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Once all young have fledged, they begin to move away from the nest. Young can usually capture prey 10 days after fledging, and parents begin to ignore begging 8-10 days after fledging. Breakup of the family occurs about 3 weeks after the young fledge (Foote et al. 2020).

Juvenile dispersal begins shortly after fledging and occurs in random directions. This dispersal may partially explain why the Black-capped Chickadee occasionally occurs south of its normal range during winter. In Wisconsin, 3 weeks after attaining independence, juveniles were seen 180-760 m from their nest sites and 50-590 m from the nearest location where they had been last seen with their parents. Within 30 minutes, 1 juvenile travelled 500 m through 3 territories, and then another 200 m before it was lost from view. These rapid dispersals are typical. Juveniles are not accosted by adults who remain on their territories at this time. Dispersal lasts only a few weeks and is usually complete by mid- to late July. In 1 area, juvenile females dispersed an average of 2.3 km compared with 1.3 km for males. Most years, juveniles band together to form flocks from July to mid-August. These flocks are often joined by woodpeckers, vireos, kinglets, and warblers. Flocks of juveniles disband later in autumn, but at that time they are joined by adults who form the nucleus of winter flocks. Most juveniles winter and subsequently breed in the area where they settled after dispersal (Butts 1931a; Odum 1941b, 1942; S.M. Smith 1991; Weise and Meyer 1979).

During the autumn dispersal and flocking periods, the Black-capped Chickadee prefers wooded areas and forest edges. In British Columbia, preferred habitat includes deciduous, mixed, and open coniferous forests; shrub thickets; riparian woodlands; and willow, aspen, and birch stands with a shrub understorey. In coniferous forests, it prefers edges and openings along beaver ponds, lakeshores, river banks, bogs, meadows, and other human-made clearings. In Pennsylvania during autumn, it was most abundant in forest edge, followed by forest interior, shrub-sapling-stage forest, forest-agricultural edge, pole-size forest, and suburban forest. In New York, late-summer flocks usually remained in woods; October flocks were seen in all parts of the study area, including weedy fields (Campbell et al. 1997; Foote et al. 2020; Odum 1942; Rodewald and Brittingham 2002).

During the postbreeding period, juveniles were equally likely to occur in riparian (59% of birds) and upland (41%) forests (Akresh et al. 2009). In Minnesota, Streby et al. (2011b) captured only 1 chickadee in clear-cuts during the breeding season, but caught 42 adults and 25 fledglings during the postbreeding period. This suggested that they moved to areas with dense shrub cover in the postbreeding period. In Pennsylvania, Stoleson (2013) captured 78 adults and 61 juveniles in clear-cuts and 3 adults and 5 juveniles in mature forest.

After fledging, the family roosts wherever it happens to be. Once flocks form, birds tend to roost solitarily but in the same general area of forest or group of trees, and the same area is used every night, particularly in winter. Birds roost near the ends of limbs in dense foliage, often in low conifers such as in pine plantations (Odum 1942).

During autumn at Prince Edward Point, 27% of foraging occurred on outer leaves, 15% on outer branches, 8% in inner branches, 17% on tree trunks, 10% on sapling foliage, 14% on sapling branches, 6% on shrubs, and 3% on the ground. Foraging occurred at heights of 0-12 m, with peaks at 3 and 10 m (Keast 1980).

In late summer and autumn, the Black-capped Chickadee's diet changes from being dominated by invertebrates to a mix of animal and vegetable matter. Invertebrate food consists predominantly of insect and spider eggs and pupae. As fruit becomes available, it feeds on fruit of staghorn sumac, common buckthorn, yew, hawthorn, winterberry holly, pin cherry, poison ivy, yellow birch, tree-of-heaven, sweet gale, blueberries, and blackberries. It also feeds on seeds of giant ragweed, early goldenrod, flat-topped goldenrod, and other members of the aster family. In late autumn and winter, hemlock seeds are highly preferred (Barnea and Nottebohm 1995; Fitch 1958; Foote et al. 2020; Mudrzynski and Norment 2013; Odum 1942; S.M. Smith 1991; Tyler in Bent 1946).

The onset of shorter days stimulates the Black-capped Chickadee to store food. This starts in mid-October. In some areas, this only lasts through November. In other areas, including Ontario, food storage may occur throughout winter and can potentially occur at any time of the year. Most items cached are seeds, although insect and spider eggs and pupae may be cached, as well as suet from feeders in winter. Each item is cached separately, usually 15-20 m or less from the food source, occasionally as far away as 70 m. Most individuals cached food in a certain orientation from a food source every day, but this orientation may vary daily and there is no favoured cache location within the home range. Most caches are retrieved within a few days. Although initial cache sites are used briefly, food may be cached at a secondary site for as long as a month before recovery. In Ohio, 48%

of seeds were stored on branches, 25% on twigs, and 21% on small trunks less than 2.5 cm DBH. More than 85% of storage substrates were less than 8 cm in diameter. It showed a strong preference for caching on the underside of branches and also cached in dead leaves that were still hanging from trees. Mean height of caches was 7.0 m. Although most food is stored in small cracks and crevices in trees, it occasionally caches on the ground or under snow, or rarely under shingles, in eavestroughs, or in drain pipes (Barnea and Nottebohm 1995; Foote et al. 2020; Kilham 1975; Odum 1942; Petit et al. 1989; Shettleworth et al. 1995; S.M. Smith 1991).

MIGRATION

The Black-capped Chickadee is typically a permanent resident that remains year round in its breeding range, even in the north. Several types of movement may occur; some occur regularly, others are more sporadic. Autumn dispersal of juveniles occurs regularly and, in some areas with significant altitudinal gradients, birds may move down in autumn and back up in spring. In some areas, there is evidence of a slight southward movement in late autumn or winter. In New York and Illinois, the Black-capped Chickadee occurred further south in winter than in the rest of the year. In the Yukon, it persists in winter at the northern extent of its range, but many disappear during cold spells suggesting sporadic seasonal movements or mortality. Most noteworthy are massive and irregular autumn movements southward. These are best termed irruptions rather than true migration and appear to be a response to low cone crops in the north. During irruptions, birds may move 50-500 km and 1 bird moved more than 2,000 km. Irruptions are usually followed by a spring return of lesser numbers that usually occurs in April and May. It is unknown if birds involved in irruptions return to their area of origin. Most birds involved in irruptions are juveniles, but some adult movement may occur. Short-distance movements during non-irruption years are rather aimless and these may represent dispersal rather than migration. All movement is during the day and chickadees may move singly, often in ragged groups, or occasionally in large flocks, especially along lake shorelines. Movements may terminate when chickadees reach the shoreline of a large lake, but flocks have been observed flying across the Great Lakes from Point Pelee and Presqu'ile Provincial Park (Brewer et al. 2018; Brooks 1991a; Butts 1931a; Foote et al. 2020; Graber and Graber 1963; Hussell 1996; Lawrence 1958; Odum 1942; Sinclair et al. 2003; S.M. Smith 1991; Weir 2008).

After a major irruption southward in October 1961, there was a pronounced spring migration at Long Point. Between 20 April and 3 June 1962, 505 Black-capped Chickadees were banded. The major influx was between 10 and 20 May, with numbers considerably reduced after 20 May. Some stayed in the area 24-25 days (mean 6.7 days). Spring invasions at Long Point are infrequent, with an average of less than 1 chickadee a day recorded most years. Only 1964 came close to the 1962 results with an average of 42.3 per day. Average number of birds in spring was correlated with average numbers occurring the previous autumn. During spring migration years, peaks at Long Point tend to be from 26 April to 20 May. Some of these birds may be paired; 2 chickadees banded at Point Pelee were recaptured together at Long Point 20 days later (Hussell 1991d, 1996; Hussell and Stamp 1965). At Pimisi Bay, there were few, if any arrivals from the south, and peak numbers occurred in March. This appeared to represent the return of wintering birds back to the breeding areas (Lawrence 1958).

Near Guelph, a regular influx of chickadees occurred in October and March suggesting that regular migration was taking place. Recoveries of birds also suggested migration. One banded in Fergus was recaptured in Guelph, 1 banded in Eramosa was recaptured in Ottawa, and 1 banded in Toronto was recaptured in Eramosa. Salvadori et al. (2002) concluded that large-scale migration occurs in the Black-capped Chickadee, but that a large number wander around in no specific direction. Of 60,000 Canadian banding records, 90% of chickadees exhibited no movement (Foote et al. 2020).

In New York, only 32 of 1,378 chickadees (2.3%) were re-encountered more than 16 km from the banding location. Most moved northeastward and the average distance travelled was 119 km over 50 days, about 1.6 km a day (Brooks 1989, 1991b). Due to the late migration of spring migrants, probably most do not return to their area of origin to breed (Hussell and Stamp 1965).

Autumn irruptions are irregular and may occur across a wide geographic area or be more localized. At Long Point, large flights occurred in 1961, 1965, 1972, 1973, 1980, 1983, and 1993, with lesser influxes in 1963, 1969, 1980, and 1990. The 1961 flight was massive and covered much of the east. In 1985, an irruption occurred that appeared to be restricted to western Ontario and western Pennsylvania. In New York, some birds moved more than 320 km during an autumn irruption. At Point Pelee from 1909 to 1920, autumn migration was very irregular. On most days, there were no migrating chickadees, but occasionally 300-400 would be present for several days; flocks were occasionally observed flying across the lake. In the Kingston area, irruptions were documented in 1961, 1968, 1972, 1975, 1981, 1983, and 1986. During autumn irruptions, movement is leisurely and generally in a southwest direction (Brooks 1991a, 1991b; Hussell 1996; Tyler in Bent 1946; Weir 2008).

Migration is not fully understood. Juvenile dispersal occurs in July and autumn irruptions occur in October and November, with spring return in May. In non-irruption years, there may be high and low winter populations suggesting some short-distance movements in response to mast abundance. At Pimisi Bay, there were 3 peaks in abundance over 5 winters that occurred in November, January, and March, along with a fourth peak of juveniles in September (Lawrence 1958; Smith 1986a).

During irruptions, Black-capped Chickadees use the same habitats as regular autumn flocks, but also may be found in urban and more disturbed areas (Foote et al. 2020; Weir 2008).

The Black-capped Chickadee is highly vulnerable to striking residences 1-3 storeys tall. It was 14.9 times more likely to suffer a collision than on average for birds. It was not on the lists of the 20 most vulnerable species for striking low-rises or high-rises (Loss et al. 2014).

During irruptions, the Black-capped Chickadee may be abundant locally or occur over a widespread area. In the Kingston area, as many as 2,000 have been seen in a day (Weir 2008). In Elgin County, more than 1,500 were observed on 21 October (Lancaster et al. 2004). In 1954, 31,000 were reported along the New York shoreline of Lake Ontario, and more than 36,000 were seen in the same place in October 1961 (S.M. Smith 1991).

WINTER

Winter flocks begin to assemble in September or October or even as early as August. Flocks have mostly stabilized by mid-September to early October in British Columbia and by late October in Alberta. Flocks remain stable until nesting territoriality begins in spring. Flock sizes range from 3 to 16 birds. Winter flocks are comprised of 1 or occasionally 2 adult pairs and a small number of juveniles. Sex ratios in flocks are typically 1:1, and juvenile birds form pair bonds over the winter and breed in the vicinity in spring. Within each flock, there is a well-defined dominance hierarchy. Males typically dominate females, although the reverse is occasionally true, and adults always dominate young of the same sex. Usually the hierarchy is adult male, juvenile male, adult female, and juvenile female. Once established, dominance relationships continue for 7-8 months. Dominance is very important because dominant birds obtain superior breeding territories and have better access to food and cover from predators. At feeders, dominant birds may make fewer visits, but have access to the feeder all the time; subdominants have to wait until the feeder is not occupied by a superior bird (Barnea and Nottebohm 1995; Desrochers 1989; Desrochers and Hannon 1989; Desrochers et al. 1988; Ekman 1989; Ficken et al. 1990; Hogstad 1989; Odum 1941a; S.M. Smith 1967a, 1976, 1991).

In winter, the Black-capped Chickadee is a snow-associated species. Important predictors of its presence include a long snow season and lack of frozen ground without snow (Keyser et al. 2022). Winter habitat is similar to that used in autumn, although there may be more usage of urban, suburban, and rural residential areas where bird feeders are provided. In suburban areas of California, its winter distribution was closely associated with the presence of feeders (Kalinowski and Johnson 2010). Prior to the era of bird feeding, McIlwraith (1894) stated that it was most frequently found in tamarack swamps during severe winter weather. Bush camps may be visited in autumn and winter where it feeds on human food scraps and meat and fat from carcasses and hides (Campbell et al. 1997). In an area of New York without feeders, flocks remained primarily in woods, orchards, shade trees, hedgerows, and shrubbery. Birds crossed open spaces at the narrowest point; the widest opening they were observed to cross was 175 m (Butts 1931a). Chickadees feeding on goldenrod gall flies in southwestern Ontario preferred open fields to forest edge (Schlicter 1978). Some portions of the winter home range may be used more than others if there is a rich food source such as a feeder, hemlock trees with numerous cones, or a temporary bonanza such as an animal carcass. It winters in areas with an average of more than 51 cm of snow a year and where the average minimum January temperature is −7 to −12°C (Odum 1942; Root 1988). In Missouri, its detectability increased with tree stocking and was lowest in savannah habitat, intermediate in woodlands, and highest in forests (Kendrick and Thompson 2013).

Roosts are a more important habitat requirement in winter. Roosts may be in dense vegetation, but more frequently in cavities. When roosting externally, flocks usually roost loosely together in the same area of a woodlot. Often conifers are selected for roosting, especially hemlock, pine, and spruce. Many of the cavities used are excavated by the chickadees. Winter roost cavities are much smaller than nesting cavities, presumably to conserve heat. Winter roosts have been documented in beech, oak, and ash, but probably a variety of species are used. Winter roosts may be in old woodpecker cavities or nests of other species such as House Sparrow. Almost all records of roosts are of a single bird in a cavity, but at least 5 were found roosting together in a stump in British

Columbia (Brewer 1963a; Campbell et al. 1997; Foote et al. 2020; Odum 1942; Schroeder 1982a; S.M. Smith 1991; Tyler in Bent 1946).

Winter flocks occupy well-defined home ranges 7.7-22.6 ha in size that average 8-10 ha. Individuals may have winter home ranges of 1.2-38.9 ha. Birds with the largest home ranges are either floaters or dominant wanderers; smallest home ranges occur near feeders. Birds in flocks usually remain in the central portion of the home range all winter, but occasionally leave and commute to rich food resources such as feeders. In New York, the greatest distance a flock travelled outside its normal range was 0.8 km. Flocks may be territorial, but flock winter ranges often overlap considerably. When this occurs, flocks tend to avoid each other. Most flocks share food resources such as feeders, but there may be agonistic interactions between flocks. When flocks encounter each other or intermingle, usually the flock that is closest to the centre of its home range is dominant. In these cases, even the most subordinate member of the dominant flock is dominant to the alpha bird of the other flock (Barnea and Nottebohm 1995; Brittingham and Temple 1992; Desrochers and Hannon 1989; Butts 1931a; Fitch 1958; Foote et al. 2020; Mueller 1973; Odum 1941a, 1942; S.M. Smith 1991).

Individuals are highly faithful to their flock through the winter; inter-flock exchange is rare. In Maine, only 19 of 3,976 visits (0.48%) to a feeder were at sites other than where the bird was banded. This occurs even where feeders are close together. In New York, birds moved freely between feeders 220 m apart, but not between those 550 m apart. In Alberta, only 0.6% of 683 individuals switched flocks regularly and permanent changes of membership from 1 flock to another occurred twice. In Wisconsin, birds banded at feeders 2 km apart were never seen at the other feeder. Connecticut birds captured at 1 feeder and moved to another 2.4 km away returned within 24 hours. The rare wanderers that move among flocks include floaters that are low-ranked juveniles, high-ranked former breeders that have a large home range, and visiting migrants (Brittingham and Temple 1988; Butts 1931a; Desrochers et al. 1988; Loery et al. 1987; Mueller 1973; S.M. Smith 1967a, 1976, 1991; Wilson 2001).

When foraging, flocks move continuously from patch to patch and rarely remain in 1 place for more than a few minutes. In Algonquin Park, much foraging occurred in the foliage of conifers and on the twigs and loose bark of deciduous trees. Ground feeding also occurred as patches of ground became clear of snow. In the Gogama area, the Black-capped Chickadee frequently fed in jack pines in winter. Ground foraging on hemlock seeds was common in New Hampshire. Dominance hierarchies affect where chickadees forage. In Alberta, males foraged lower and closer to the trunk than females and used trunks and main branches for foraging more often. Females foraged high and on the outermost tree parts. When males were removed, females foraged where males typically searched for prey. It is readily attracted to winter feeders, especially those that are established early in the season. In Ontario, more than 90% of feeders are visited by Black-capped Chickadees, with lower utilization of feeders at the northern extent of its range. Urban and rural feeders are visited at equal rates, but rural flocks are about twice as large. Flock sizes are also slightly larger in the north, suggesting greater dependence on feeders (Brittingham and Temple 1992; Desrochers 1989; Dunn and Tessaglia-Hymes 1999; James and Peck 1995a; Kilham 1975; Martin 1960; Wilson 2001).

In Michigan, Black-capped and Boreal chickadees often forage together in mixed-species flocks. The Black-capped Chickadee foraged in 6 conifer and 3 deciduous tree species; the Boreal Chickadee restricted its foraging to 3 species of conifers. The Black-capped Chickadee spent 4.5% of its time foraging at the top of trees compared with 36.5% for the Boreal Chickadee, but the 2 species foraged at similar rates in other vertical zones. The niche overlap of the 2 species was 67.6%, higher than expected. The 2 chickadee species eat similar foods but competition is reduced due to the abundance of food resources, the fact that foraging overlaps in only 3 species of conifers, and that Black-capped Chickadees use the crowns of these conifers significantly less than Boreal Chickadees (Gayk and Lindsay 2012).

In Connecticut, Correia and Halkin (2018) compared the winter habitat and foraging niches of the Tufted Titmouse and Black-capped Chickadee. Chickadees spent 83% of their foraging time in the upper and middle canopy and in shrubs. They spent a much greater percentage of their time in the outer-upper canopy (26.7%) and shrubs (25.0%) than titmice (9.1% and 9.9% respectively). From the ground up, there was a steady increase in the amount of time that chickadees spent foraging at each successive level. Titmice spent less time in the upper canopy than at lower levels. Compared with chickadees, titmice used canopy foraging locations more evenly, spent less time in shrubs, and spent much more time on the ground. Chickadees spent significantly more time in the outer-upper canopy and shrubs than titmice, and titmice spent significantly more time on the ground than chickadees. The 2 species had different preferences at feeders. Chickadees selected sunflower seeds without shells on 61% of visits; titmice selected safflower on 54% of visits. At feeders, titmice won all challenges against chickadees. The significant differences found in the 2 species' foraging behaviours and seed preferences may mitigate competition.

Natural winter food of the Black-capped Chickadee includes insect eggs and larvae, mites and other arthropods, and seeds. Most winter food consists of seeds of conifers; hemlock is highly favoured. It may also eat buds and scales of other plants. It eats animal fat if it finds a carcass; flocks have fed on the fat of a dead skunk and dead fish. In southern Ontario, it actively feeds on the larvae of the gall fly in galls on Canada goldenrod. Predation of gall flies declines by the third week of December at forest edges, because 80.5% of galls have been attacked by this time. In open fields, about 60% of galls are preyed upon by the end of January (Brittingham and Temple 1988; Kilham 1975; Schlicter 1978; S.M. Smith 1991; Tyler in Bent 1946). In western North America, gall flies have been introduced in an attempt to control the invasive spotted knapweed. The Black-capped Chickadee actively selects seedheads of knapweeds that support high densities of gall fly larvae for foraging in winter (Templeton 2011).

In Pennsylvania, Nastase and Linville (1995) provided a feeder with trays at heights of 2, 4, and 6 m. Chickadees fed 41.4% of the time on the ground, more than the other 6 species they studied. Rates of foraging at other heights were 32.7% at 2 m, 14.6% at 4 m, and 11.3% at 6 m. They showed an overwhelming preference for sunflower seeds, taking them on 98.1% of visits. Other foods taken were niger seeds on 0.8% of visits, canary seed on 0.6%, corn on 0.3%, and millet on 0.2%.

At feeders, the Black-capped Chickadee's favourite food is sunflowers of any type, but especially striped and black oil sunflowers. Other favoured feeder foods are safflower, hulled peanuts, suet, peanut butter mixes, bird puddings, and water. Foods eaten infrequently include mixed seeds,

millet, canary seed, cracked corn, milo, niger, peanuts in the shell or peanut hearts, oats, canola, pet food, fresh or dried fruit, meat scraps, baked goods, and popped corn (Dunn and Tessaglia-Hymes 1999). A total of 79,570 feeding observations were made for the Black-capped Chickadee. It preferred black oil sunflowers and preferred hopper feeders to tube or platform feeders. It was least abundant at feeders filled with sorghum (Horn et al. 2014). It selects the largest and heaviest sunflower seeds available (Wysinger et al. 2022).

Winter food availability may be a significant limiting factor in the northern and even central portions of the Black-capped Chickadee's range. It stores fat, but only enough to survive less than 24 hours without feeding. In Wisconsin, chickadees obtained about 21% of their daily energy requirements from feeders. Winter survival rates were significantly lower in areas without feeders in Pennsylvania. During all months of the year, survival rates in Pennsylvania were higher in areas with supplemental food. The difference was most pronounced in October and March with 60% survival under natural conditions and 90% where food was supplied. In the north where there are no feeders, winter starvation is likely a regular and potentially significant source of mortality (Brittingham and Temple 1988, 1992; Desrochers et al. 1988; Egan and Brittingham 1994; S.M. Smith 1991).

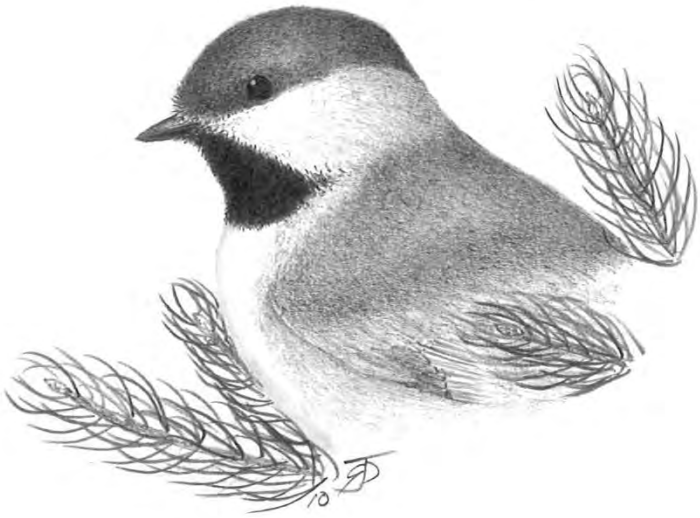
Survival rates of the Black-capped Chickadee are affected by cold weather, particularly where feeders are not available. In Wisconsin, birds that had access to supplemental food continued to feed during very cold weather. Those without a supplied source of food reduced energy expenditure by sitting motionless with the feathers fluffed out. Birds had higher survival rates in winters with 5 or fewer days with temperatures below –18°C than in winters with more days at these temperatures. In winter, it conserves heat at night by dropping its body temperature through controlled hypothermia. Summer abundance has declined occasionally in the eastern states following severe winters (Brittingham and Temple 1988; Holmes and Sherry 2001; Holmes and Sturges 1975; S.M. Smith 1986, 1991).

During winter in Alberta and Quebec, the Black-capped Chickadee was as likely to travel in corridors as narrow as hedgerows as in continuous forest, but less likely to cross gaps. Birds were unwilling to cross gaps wider than 50 m when they had forested alternative routes, even if the distance was much longer. They sometimes crossed gaps as wide as 200 m when there was no alternative route. Chickadees were 4 times more likely to travel 200 m in a forest and 3.5 times more likely to travel that far in a corridor than they were to cross a similar-sized gap. It preferred to remain close to forest cover (St. Clair et al. 1998). In British Columbia, gaps in forest habitat ranged from 10 to 84 m. Birds made significantly fewer movements between feeders on the opposite side of a gap (31.8%) than between feeders on the same side of the gap (68.2%). Birds were 1.8 times less likely to cross gaps as gap distance increased from 10 to 40 m, and 3.7 times less likely to cross as gap distance increased to 70 m. Birds were more likely to cross gaps as the amount of vegetation 1-2 m tall increased. For each 5% increase in vegetation density at 1-2 m, crossing likelihood increased by 1.7 times. Bailey et al. (2018) concluded that gaps in forest canopy impede movements of this chickadee, but this may be partially mitigated by the presence of shrubby vegetation 1-2 m tall.

The Black-capped Chickadee is common in winter. Christmas Bird Count data indicate that it decreased annually in Ontario by 0.25% 1970-2021 and by 0.10% 2009-21 (National Audubon Society 2022).

Boreal Chickadee

Poecile hudsonicus



BREEDING SEASON

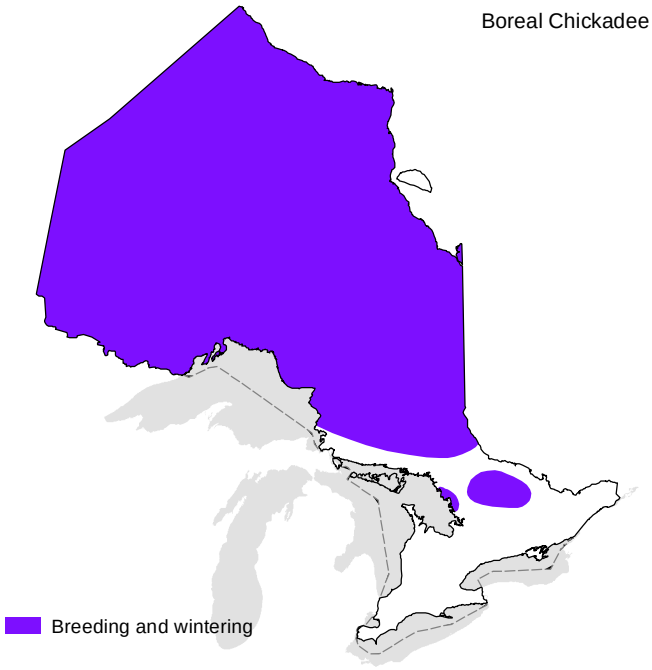
Habitat Requirements

In Ontario, the Boreal Chickadee nests primarily in closed and open coniferous and mixed forests and black spruce bogs. There are single reports of nests in an open field and an open wooded marsh. Some nests were at forest edges, near shorelines, and near a railway right-of-way. Wet habitats were selected more frequently than dry areas (Peck and James 1987).

Along the coasts of Hudson Bay and James Bay, the Black-capped Chickadee nested in dry spruce stands. This habitat was scarce except near the major rivers (Manning 1952).

In the Boreal Forest Region at Pickle Lake, James (1980) observed the Boreal Chickadee regularly in coniferous forests, especially those that were open and disturbed. On the north shore of Lake Superior, Baillie and Hope (1943) found it mostly in or adjacent to black spruce bogs. It also occurred in open, park-like stands of jack pine adjacent to spruce bogs. Near White River, it was significantly more common in clear-cuts 18-20 years old than in younger or older cuts or in mature forests (Venier and Pearce 2005). In the Clay Belt, it was associated with wet areas in forests that were moderate to rich in nutrients (Welsh and Lougheed 1996).

In the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region in Quetico Park, the Boreal Chickadee was most abundant in intermediate-aged stands (67-73 years), but occurred in all age classes (Apfelbaum and Haney 1985). Near Gogama, it occurred only where jack pine was



the dominant tree type. It was absent from very young stands; pines were 4-6 m tall before they were inhabited. Densities were highest where pines were about 10 m tall, and declined somewhat as forests matured. Nest boxes were used more frequently in 20-year-old than 40-year-old stands. Older stands would have more potential nest sites. In most nesting areas, canopy closure was greater than 75% and often approached 100%. It occasionally nested among well-spaced pines with canopy closure only slightly greater than 50%. Tall shrubs were absent or scarce in nesting areas and appeared unnecessary because foraging occurred only in pines (James and Peck 1995a). In Algonquin Park, it occurred chiefly at or near spruce bogs (MacLulich 1938), and in black spruce–balsam fir forests with considerable interspersion by white spruce, trembling aspen, and white birch (McLaren 1976).

The Boreal Chickadee is a permanent resident of the Boreal Forest Region. It occurs in both young and mature coniferous forests and in mixed forests, rarely in deciduous stands. It is most frequently associated with spruce, but also with jack pine and balsam fir. Its preference for spruce and fir forests partially explains its spotty distribution in the south. In the south, it is replaced by the Black-capped Chickadee in hemlock stands and in pines other than jack pine. The Boreal Chickadee displaces the Black-capped Chickadee in fir stands. The Boreal Chickadee occurs in Quebec wherever there are large expanses of coniferous forest. Densities are higher in open spruce-lichen woodlands and taiga than in the more southern black spruce–moss forests. In Quebec black spruce forests, it breeds in clear-cuts and recent burns, and was equally abundant in all habitats that it occupied. In British Columbia, it occurs in open stands or at edges of closed stands. It was considered a forest-interior species in 1 Saskatchewan study. In this area, it was randomly distributed within fragmented landscapes. Its presence was not associated with forest size, the amount of forest cover within 5 km, nor forest type. Nesting in Saskatchewan occurred in tamarack, mixed, and white spruce forests. In Newfoundland, it was more common in 40-60-year-old stands than those 80 years or older. It is in a guild of 34 species that are predominantly associated with conifers. In the Yukon and Alaska, it is a dominant species in spruce forests. The northern extent of its range coincides with that of spruce. In the Yukon, it is a habitat specialist in mature white spruce along rivers and rarely occurs in the deciduous shrub habitats favoured by Black-capped Chickadees. In northern Maine, both chickadee species are present in the same spruce–balsam fir stands. The Boreal Chickadee is more abundant in the lowland flats; the Black-capped Chickadee is more abundant on ridges. In Algonquin Park, both chickadee species are present, but no interactions appear to occur between them. In New Hampshire, the Boreal Chickadee occurred in high-altitude conifers dominated by

taiga or boreal spruce forest. Mean canopy height where it occurred was 8.8 m, mean canopy closure was 63%, and the average diameter at breast height (DBH) of trees was 11 cm. In some areas, it occurs in forests dominated by white cedar (Bent 1946; Campbell et al. 1997; Desrochers in Gauthier and Aubry 1996; Erskine 1977; Ficken et al. 2020; Gage et al. 1970; Hobson and Bayne 2000; Imbeau et al. 1999; Kirk et al. 1996; McLaren 1976; Niemi and Pfannmuller 1979; Sabo 1980; Sinclair et al. 2003; Thompson et al. 1999).

In Minnesota, the Boreal Chickadee was positively correlated with the amount of coniferous cover within 200 m and the density of streams. It used black spruce stands and avoided tamarack forests (Zlonis et al. 2017). In New York, Vermont, Maine, Nova Scotia, and Newfoundland, it occurred at 11 of 20 sites indicating broader habitat preferences than many species and an ability to use multiple boreal forest habitats. It preferred young, dense spruce-fir forests (Ralston et al. 2019).

The female roosts in the nest cavity beginning with laying of the first egg. No information is available on where males roost, or where roosting occurs outside the breeding season (Ficken et al. 2020).

Ontario nests in natural areas were in cavities in standing tree stumps (61.9% of nests), in tree trunks and branches (33.3%), and in an uprooted stump (9.8%). Most nest stumps and trees were dead, but 3 (14.3%) were living or partly alive. Most nests were excavated or natural cavities in the side of stumps or trees (72.2%); the remainder were in cavities at the top of broken stumps. Twelve cavities were excavated or enlarged by the chickadees, but 3 were not; an old woodpecker cavity was used once. Six nests were in birches, 4 in poplars, 2 in balsam fir, 2 in black spruce, 2 in white cedar, and 2 in pines. Nests were 0.3-10.5 m from ground, with most 0.9-4.3 m up. Two nests in hollow stumps were at ground level (Peck and James 1987). In the Sudbury and Gogama areas and elsewhere in the province, the Boreal Chickadee readily accepts nest boxes (Peck and James 1997). In Algonquin Park, tree species were not important in nest-site selection. Chickadees selected trees based on the softness of the heartwood. All nests were in trees or stumps where the heartwood was soft from rotting, but the outer layers and bark were still hard. About 40% of cavity entrances were at the top of stumps; in any given population, approximately 20-40% of nest entrances face upwards (McLaren 1975). In Algonquin Park, nest holes were 0.1-10.5 m above ground, but seldom higher than 3 m (Ficken et al. 2020). Along the north shore of Lake Superior, Baillie and Hope (1943) found 2 nests 1.8 m and 2.4 m up in black spruce stubs in bogs and another was in an old woodpecker cavity 1.5 m up in a dead jack pine (James and Peck 1995a). Nest cavities do not appear to be reused in subsequent years, but nest boxes were occasionally reused (Ficken et al. 2020; McLaren 1975).

Nests reported elsewhere are similar to those found in Ontario. The Boreal Chickadee has nested in white birch stubs in a beaver pond, in spruce and tamarack stubs and stumps, in cedar stumps, in knotholes and splits in live black spruce and trembling aspen, in willow, and in an old Hairy Woodpecker nest. Nest heights in British Columbia were 1.0-8.0 m, with most 1.2-5.5 m up. Optimum stump or snag size appears to be about 10 cm, but larger ones may be used (Bent 1946; Campbell et al. 1997; Evans and Conner 1979; Sinclair et al. 2003; Walkinshaw 1948a).

Pairs break away from the winter flock in early spring and establish a territory. In Algonquin Park, territories were larger than 5 ha. They were not advertized vocally, so considerable trespassing

occurred and it is possible that territories overlap. When intruders are detected, they are vocalized at and chased away. Territoriality may continue until shortly after the young fledge (McLaren 1975). In subalpine areas of New Hampshire, territory sizes averaged 1.2 ha (Sabo 1980).

Essentially nothing is known about natal philopatry and juvenile dispersal. Ficken et al. (2020) reported that no young from 3 broods seen in winter flocks were found later on their natal territory, and it was unknown where they first nested. In Algonquin Park, McLaren (1975) observed 1 pair on the same territory in 2 consecutive years. It is likely that pairs mate for life and remain in the same area for their entire life.

Limiting Factors

Eggs have been reported in Ontario nests from the third week of May until early July, with most present in the last week of May and first week of June (Peck and James 1997). Once pairs split from the winter flock, 2-3 weeks may elapse before nesting behaviour begins (McLaren 1975). In Algonquin Park, nests are under construction from late April to late May, eggs are present from late May to mid-June, nestlings are typically present from early to late June but a nest with young was found on 3 August, and dependent fledglings are present from late June to mid-August (Tozer 2012).

The earliest that nest excavation in Algonquin Park was observed on was 20 April. The time required to excavate a cavity is 1-10 days, depending on the hardness of the heartwood. Several cavities may be examined or excavated before one is selected for nesting. Pairs may spend as long as 5 days excavating a cavity, and then abandon it. Nest construction often starts as soon as the cavity is complete, but may be delayed several days. Egg laying usually begins after 2-3 days of nest building, and always before the nest is complete. One egg is laid per day; incubation begins with the laying of the penultimate or last egg. Incubation periods of 11-16 days have been reported in Ontario, with most eggs hatching in 15 days. In Algonquin Park, eggs in a clutch frequently did not hatch in the same day, and it took 3 days for all eggs to hatch in 1 clutch. Most young leave the nest when they are 18 days old; fledging occurred between 22 June and 3 July in Algonquin Park (Ficken et al. 2020; McLaren 1975; Peck and James 1997).

A single brood is raised annually. It is unknown if renesting occurs if a nest is lost. Clutches of 4-8 eggs have been documented in Ontario, with most containing 6 or 7 eggs. Overall, clutches of 2-9 eggs have been reported, but the clutch sizes reported in Ontario are typical (Bent 1946; Campbell et al. 1997; Ficken et al. 2020; McLaren 1975; Peck and James 1997).

The Boreal Chickadee probably first breeds when it is 1 year old. It is presumed to be monogamous, but data are lacking (Ficken et al. 2020).

In Ontario and the Northwest Territories, foraging occurred in conifers 90.5-96.0% of the time. In the Northwest Territories, 41.5% of foraging was conducted while hanging upside down compared with 20.5% in Ontario (Greenberg et al. 1999). In subalpine New Hampshire, foraging methods included 0.4% aerial flycatching, 39.0% leaf gleaning, 2.6% leaf hawking, 3.7% leaf hovering, 12.5% twig pecking, 15.4% twig gleaning, 3.7% branch pecking, 4.4% branch gleaning, 11.8% bole pecking, and 6.6% bole gleaning. It foraged equally close to (58.6%) and distant (41.4%) from tree trunks. Eighty-two percent of foraging was on coniferous foliage and 11.8% was on deciduous

foliage. Time spent foraging by height was 2.6% at 0.1-2 m, 47.4% at 2-5 m, 31.3% at 5-8 m, and 18.8% above 8 m (Sabo 1980). In Newfoundland, Vasallo and Rice (1982) compared foraging strategies of 2 Boreal Chickadee populations: one where Black-capped Chickadees were present and one without Black-capped Chickadees. Where both chickadee species were present, Boreal Chickadees foraged mostly on conifers and significantly higher than Black-capped Chickadees; Boreal Chickadees foraged on the outer portions of trees and Black-capped Chickadees foraged in the inner portions. Where Black-capped Chickadees were absent, Boreal Chickadees fed mostly in deciduous species and were more generalized in their foraging behaviour, using all portions of trees equally. Bent (1946) also noted that the Boreal Chickadee forages higher than the Black-capped Chickadee, and hangs upside down considerably less than the Black-capped Chickadee. Where the Boreal Chickadee forages within trees is probably a response to competition from other bird species. In New Brunswick, it foraged at the top of trees. In Saskatchewan, it favoured the mid-portions of trees and avoided the canopy and bottom of trees. In Saskatchewan, the mean foraging height was 6.1 m in conifers and 9.1 m in deciduous trees. Foraging occurred in the canopy 36.7% of observations and the remainder were in the subcanopy (Cumming 2004; Gage et al. 1970). In boreal forests in Saskatchewan, it selected balsam fir more for foraging than expected, tended to avoid trembling aspen, and used other tree species in proportion to their availability. In other areas, it is strongly associated with mature spruce and selects mature trees regardless of their height (Cumming 2004; Desrochers in Gauthier and Aubry 1996; Ficken et al. 2020; Matsuoka et al. 2001). In Algonquin Park, pairs foraged closely together in early spring, usually on the ground where melting snow had exposed material that had dropped from trees. Occasionally they fed in the upper third of trees (McLaren 1975). In Saskatchewan, it fed among piles of bark in the snow that were chipped off by woodpeckers. It also landed on tree trunks and pecked in the same locations that woodpeckers had, and followed woodpeckers to continue this foraging technique (Hooper 1988).

The Boreal Chickadee feeds predominantly on insects and spiders, their pupae and eggs, some fruit, and seeds of conifers and birches. Important insect foods include moth and butterfly larvae, aphids, and beetle larvae. It readily consumes budworms, depending on their size. In New Brunswick, no first-instar budworms were eaten even though their density was at a maximum. Consumption increased to a maximum as prey size increased then declined to zero as budworms decreased. In Maine and New Hampshire, it did not consume many budworms and its abundance was not associated with budworm abundance; no response to budworm numbers was observed in New Brunswick. At another Maine site, spruce budworm larvae and pupae constituted 25.3% and 37.0% of the invertebrates consumed in 2 years. It eats ashes from fire pits if ashes have high calcium content. This observation was made in mid-October and suggests that calcium is important in the diet year round (Bent 1946; Crawford and Jennings 1989; Ficken 1989; Ficken et al. 2020; Gage et al. 1970; Mitchell 1952; Morris et al. 1958).

The Boreal Chickadee regularly stores food and this is probably critical to its winter survival. The frequency of storage increases in July and August; as many as 45 items may be stored within an hour. Food may be stored in the same tree where it was found, or transported to another tree an average of 7 m away. It tends to store food at a consistent height, usually lower than foraging height. More than 1 item is usually stored in a cache and most food is stored on dead main branches near

the tree trunk. Seeds are placed closer to the trunk than arthropods. Most stored food is visible from below, thereby increasing chances of finding it when snow covers upper portions of branches. Stored food consists of predominantly moth and butterfly larvae, aphids, some beetle larvae, and spruce seeds. Most invertebrates are stored in bark crevices; aphids are often stored at branch junctions and between conifer needles. Seeds are usually better hidden in bark crevices and under lichens and are secured in place by saliva and sometimes web material from spiders, insect cocoons, or plant down. Cached items are sometimes covered with a small piece of bark, lichen, or spruce needles. Stored items, especially seeds, are sometimes retrieved and moved to another site (Dunn and Tessaglia-Hymes 1999; Ficken et al. 2020; Sherry 1989).

In Ontario, availability of old-growth black spruce may be particularly important for the Boreal Chickadee's survival, particularly in winter. These forest stands are under increased pressure for logging (Ficken et al. 2020). Similar concerns have been raised about mature white spruce stands in the Yukon (Sinclair et al. 2003).

In Minnesota, blowdown of spruce-fir forest resulted in an 80% decrease in canopy cover and a 100% increase in shrubs. The Boreal Chickadee bred in both the blowdown and control areas with no significant differences in abundance (Burris and Haney 2005).

On Anticosti Island, the Boreal Chickadee was unaffected by heavy browsing by high deer populations. Browsing suppressed deciduous regeneration, particularly of white birch, but coniferous regeneration was unaffected. High deer densities may have resulted in better habitat for it (Cardinal et al. 2012).

In Newfoundland, 68% of mist-netted Boreal Chickadees were captured in natural forests and 32% were in clear-cuts. There was no difference in annual survival rates of birds in natural and clear-cut habitats. Whitaker et al. (2008) concluded that it was resilient to a moderate amount of clear-cutting. In Quebec, Hadley and Desrochers (2008a) concluded that increasing the amount of edge due to clear-cutting did not affect its use of remaining mature forests, even under inclement winter conditions. Movements may be restricted in regenerating forests after clear-cutting during adverse weather. In the Boreal Forest Region with particular reference to Ontario, it decreased in abundance when 30%, 50%, or 70% of trees were removed (Vanderwel et al. 2009). In Ontario in the Canadian Shield, there was no difference in its abundance in early and mid-successional clear-cuts compared with similarly aged stands after fire. It was equally abundant in mid-successional and mature stands but significantly less abundant in early successional than mature stands (Zimmerling et al. 2017).

The Black-capped Chickadee does not appear to compete for nest sites but its presence may reduce Boreal Chickadee densities because the 2 species apportion trees and food resources where they coexist. In Newfoundland, the density of Boreal Chickadees on an island without Black-capped Chickadees was significantly greater than the combined density of both chickadee species on the mainland (McLaren 1975; Vasallo and Rice 1981).

In Alberta, the Boreal Chickadee was significantly more abundant at seismic lines than in adjacent forest interior. There was no difference in its abundance at pipelines and well pads than in forest interior adjacent to these facilities (Bayne et al. 2016).

Price (2004) predicted that the Boreal Chickadee might disappear as a breeding species in southern Ontario if the average summer temperature increased by 2°C. DesGranges and Morneau (2010) concluded that it was not very sensitive to climate change in Quebec. In the Boreal Forest Region of Quebec and Labrador, DesGranges and LeBlanc (2012) determined that the Boreal Chickadee was associated with stands having relatively high summer temperatures and high summer precipitation.

Status

The Boreal Chickadee has always been a widespread breeder throughout the Hudson Bay Lowland and the Boreal Forest Region, with an isolated population in Algonquin Park. It is also present in the Great Lakes–St. Lawrence Forest Region north of Lake Superior. McIlwraith (1894) stated that it occurred in the Hudson Bay area and that it might be present in the districts of Muskoka and Parry Sound. Baillie and Harrington (1936) concluded that it was resident from about latitude 46°N to Hudson Bay. The southern limit of the general population was in the central portions of the districts of Algoma, Sudbury, and Timiskaming. Bailey and Hope (1947) found it regularly at Chapleau, but concluded that it was absent in southern Sudbury District. James (1991) considered the Boreal Chickadee an uncommon permanent resident southward to the Sudbury area, and rare to uncommon in the Algonquin Highlands.

The second atlas demonstrated that there had been no change in the range or probability of observation of the Boreal Chickadee since the first atlas. It was most abundant in the northern Boreal Forest Region and southern Hudson Bay Lowland (McLaren in Cadman et al. 2007).

Despite logging and forest fires, distribution of the Boreal Chickadee in northern Ontario is probably similar to presettlement times. Long-term (1970-2021) population trends determined from the Breeding Bird Survey indicated annual decreases of 1.5% in Canada and 1.44% in Ontario. The short-term (2011-21) trends were annual decreases of 0.933% in Canada and 2.64% in Ontario. Results were of low to medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

The family remains together in the territory for at least 2 weeks after fledging. Adults feed the young less and less during this period, and fledglings leave the territory 3 weeks after they leave the nest (Ficken et al. 2020).

MIGRATION

The Boreal Chickadee is predominantly a permanent resident that remains on its breeding territory in winter. Short-distance migratory movements occur in some parts of its range. It exhibits regular migration patterns in northern Minnesota, northern Michigan, Saskatchewan, and Alberta. In the Yukon, no significant seasonal movements occur, although there may be withdrawal from the northern portions of its range during extreme cold. In British Columbia, it is nonmigratory even in the north, but populations at high altitudes may move to lower areas in winter. To further confound migration patterns, juveniles form flocks and wander shortly after fledging, and it periodically irrupts considerably south of its normal range. Postbreeding movement appears to occur in the first half of September in the Moosonee area (Bent 1946; Campbell et al. 1997; Dunn and Tessaglia-Hymes 1999; Ficken et al. 2020; Sinclair et al. 2003; Wilson and McRae 1993).

Irruptions occur in autumn and birds may remain south of their breeding range much of the winter or until spring. Southward irruptions are probably a response to low food supplies; most birds that move southward are less than 1 year old. Irruptions between 1964 and 1972 corresponded to irruptions by 8 pine-seed-eating species, suggesting that irruptions may be associated with fluctuations in pine seed crops. Irruptions occur in different areas in different years. All Boreal Chickadee irruptions are associated with Black-capped Chickadee irruptions, but not all Black-capped Chickadee irruptions contain Boreal Chickadees. In New York, irruptions occurred at intervals of 2-7 years, and averaged every 3.8 years from 1950 to 1981. Minor irruptions occurred there at intervals of 2-3 years, while Christmas Bird Count (CBC) data indicate major irruptions every 4-6 years. In some areas, large irruptions occur every 6-8 years. Frequency of irruptions is only about half that of the Black-capped Chickadee (Bent 1946; Dunn and Tessaglia-Hymes 1999; Ficken et al. 2020; Root 1988; Yunick 1984).

In northern Ontario, movements associated with irruptions may start in mid- to late September. On 18 and 25 September 1938, a large southward movement was observed at Moosonee (Manning 1952). On 30 September 1947, a flock of 150-200 was seen moving southward along the Kesogami River near Hannah Bay. None had been seen there the previous 4 days. Several were seen the following week, but only in groups of 2 or 3 (Hewitt 1948). Irrupting birds may appear in southern Ontario from mid- to late October, but the peak is in November; occasionally birds do not appear until December or January. Birds often disappear from the south in January, but many stay much longer, particularly following large irruptions. In most irruption years, numbers start to decline after November. After a large irruption, there may be a weak return flight from mid-April until early May, with occasional stragglers to the end of May (Bent 1946; Ficken et al. 2020; Weir 2008; Yunick 1984).

Resident Boreal Chickadees and those that regularly migrate short distances frequent the same habitat types as they do during the breeding season. Irrupting birds occur in a much wider range of habitats, but still prefer areas with coniferous cover (Campbell et al. 1997; Dunn and Tessaglia-Hymes 1999; Ficken et al. 2020; Yunick 1984).

During the winter of 1951-52, 97 were recorded in the Hamilton area; 118 were observed in the 1972-73 invasion. Extreme dates of occurrence were 1 October to 25 April (Curry 2006).

WINTER

In winter, the Boreal Chickadee (except for irrupting birds) remains mostly in boreal coniferous habitat identical to that used in the breeding season. In Alaska, it has spent the winter in dense willows along a river and in willow and alder copses in addition to spruce–white birch forests (Bent 1946).

In winter near Quebec City, the Boreal Chickadee used mature forests more frequently than regenerating areas or open areas; regenerating areas were used more than open areas. It preferred mature forest stands and avoided young successional forests and open areas, although flocks frequently spent time in regenerating areas. Hadley and Desrochers (2008a) concluded that forestry practices result in substantial reduction of optimal Boreal Chickadee wintering habitat. Declines in its population may be due to loss of high-quality wintering habitat. Flocks showed no response to forest edges in mature forest stands. In regenerating forests 4-7 m tall, flocks mostly used edges near

mature forest and were significantly closer to both open edges (41 m) and mature forest edges (11 m) than would be expected from a lack of response to edges. On the coldest and windiest days, flocks did not avoid exposed edges of mature forest, but avoided edges of regenerating stands and were found disproportionately more along edges between mature and regenerating stands (Hadley and Desrochers 2008b).

Brotons (2000) stated that the Boreal Chickadee exhibited winter territoriality, but provided no explanation. Winter flocks form soon after the young fledge and persist until spring when pairs break off from the flock to breed. In autumn, it forms flocks with Black-capped Chickadees, warblers, Red-breasted Nuthatches, Golden-crowned Kinglets, White-winged Crossbills, and occasionally woodpeckers. The average flock includes 6 Boreal Chickadees (range 4-10). As winter progresses, flocks become composed primarily of Black-capped and Boreal chickadees and Golden-crowned Kinglets, with Black-capped Chickadees more numerous than Boreal Chickadees. One flock that was observed many times over a winter in Algonquin Park had 6-7 Black-capped Chickadees and 2-3 Boreal Chickadees. This indicated flock cohesion and possibly that the flock maintained a winter home range. Birds that irrupt southward exhibit no winter territoriality or site fidelity. These individuals wander widely. Birds that find a feeder seldom stay more than 1 or 2 days, although some become associated with a feeder during winter (Bent 1946; Dunn and Tessaglia-Hymes 1999; Ficken et al. 2020; Yunick 1984).

Near Quebec City, the average size of 85 Boreal Chickadee winter flocks was 4 chickadees (range 3-8). Some flocks contained Black-capped Chickadees or Red-breasted Nuthatches; some contained all 3 species. Boreal Chickadee flocks were cohesive units and occupied a mean home range of 14.7 ha (range 7.9-30.4 ha) with a mean core area of 2.3 ha (range 1.0-5.8 ha). Home range size was not affected by flock size. Home ranges contained 61% mature forest (range 21-94%), 23% regenerating forest (range 0-79%), and 15% open habitat (range 0-43%). Smaller home ranges contained higher proportions of mature forest; flock home range sizes increased with increasing amounts of open habitat. Flocks with larger home ranges had several distinct core areas within the home range. Those with small home ranges used their home range more evenly (Hadley 2006; Hadley and Desrochers 2008a).

Boreal and Black-capped chickadees often forage together in mixed-species flocks. In Michigan, the Boreal Chickadee foraged in only 3 conifer species with 76% of foraging occurring in black spruce and lesser time spent in white spruce and tamarack. The Black-capped Chickadee foraged more widely in 6 conifer and 3 deciduous tree species. The Boreal Chickadee spent 36.5% of its time foraging at the top of trees compared with 4.5% for the Black-capped Chickadee; the 2 species foraged at similar rates in other vertical zones. The niche overlap of the species was 67.6%, higher than expected. The 2 species eat similar foods but competition is reduced due to the abundance of food resources, the fact that foraging overlaps in only 3 species of conifers, and that Boreal Chickadees use the crowns of these conifers significantly more than Black-capped Chickadees (Gayk and Lindsay 2012).

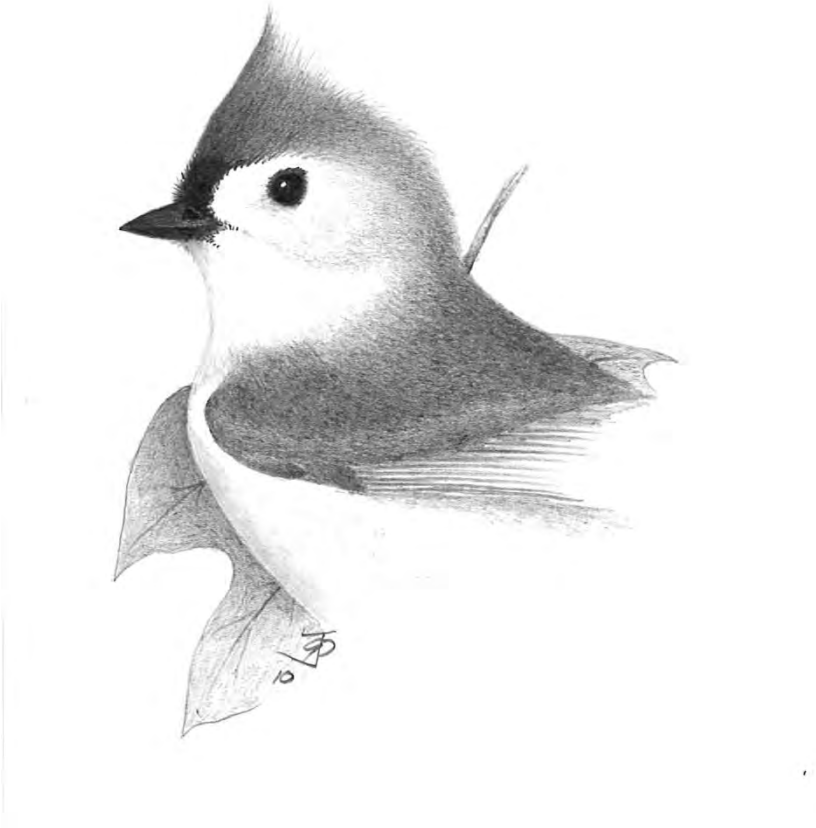
In winter, the diet is dominated by seeds, especially those of conifers, and hibernating insects, pupae, or egg masses. The Boreal Chickadee has been observed feeding on goldenrod and aster stems, on gray birch seed cones, and on red cedar berries in winter. It is a common visitor to winter

bird feeders in Alaska and in the Boreal Forest Region, and visited trappers' cabins for handouts long before winter bird feeding became fashionable. It rarely visits urban feeders, but appears in small flocks of usually 1-3 birds at feeders in rural and natural areas. Favourite foods at feeders include suet, black oil sunflowers, possibly hulled sunflowers, peanut butter mixes, and bird puddings. It occasionally eats sunflowers and baked goods. At 1 Thunder Bay feeder, it fed mostly on doughnuts and raisin bread, although suet and sunflowers were available (Bent 1946; Dunn and Tessaglia-Hymes 1999; Whittam 2000).

CBC data for 1970-2021 indicated that the Boreal Chickadee population decreased annually by 2.24% in Ontario; it decreased by more than 4.40% 2009-21 (National Audubon Society 2022).

Tufted Titmouse

Baeolophus bicolor

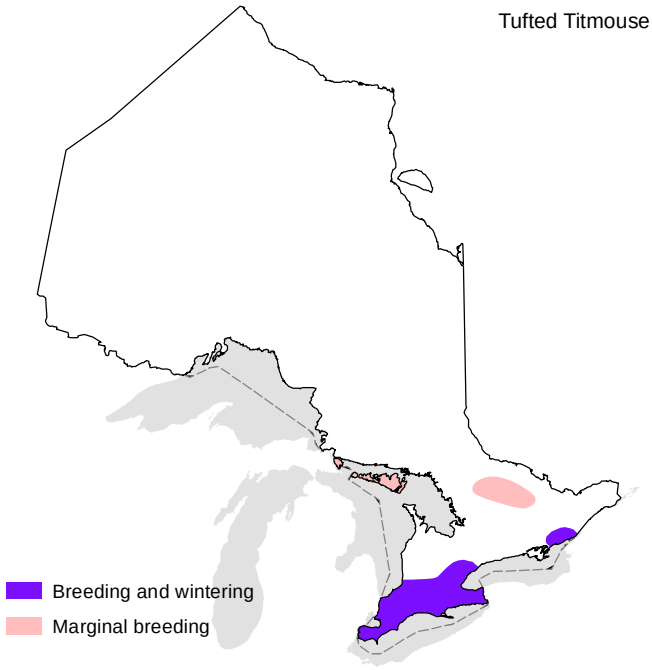


BREEDING SEASON

Habitat Requirements

The Tufted Titmouse has nested in deciduous and mixed woods, on a wooded sand dune, and in a residential garden in Ontario (Peck and James 1987).

It prefers deciduous woodlands, but also nests in mixed woods, and avoids coniferous stands. It occasionally nests in swamps, orchards, parks, on golf courses, and in older urban and suburban areas. Preferred habitats contain tall vegetation with a large number of tree species and a dense canopy. In Pennsylvania, it preferred dense undergrowth near water, but most studies found it in woodlands with little understorey. Occasionally it nests in very open, grassy areas with a few scattered trees. It greatly prefers forest edge to forest interior, and tends to prefer oak-hickory over maple-beech forests. More mature stands are preferred, and it may decline by 50% after forest harvesting. In New Jersey, it preferred second growth, wet disturbed areas, and climax logged areas. It first appeared in fields 40 years after agriculture was abandoned, when they were densely covered with saplings 2-26 cm diameter at breast height (DBH) and the field borders had become densely



wooded (Austen et al. 1994; Bent 1946; Doherty and Grubb 2000; Fitch 1958; Gillespie 1930; Graber and Graber 1963; Noon et al. 1979; Pogue and Carter 1995; Pravosudova et al. 2002; Ritchison et al. 2020; Suthers 1988; Temple et al. 1979).

There are conflicting reports about whether the Tufted Titmouse is a habitat specialist or generalist, or an area-sensitive species. In Tennessee, Anderson and Shugart (1974) could not characterize its habitat requirements with any of the variables they tested and concluded that it was a habitat generalist. In Michigan, Inman et al. (2002) concluded that it was a habitat generalist. In Texas, its abundance was positively correlated with vegetation height, number of tree and shrub species, canopy closure, foliage density at 7 m to above 20 m, percent coverage by hardwoods 5-32 cm DBH, and number of tree stems larger than 32 cm DBH. It was negatively correlated with percent coverage by pines 5-16 cm DBH. It was in a guild that preferred fairly mature pine-hardwood forest (Conner et al. 1983). In the Pennsylvania Appalachians, it was more likely to occur in stands that were not old growth. It occurred in 27.3% of old-growth forests compared with 80.9% of Pennsylvania forests and 64.1% of forests on the Appalachian Plateau (Haney 1999). In the mid-Atlantic states, its presence was positively associated with forest size, percent canopy cover, and canopy height, and negatively associated with slope, percent forest cover within 2 km, presence of coniferous trees, moisture gradient, and the number of standing dead trees larger than 3 cm DBH per ha (Robbins et al. 1989). Its presence was associated with larger woodlands in Pennsylvania (Keller and Yahner 2007). In Indiana, it was most abundant in forests with more than 90% canopy closure but it was not significantly more abundant than in areas of densely regenerating oak saplings. There were no significant differences in its abundance in savannahs, woodlands with 50-90% canopy closure, or regenerating oak areas. It was least abundant in open areas with 20% or less canopy closure. Its abundance increased with tree density. Its probability of occurrence was about 25% when trees were widely scattered compared with 100% at 500-600 trees per ha (Grundel and Pavlovic 2007a, 2007b). In southern and central Illinois, it occurred in a variety of habitats including upland and floodplain forests, savannah, and low-density developed areas. In the northern portion of the state, it was found only in developed areas (Walk et al. 2011).

In a Connecticut woodlot over a 59-year period, there was a progressive shift to larger trees, a sparser shrub layer, and a less diverse tree canopy dominated more by oaks and maples as a result of a severe decline in hemlock. There was no change in the abundance of the Tufted Titmouse (Buchanan et al. 2016).

In Ohio, the titmouse prefers forest fragments, yet the number detected per Breeding Bird Survey (BBS) route increases with increasing forest cover (Pravosudova et al. 1999; Ritchison et al. 2020). In Maryland, its frequency of detection on BBS routes increased with forest size. Robbins (1979) concluded that a minimum of 4 ha was required to maintain a viable population. In the mid-Atlantic states, its maximum probability of detection was in forests 52 ha in area, but the probability of detection did not decline to 50% until woodlot size was only 0.5 ha. It greatly preferred isolated forests (less than 33% forest coverage within 2 km) to moderately isolated forests (33-66% coverage; Robbins et al. (1989). In southern Wisconsin, Mossman and Hoffman (1989) concluded that it required a minimum forest size of 32.4 ha to maintain a population. It was rare there at the time that this study was completed. In Missouri, Hayden et al. (1985) considered it area sensitive and estimated that it required a minimum forest size of 1.2 ha. This suggests that it actually is not area sensitive there. In Ohio farmland habitat, it is uncommon in forest fragments smaller than 2 ha (Ritchison et al. 2020). In South Carolina, it was not area sensitive. It was significantly more abundant in small, fragmented woodlots surrounded by agricultural lands than in same-sized woodlots surrounded by plantations. Probabilities of detection in field-surrounded versus plantation-surrounded woodlots of different sizes were: 0.5 ha, 82% and 47%; 1.0 ha, 87% and 55%; 2.5 ha, 94% and 75%; 5.0 ha, 98% and 92%; and 10 ha, 100% and 99%, respectively. Kilgo et al. (1997) concluded that it was an edge species and that woodlots surrounded by agriculture were all edge and better habitat than those surrounded by plantations. In Ohio, it occurred in 100% of isolated woodlots 3-4 ha in area, in 86% of 2-3-ha woodlots, in 40% of 1-2-ha woodlots, and in 12.5% of woodlots smaller than 1 ha. This study was done in late autumn so results may not have been representative of the breeding season (Ritchison et al. 2020). Keller et al. (1993) found that its probability of detection was unrelated to forested width along rivers. Lindell et al. (2007) reviewed studies that determined edge preferences of the Tufted Titmouse. In 2 studies, it showed no preference for edge or interior; a third study found that it actively exploited edge. In Tennessee, there were significantly more territories close to edge than distant from it (Kroodsma 1984).

In summary, the Tufted Titmouse is a bird of mostly deciduous forests and occasionally mixed forests that prefers forest edge to interior. It may also nest in sparsely treed areas. It is not area sensitive and appears to prefer isolated woodlots rather than those in more forested landscapes. There is a possibility that it prefers larger woodlands at the periphery of its range than in its core range. It preferred areas that were 71-94% forested in New York (Cunningham and Johnson 2019).

One Ontario nest was in a leaning pipe stuck in the ground but the rest were in natural cavities in living trees. Two were in maple trees, one in an oak, and one in an apple tree. Nests in natural cavities were 2-16.8 m from ground, mostly 9-13.5 m up. The nest in the iron pipe was 30 cm below the top of the pipe, which was 1.5 m up (Peck and James 1987). A nest on Manitoulin Island was in a nest box (Peck and James 1997).

The Tufted Titmouse does not appear to excavate its own nest, and relies on cavities excavated by other birds or natural cavities in trees; it occasionally nests in fence posts. It readily uses nest boxes, but prefers tree cavities. Unusual nest locations include cavities in the sides of old large bird nests, in a tin newspaper box at a roadside, in metal pipes, and in Spanish moss. Natural tree cavities are those created by knotholes or lightening strikes, or excavated by woodpeckers. Nests have been

reported in a variety of tree species, mostly deciduous, including beech, red and white oak, sycamore, pine, hemlock, apple, mulberry, red and sugar maple, white ash, chestnut, white elm, dogwood, birch, and black locust. Most nest trees are large with an average DBH of at least 30 cm and occasionally as large as 38 cm. In Missouri, average tree diameter at the nest was 24.8 cm, but in other areas tree diameters were 10-12.5 cm. Preferred cavities are in sound wood with little evidence of decay. The optimum cavity entrance is 4.4-5.6 cm in diameter with a minimum of 3 cm. Nest heights of 0.6-29.6 m have been reported, mostly about 10 m or higher (Bent 1946; Brown et al. 1984; Eshbaugh and Eshbaugh 1979; Evans and Conner 1979; Lancaster et al. 2004; Laskey 1957; Middleton 1949; Pravosuodova et al. 2002; Ritchison et al. 2020; Smith 1985). It readily accepted nest boxes in pine stands in Florida. There was a slight population increase as a result of the addition of nest boxes (Miller 2010).

The female starts roosting in the nest cavity when the first or second egg is laid, and continues to do so until the young are 12-13 days old (Brackbill 1970; Laskey 1957). In autumn and winter, both sexes roost in woodpecker holes and in natural cavities in posts, snags, and trees (Bent 1946).

In Kansas, the average breeding territory was 1.7 ha (Fitch 1958). In Michigan, 14 breeding territories averaged 4.2 ha (range 3.2-5.0 ha). The titmouse may be able to tolerate smaller territories or home ranges in isolated woodlots. In Missouri, 4 dominant pairs had average breeding territories of 3.3 ha (range 2.9-3.6 ha); 4 subordinate pairs had average territories of 3.4 ha (range 3.1-3.8 ha). The mean distance from the centre of the winter flock territory to the centre of dominant pairs' breeding territories averaged 17.8 m (range 12-23 m) compared with 555 m (range 428-675 m) for subordinate pairs (Brawn and Samson 1983).

Natal philopatry is variable and complicated because 1 young frequently remains with the adults over winter and becomes a helper at the nest in the next breeding season. In Tennessee, 1 young helper at a nest returned to the same winter feeder for an additional 6 years, usually returning in late summer with 1 or 2 fledglings; occasionally one of these remained with him over winter. Distances of first nests from the natal area may be in the order of 0.5-1.2 km. Most authors assumed that a winter trio of birds represents a pair and 1 of its offspring. But in small, isolated woodlots in Ohio, only 5 of 12 trios were families. Therefore, studies that report the distance of a bird's first nest from its winter territory may include birds hatched within the area and those that dispersed to the area the previous autumn. Young that dispersed from the vicinity of the natal area travelled a median distance of 75 km in Pennsylvania. Once a bird has bred in an area, it tends to have very high site tenacity. There are records of birds using the same nest box or cavity for 6-7 years. In Missouri, some birds nested and then were absent for 1-5 years before returning to breed again, suggesting that some local movement occurred between nesting seasons. Of 632 bird-years, 49 birds (7%) were missing for a year or more before returning. Forty were absent for 1 year, 4 for 2 years, 2 for 3 years, 2 for 4 years, and 1 for 5 years. Of 112 titmice observed in 3 or more years (making a skip possible), 27% skipped 1 or more years (Brackbill 1970; Brawn and Samson 1983; Davis 1978; Ekman 1989; Elder 1985; Gillespie 1930; Laskey 1957; Middleton 1949; Pravosudova et al. 1999; Ritchison et al. 2020; Tarbell 1983).

Limiting Factors

Eggs are most likely to be present in Ontario nests from mid-May until the third week of June (Peck and James 1987). Pair formation of juveniles may occur as early as the end of July of their first year and continues until January or February. Pairs abandon the winter flock in February or early March and establish a breeding territory. In Oklahoma, about 2 weeks elapsed between the start of nest building and laying. In Maryland, 3 nests took 6-11 days to build and laying began 3 days after they were complete. Eggs are laid at the rate of 1 a day. Incubation starts with laying of the last or penultimate egg. The incubation period is 12-14 days, but mostly 13 days. Young fledge when they are 15-18 days old, but mostly at 17-18 days (Bent 1946; Brackbill 1970; Brawn and Samson 1983; Laskey 1957; Nice 1933; Pogue and Carter 1995; Ritchison et al. 2020; Samson and Lewis 1979).

Usually only 1 brood is raised a year. Circumstantial evidence in Maryland suggested 2 cases of double broods, but these may have been renests. One banded bird in Pennsylvania nested 7 years, and produced 2 broods in 2 of those years. Two Ontario nests contained 3 and 4 eggs, but these probably were not full clutches. Most clutches contain 5-7 eggs. The overall average clutch size is 5.7 eggs, the median is 6, and the range is 3-9 eggs (Bent 1946; Brackbill 1970; Laskey 1957; Middleton 1949; Peck and James 1987; Ritchison et al. 2020).

The age at first breeding is 1 year. The Tufted Titmouse is monogamous and many birds pair for life. Divorce is common and some birds may have 2-5 mates during their lifetime. In 7 Ohio broods, 3 of 29 nestlings (8.8%) were unrelated to their behavioural father. In these cases, the male was a close relative of the female (Brackbill 1970, 1987; Laskey 1957; Provosudova et al. 2002; Ritchison et al. 2020; Short 1933).

The Tufted Titmouse forages by searching bark crevices, exploring dead leaves in hanging clusters or in squirrel nests, and by hammering with the bill to open seeds and acorns. Foraging techniques include 63% gleaning, 21% hanging and gleaning, 3% hovering and gleaning, 8% probing, 2% pecking, 1% scratching and gleaning, and 1% turning leaves. It rarely hawks moths from the air. In Ohio, it foraged 56% of the time on trees, 17% on shrubs, and 27% on the ground. Of tree foraging, 4.4% occurred on the trunk, 12.1% on primary branches, 40.5% on secondary branches, and 43.0% on tertiary branches. In a laboratory experiment, titmice were allowed to forage freely on branches 0.5, 1.0, 2.5, 5.0, 10.0, and 20.0 cm in diameter. All foraging occurred on tops of branches and 2.5-cm diameter branches were used considerably more than expected. Although it occasionally forages at the extremity of a branch or at the trunk, most time is spent between these extremes. Titmice feed mostly in the lower and interior areas of trees, but tend to forage in taller trees in spring and summer. During the breeding season in Illinois, foraging occurred mostly in the shrub (0-5 m) and subcanopy (6-10 m) foliage layers, with 24% of foraging activity at 0-5 m, 52% at 6-10 m, 12% at 11-15 m, and 12% above 16 m. Foraging occurred in hickory more than expected; no foraging occurred in sugar maple and red elm. Tree species preferred for foraging, in order of preference were shellbark hickory, white elm, red maple, silver maple, and bitternut hickory. In order of decreasing avoidance, pumpkin ash, black gum, blue beech, green ash, Manitoba maple, sycamore, and pin oak were used less than their availability. Three preferred species, shellbark hickory, silver maple, and bitternut hickory were uncommon and ranked 11th, 18th, and 19th in abundance, respectively. Pumpkin ash and blue beech were highly avoided yet ranked 2nd and 7th

in abundance (Anderson and Shugart 1974; Bent 1946; Brackbill 1950b; Dickinson 1969; Gabbe et al. 2002; Hartung and Brawn 2005; Pierce and Grubb 1981; Ritchison et al. 2020).

The diet of 186 adults consisted of 66.6% animals and 33.4% vegetable matter. Caterpillars represented over half the animal food, and caterpillars and wasps comprised over half of all food. Ants and other hymenopterans constituted 12.5% of food; beetles totalled 7.1% (mostly weevils). Other animals consumed included stink bugs, treehoppers, scale insects, katydid eggs, cockroach eggs, spiders, and a few snails. It eats soft mast in late summer and early autumn. Hard mast is the principal food item from August until February. It eats some corn, as well as raspberries, blackberries, dogwood berries, Virginia creeper berries, honeysuckle berries, tulip-tree seeds, giant ragweed seeds, grapes, cherries, strawberries, elderberries, hackberries, blueberries, huckleberries, mulberries, juneberries, alder seeds, sumacs, and poison ivy. Acorns and beechnuts comprised 23.4% of the total diet and constituted 95% of the November diet. In late summer and early autumn, juveniles may congregate in oak-hickory woods or stands where beech is common. Beechnuts are a preferred autumn and winter food. In Illinois, acorns from different species of oaks were provided at a feeder. The Tufted Titmouse preferred acorns from white and pin oaks to those of black oak. It was 19.0 and 6.2 times more likely to select pin and white oak acorns, respectively, than black oak acorns. Black oak acorns are intermediate in size but have a harder shell than the other 2 oaks. It caches acorns in areas where they may germinate and may be an important agent for white oak dispersal. In Missouri, a titmouse caught and ate a salamander. One captive bird picked at the carcass of a dead titmouse and ate considerable flesh (Beal et al. 1916; Bent 1946; Dance et al. 2012; Gillespie 1930; Hendricks and Hendricks 1985; Richardson et al. 2013; Ritchison et al. 2020; Stewart 1955).

The Tufted Titmouse is rarely parasitized by the Brown-headed Cowbird. Bent (1946) reported 4 cases of parasitism and Lowther (1997) reported another 2 incidences from Illinois. Clapp (1995) reported a case of parasitism in Virginia. This nest was in a box designed for the Great Crested Flycatcher. Although cowbird eggs have been found in titmouse nests, there appear to be no records of cowbirds successfully fledging.

Cold spring weather may affect nesting success. In Oklahoma, some eggs froze in nest boxes (Pogue and Carter 1995).

Kilpatrick et al. (2007) determined that the Tufted Titmouse was vulnerable to the West Nile virus and that significant effects on populations had been identified due to the virus. The titmouse may be resident in suburban areas where it is most likely to come in contact with the vector. Approximately 80-90% of the Windsor population was decimated in 2002 with an outbreak of this virus (Read in Cadman et al. 2007).

In New Jersey and Pennsylvania over a 15-year period, hemlock declined from 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The Tufted Titmouse responded favourably to hemlock decline and increased, possibly due to the greater prevalence of snags (Toenies et al. 2018).

Harrison and Kilgo (2004) tested the effects of retaining patches of bottomland hardwood forest within traditional clear-cuts. Titmouse densities were higher in clear-cuts where patches were left.

Robinson and Robinson (1999) created small (0.02-0.4 ha) openings in contiguous forest in Illinois. There was no difference in numbers of titmice in cut and uncut forests.

In Delaware, browsing by white-tailed deer had no effect on the Tufted Titmouse. It was equally abundant in areas of low, moderate, and high deer densities (Tymkiw et al. 2013).

In New York, Damsky and Gall (2017) played Tufted Titmouse mobbing calls and mobbing calls accompanied by anthropogenic noise, including traffic with occasional airplane and lawnmower noise. The addition of noise resulted in an approximately 80% decrease in the number of titmice approaching the speakers; there was no effect on foraging behaviour. The decrease in response to the mobbing call as a result of noise was considered a concern. These calls are given in response to a threatening stimulus. If birds are slow to respond to the warnings, they may be unable to take advantage of them.

Price (2004) predicted that the range of the Tufted Titmouse could expand in southern Ontario if the average summer temperature increased by 2°C.

Status

The Tufted Titmouse is a recent arrival to Ontario. The first provincial record was in May 1914 when one was observed at Point Pelee. The first summer record was at Fisher Glen in Norfolk County in 1932. Adults with young were seen in Hamilton in 1936, and the first undocumented nest was reported from Sarnia in 1953. Nesting was officially confirmed in 1971 when a young bird was photographed leaving a Port Colborne nest. There was an influx of titmice to the Hamilton area in autumn 1961 and it has been a rare resident in that area ever since. Numbers of breeding pairs continued to increase in the province and by the first atlas it was estimated that there were 26-40 pairs. The greatest concentrations occurred in Niagara Region with scattered sightings around Lake Simcoe, Rondeau Provincial Park, Essex County, Sarnia, and Walpole Island (Austen et al. 1994; Baillie 1960; Currie in Cadman et al. 1987; Curry 2006; Peck and James 1987). James (1991) considered it a rare permanent resident in the Carolinian Forest Region with wanderers north to Lake Simcoe. The first Elgin County breeding record was in 1990 and it is now a rare and regular breeder there (Lancaster et al. 2004). A nest in a bird box on Manitoulin Island was the most northern breeding record at the time (Peck and James 1997), but was surpassed by a nest found in Algonquin Provincial Park in 2004 (Peck 2005b).

The second atlas demonstrated that the range of the Tufted Titmouse had expanded since the first atlas. During the second atlas, its range included the Carolinian Forest Region, with numerous gaps in distribution within this area, and a few scattered records in the Great Lakes–St. Lawrence Forest Region south of the Canadian Shield. It was most numerous and widespread in Niagara Region, with other concentrations along the shoreline of Lake Erie, and in Chatham-Kent, Essex, and Lambton, where it was not encountered during the first atlas. There were a few records from eastern Ontario; these birds may have originated from the expanding New York population. Its probability of observation increased almost 5-fold from the first atlas. It was recorded in 21 squares during the first atlas and in 99 during the second. Numbers increased steadily in the Windsor area beginning in the mid-1980s, but 80-90% of the population was killed during the 2002 West Nile virus outbreak.

This population appears to be recovering slowly. The current distribution of the Tufted Titmouse is very close to that of the pin oak in Ontario (Read in Cadman et al. 2007).

The Tufted Titmouse has experienced a widespread northward range expansion. It was first observed in Massachusetts and Maine in the 1950s, but it is now well established in New England. The first records in Wisconsin and Michigan were in the early to mid-1940s and it has since become well established in the southern portions of these states. The northward range expansion appears to be due to a combination of climate warming and an increase in winter bird feeding. It is more likely to visit feeders northward, suggesting that feeders are more important in colder climates (Berger and Dunn 1991; Dunn and Tessaglia-Hymes 1999; Hamilton 1994; Ritchison et al. 2020; Root 1988; Van Tyne 1948; Wilson 1999).

Long-term (1970-2021) population trends determined from BBS results indicate annual increases of 4.19% in Canada and 2.1% in Ontario. The short-term (2011-21) trends were an annual increase of 2.11% in Canada and an annual decrease of 0.0454% in Ontario. All results were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young may be fed as late as 36 days after fledging but they start feeding themselves 5 days after leaving the nest. They are fully independent at age 6 weeks. From the end of July into August, the Tufted Titmouse is frequently found in feeding flocks, typically in areas with an open understorey and well-developed canopy. These small flocks persist through winter until the following spring. A typical flock consists of a pair of adults and 1 or more juveniles that may include both their own offspring and unrelated young. Young that disperse from the natal area do so in late August and early September (Ritchison et al. 2020).

In Ohio, both adult and particularly juvenile Tufted Titmice used densely regenerating clear-cuts during the post-breeding season. Early successional habitats may be important because they provide dense cover and an abundance of food (Vitz and Rodewald 2006, 2007). In Missouri, Porneluzi et al. (2014) netted birds during the postfledging period in an oak-pine-hickory forest 2-15 years after it was clear-cut. The Tufted Titmouse exhibited a significant curvilinear abundance trend, increasing gradually to a peak 6-9 years after harvesting and declining thereafter. During years of heavy beech or oak mast crops in Ohio, juveniles congregate in pine-oak and beech groves (Ritchison et al. 2020).

AUTUMN

The Tufted Titmouse is a permanent resident that exhibits no regular migratory patterns. Many birds never move much more than 1-2 km from their natal site. In some years, there may be a slight southward movement in autumn, presumably by juveniles. There are 2 classes of birds: adults and juveniles that have been accepted into a winter flock, and nonterritorial juvenile floaters. The floaters exhibit considerable local movement. In Missouri, 80% of birds arriving at a site in December and 67% of January arrivals were absent in February (Berger and Dunn 1991; Elder 1985; Fitch 1958; Gillespie 1930; Graber and Graber 1963; Hogstad 1989; Ritchison et al. 2020; Van Tyne 1948). In West Virginia, 96 were captured in autumn at a banding station over a 21-year period in an area where the species does not breed. This suggested that birds were dispersing but the movement probably

was not true migration. Northward spring movements have been documented in Connecticut, Massachusetts, Vermont, and New Hampshire.

Although the Tufted Titmouse is typically very sedentary, Post (1979) reported the only known irruption of this species. In New York City in 1978, titmice started to arrive in the last week of September and first week of October. The movement peaked between 10 and 23 October, but birds continued to move through until late November. On the local Christmas Bird Count (CBC), 135 were reported compared with the previous high of 17. Higher than normal numbers also occurred in Maine and New Hampshire.

During autumn in Pennsylvania, the Tufted Titmouse was most abundant in mature forest habitats. It was significantly more abundant in suburban forests, followed by forest-agricultural edge, forest edge, shrub-sapling-stage forest, forest interior, and pole-stage forest (Rodewald and Brittingham 2002). It was associated with larger woodlands in spring and autumn in Pennsylvania (Keller and Yahner 2007).

WINTER

Winter habitat is similar to that used the rest of the year, but movements among habitats may occur during severe winter conditions. Portions of the winter flock territory are typically used as a breeding territory by the dominant pair. In Illinois, Tufted Titmice stayed more in woody habitats during winter than chickadees (Graber and Graber 1963). Root (1988) noted that it occurred only in areas receiving more than 61 cm of rain a year, and that it was most common where there was at least 81 cm of rain. It relies heavily on beechnuts and acorns in winter, so it may be most common in oak-hickory woods and forests where beech is abundant.

In Missouri, the Tufted Titmouse increased with increasing tree density and was most abundant in forests, followed by woodlands and savannahs (Kendrick and Thompson 2013). In Michigan, it was more likely to be found in smaller than large woodlots in winter (Ritchison et al. 2020).

Winter flocks form shortly after juvenile dispersal, usually in late July and August, but occasionally as late as September or October. These flocks remain intact and fairly stable until they break up in February at the onset of the breeding season. A typical flock consists of a pair, or occasionally 2 pairs, and their offspring or unrelated juveniles. Once a flock is established, the membership is stable and no new birds are accepted, even if some of the regulars die. Winter flocks usually consist of 2-6 birds and occasionally as many as 8. The sex ratio is usually equal within winter flocks and there is a linear dominance within them. The adult pair is dominant, but all males are dominant to females, and the female mated to the alpha male is the alpha female. Dominance has several advantages: dominant birds arrive at feeders earlier in autumn than subordinates and continue to use feeders longer in spring, dominants may use feeders whenever they wish and obtain more seeds, and dominants select the best area within the winter flock territory for their breeding territory. Occasionally pure juvenile flocks form where there are no survivors from the previous winter. Pairing occurs over the winter and most birds prefer to pair with a bird within the same flock (Brackbill 1970; Brawn and Samson 1983; Condee 1970; Ekman 1989; Fitch 1958; Gillespie 1930; Hogstad 1989; Nice 1933; Ritchison et al. 2020; Samson and Lewis 1979). The Tufted Titmouse is a core species in flocks of other species, and it defines flock movement patterns. It is dominant to

chickadees and affects their foraging behaviour and condition; titmice may steal food from subordinate flock members (Ritchison et al. 2020).

Winter flocks maintain definite home ranges or territories. Birds rarely move out of this area and those that do are usually males that briefly trespass on adjacent winter flocks' territories. In most cases, flocks defend their winter territory and trespassers either retreat themselves or are expelled. Territorial disputes between flocks may be common, especially when food is limited. In 1 area of Pennsylvania where food was abundant, 2 flocks overlapped and showed no signs of aggression. In Ohio, all winter home ranges in 1 area overlapped by 30-50%. Individuals may range throughout the entire flock territory, but many remain in localized areas within the territory. Many shift the portion of the territory that they use from 1 winter to the next; others have very high site fidelity. Flock territories remain fairly constant year to year. Flock territory sizes range from 2.5-17.8 ha, but mostly 5-8 ha. Smallest home ranges were reported from isolated woodlots in Ohio. In these woodlots, pairs accompanied by their first-year offspring occupied larger woodlots (4.5-10.0 ha) than pairs with unrelated juveniles (2.5-5.9 ha; Brackbill 1970; Brawn and Samson 1983; Condee 1970; Ekman 1989; Fitch 1958; Gillespie 1930; Nice 1933; Pravosudova et al. 1999; Ritchison et al. 2020; Samson and Lewis 1979).

In Ohio woodlots, wintering titmice foraged on the ground 27% of the time, 17% of the time in shrubs, and 56% of the time in trees. In trees, 4.4% of foraging occurred on the trunk, 12.1% on primary branches, 40.5% on secondary branches, and 43% in tertiary branches (Ritchison et al. 2020). In winter in Illinois, 45% of foraging time was between 0 and 5 m, 3% at 6-11 m, 16% at 12-17 m, and 40% at 18-23 m. At Pennsylvania feeders at different heights, 32.1% of foraging occurred on the ground, 42.1% at 2 m, 12.4% at 4 m, and 13.4% at 6 m. Foraging at all heights differed significantly from an expected equal distribution (Nastase and Linville 1995).

Favoured natural winter foods are acorns, beechnuts, and lepidopteran cocoons. In New Jersey pine barrens, acorns were the dominant winter food and the Tufted Titmouse was restricted to areas with oaks and acorns (Brush 1989). It is readily attracted to winter bird feeders, where it is slightly less regular and abundant in urban than rural areas. It prefers peanuts and large striped sunflowers at feeders, and usually takes the largest sunflower that is available. Favourite feeder foods include striped and black oil sunflowers, hulled peanuts, hulled sunflowers, safflower, peanut butter mixes, and bird puddings. Infrequent choices include millet, mixed seeds, canary seed, cracked corn, milo, niger, peanuts in the shell or peanut hearts, pet food, raisins, soda crackers, suet, meat scraps, baked goods, and water. At a Pennsylvania feeder, it took sunflowers on 85.6% of visits, corn on 11.8%, and niger on 2.6%. No canary seed or millet was taken (Bent 1946; Berger and Dunn 1991; Dunn and Tessaglia-Hymes 1999; Gillespie 1930; Laskey 1957; Nastase and Linville 1995; Ritchison et al. 2020). Based on 20,246 feeding observations, it preferred black oil sunflowers and whole peanuts in tube or platform feeders (Horn et al. 2014)

About half the items taken from feeders is stored, and around 80% of shelled foods are hulled before storage. Only 1 seed is taken per trip and most are stored within 40 m of the feeder. Height of caches ranged from 0 to 25 m (average 7.8 m). Most seeds (46%) were wedged under loose bark; 15% were placed in furrows, cracks, and rotted areas of trees; 12% in the ground; 12% between 2 branches; and 12% at the end of broken branches and twigs. In trees, seeds were stored on branches

less than 8 cm in diameter and on twigs in trees with diameters greater than 8 cm. In trees, caching occurred equally in the inner, middle, and outer portions of limbs. Seeds were placed more than expected at the tops and sides of branches. Overall, it showed a strong preference for storage on branches, compared with trunks by the White-breasted Nuthatch and twigs by chickadees. Stored food was rarely covered (Laskey 1957; Petit et al. 1989).

In Connecticut, Correia and Halkin (2018) compared the winter habitat and foraging niches of the Tufted Titmouse and Black-capped Chickadee. Compared with chickadees, titmice used canopy foraging locations more evenly, spent less time in shrubs, and spent much more time on the ground (25% of the time for titmice, 1.7% for chickadees). Chickadees spent significantly more time in the outer upper canopy and in shrubs than titmice, and titmice spent significantly more time on the ground than chickadees. In tulip trees, titmice foraged in the outer upper canopy but largely avoided this area in other tree species; seed clusters of the tulip tree tend to be in this area. Both species gleaned small objects on surfaces of all tree species except tulip tree and red pine where feeding was restricted to seeds. Titmice ate pulverized beechnuts and acorns found on forest trails and foraged in conifers much more rarely than chickadees. Titmice actively flipped leaf litter on the forest floor and hopped along decayed logs; no chickadees were observed on the forest floor. The 2 species had different preferences at feeders. Chickadees selected sunflower seeds without shells on 61% of visits; titmice selected safflower on 54% of visits. At feeders, titmice won all challenges against chickadees. The significant differences found in the 2 species' foraging behaviours and seed preferences may mitigate competition.

Cold winds may affect titmouse foraging behaviour and where they occur within small woodlots. In Ohio, titmice were found significantly lower in the canopy as wind velocity increased. As wind increased and the temperature dropped, birds were found significantly further from the windward edges of woodlots. On 62% of visits, titmice were found only in the leeward half of the woodlot. Titmice appeared to be sensitive to winds only when the temperature was below –6°C. On a particularly cold day (–15°C) with a low wind speed of 0.5 m/second, all birds were on the leeward side of the woodlot. Birds may leave very small woodlots when it is cold and windy but dense understorey vegetation near windward edges allows birds to use these areas (Dolby and Grubb 1999).

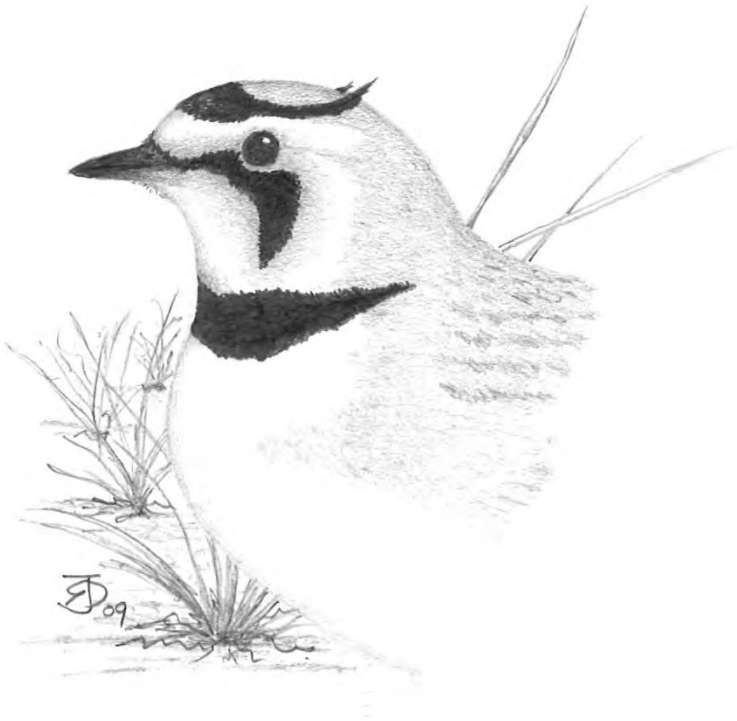
Heavy snow cover may result in changes in habitat use or direct mortality. Because the Tufted Titmouse forages primarily on acorns and beechnuts on the ground, snow cover reduces food availability. Nutritional condition of birds and their survivorship is inversely related to snow coverage. During a severe winter storm in Illinois, titmice appeared to move from bottomland hardwoods to other habitats, especially urban residential areas where none were observed prior to the storm. Numbers in bottomland forests declined by 49.4%; populations in upland forests increased by 6.2%. Some titmice carcasses were observed after the storm (Doherty and Grubb 2003; Graber and Graber 1979).

In Pennsylvania, cycles of abundance were noted, with titmice common some years and scarce others. This was probably due to availability of winter food and the fact that titmice appear to be vulnerable to the depth and length of snow cover, particularly in combination with low temperatures (Gillespie 1930; Overlease and Overlease 1987).

CBC results indicate annual increases in Ontario of more than 12.5% from 1970 to 2019 and 0.25% 2009-19 (National Audubon Society 2022).

Horned Lark

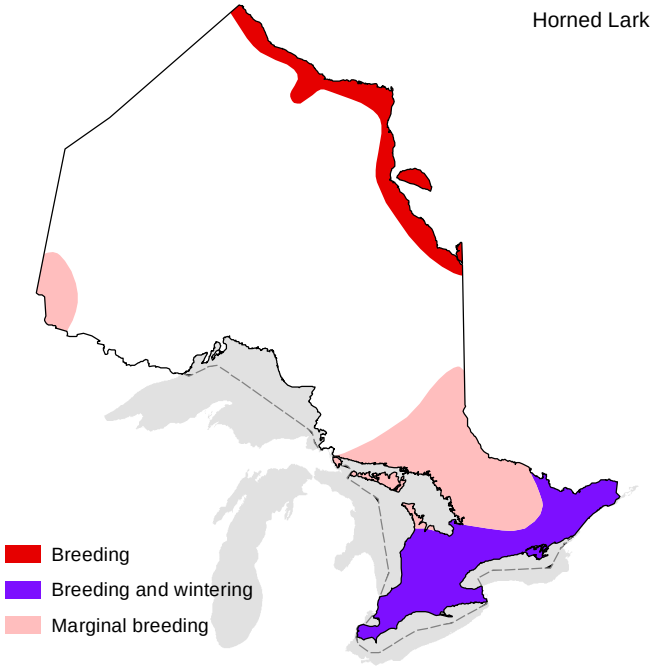
Eremophila alpestris



BREEDING SEASON

Habitat Requirements

In Ontario, the Horned Lark breeds in the tundra along the northern coast in open, treeless areas that are devoid of shrubs and tall forbs. In the south, it breeds predominantly in human-altered areas such as agricultural fields, pastures, large lawns, airports, racetracks, golf courses, gravel pits, landfills, road shoulders, railroad beds, and parking lot edges. Natural areas that may be used for nesting include tundra, short-grass prairies, and sand beaches (Peck and James 1987). In the Kingston area, it occurred mostly in flat agricultural areas and was absent in heavily forested areas (Weir 2008). This is typical of the Prairie subspecies which is found predominantly in agricultural areas in the south. Baillie and Hope (1947) reported a few on a farm in Sudbury District, but did not see it elsewhere, although it previously nested on a golf course in Sudbury. It is seldom found in the Boreal Forest Region because there are few natural areas where there is a permanent lack of trees (Erskine 1977). It is infrequent in northern farmlands, possibly because they are too small. It was almost absent in the heavily forested portions of the province during the first atlas. In forest-dominated landscapes, it is associated mostly with airfields and other large human-made clearings (Hussell in Cadman et al. 1987).



In southern Ontario, the Horned Lark was more abundant on organic than conventional farms, but not significantly. It was significantly associated with spring grain, habitat heterogeneity, row crops, field size, and the number of treatments a field received. Positive nonsignificant associations were with crop biomass and the number of tills in the fields. Negative nonsignificant correlations were with pasture and grassy strips between fields that often supported fences, herbicides, and chemical fertilizers (Kirk et al. 2011).

Elsewhere, the Prairie Horned Lark is largely associated with agricultural lands and other bare habitats. It prefers bare ground, but will nest in very short grasses. In non-agricultural areas, it may nest in shortgrass prairie, bushy flats, deserts, and alpine areas. In agricultural areas, preferred nesting areas are stubble fields, plowed fields, and fall-planted fields. In Iowa, it and the Vesper Sparrow were the only species that nested in fields of row crops. Row crops are excellent habitat in spring and early summer, but become unsuitable later as crops grow. Harvesting of hay and small grains in mid-summer opens up new habitat and it moves to the cut fields. In Illinois, many nested in pastureland in the early 20th century, but by the mid-1950s nesting was confined mostly to crop fields. The former practice of keeping roadsides closely mowed was beneficial to the Horned Lark. By 2000 in Illinois, it nested most frequently in soybean and corn fields, occasionally in grazed grass and mown hay, seldom in wheat and alfalfa, and rarely in idle grass. It nested in Iowa and Illinois cornfields and showed no preference for nesting in the centre of fields or near edges; it avoided edge habitats abutting cornfields. In grazed areas, highest densities are associated with heaviest grazing. In North Dakota, it was more abundant on grassy plots with no shrubs than on shrubby plots, but not significantly. In Washington, it was negatively associated with shrubs and was least abundant in shrubsteppe habitat. It was more abundant in old than new Conservation Reserve Program fields, although the difference was not significant. Other human-made habitats occasionally used for nesting include sod farms, lawns, racetracks, airfields, garden plots, and baseball diamonds. Natural habitats include sand dunes, shorelines with sparse vegetation, shrubsteppe habitats, and shortgrass prairie, which is its native habitat. In grassland, its presence is strongly negatively correlated with vegetation height; it prefers vegetation less than 3 cm tall. Variations in moisture, soil type, elevation, and temperature are tolerated, so vegetation appears to be the controlling factor. Near Churchill, overgrazing by geese created additional breeding habitat (Arnold and Higgins 1986; Beason 2020; Beason and Franks 1973, 1974; Best et al. 1990; Bowles 1900; Campbell et al. 1997; DuBois 1935; Fitch 1958; Graber and Graber 1963; Hurley and Franks 1976; Jehl 2004; Johnson and Gardella 1999; Leighton et al. 2002; Patterson and Best

1996; Pelletier in Gauthier and Aubry 1996; Pickwell in Bent 1942; Rotenberry and Wiens 1980; Skagen et al. 2005; Sutton 1927; Vander Haegen et al. 2015; Verbeek 1967; Walk et al. 2011; Wiens and Dyer 1975; Wiens et al. 1986).

Occupied areas typically have moderate coverage (10-37%) of bare ground. In the Midwest, the Horned Lark's abundance was negatively correlated with percent forb cover, maximum vegetation height, and height of forb and shrub coverage. In Colorado, occupied areas were characterized by 65% coverage by short grasses, 2% coverage by mid-height grasses, 6% sedge coverage, 7% forb coverage, 2% cactus coverage, 0.8% shrub coverage, 17% bare ground, 1% rock coverage, and 7.2 cm mean vegetation height. It was significantly more abundant in upland than lowland grasslands. In North Dakota, it was more abundant in pastures with less than 10% coverage by snowberry and silverberry than in pastures with 30-80% coverage by these shrubs. Highest densities occurred on transects with the lowest height and density of vegetation regardless of the presence or absence of shrubs. Where it was present, maximum vegetation height was taller and the percent coverage by native herbaceous vegetation was greater than where it was absent. Where it was absent, litter depth was greater, cover by shrubs was greater, coverage by aspen within 100 m was greater, and the coverage by Kentucky bluegrass and smooth brome was greater than where it was present. Its presence was strongly tied to the presence of native plants that did not create a deep litter layer. In Saskatchewan, it occupied areas with little or no vegetation or litter. Its occurrence was positively associated with narrow-leaved (less than 5 mm wide) grasses 10 cm or less in height and was negatively associated with vegetation height. Breeding habitat in Missouri cropland consisted of vegetation shorter than 10 cm, no woody stems, and less than 25% coverage by litter that was less than 0.4 cm deep. Areas where cattle and bison created bare ground were also used. In Colorado, it preferred areas with grass shorter than 10 cm but persisted in taller grasses. Its abundance increased with cover of short grasses and litter and decreased with cover of standing dead vegetation, mid-height grasses, and shrubs (Arnold and Higgins 1986; Davis et al. 2021; Dinkins et al. 2002; Grant et al. 2004; Wiens and Rotenberry 1980).

In Saskatchewan prairie habitats, the Horned Lark was not area sensitive. Nonetheless, its abundance increased as the ratio of edge to area decreased. It also increased with increasing distance from the nearest shrub (Davis 2004). In Colorado short-grass prairie habitat, only 6 of 46 nests (13.0%) were found within 50 m of edge. Nest success decreased with increasing patch size. Skagen et al. (2005) concluded that larger patches had a greater suite of predators that resulted in higher predation rates. Ribic et al. (2009) concluded that its occurrence was positively correlated with patch size in South Dakota. In Washington and Oregon, grassland areas used in inland areas were 131-390 ha, but habitat patches as small as 10 ha were used in coastal areas (Beauchesne et al. 2007). In Alberta, its abundance in short-grass prairies increased as distance to crop edge increased. Maximum abundance occurred 2.97 km from crop edges and abundance was 25% of maximum at 0.79 km. It did not avoid roads nor was it attracted to them. Abundance increased with distance to wetlands, indicating that wetlands were avoided. Vegetation density increased near wetlands and croplands and this may have been a factor in their avoidance (Sliwinski and Koper 2012).

The Northern Horned Lark, which nests along the northern coast of Ontario and areas much further north, prefers rocky barrens and sparsely vegetated tundra. It tends to nest in drier upland

areas of tundra, particularly dry sand and gravel ridges which are preferred habitat along the western James Bay coast. Further north, it nests on dry ridges as well as on dry, coastal slopes; on mountain tops, even if they are highly exposed to wind and cold; on old beach lines; in outwash plains; on barren points and islands; in dry meadows; and on areas of bare granite with scattered mosses and lichens. On Bylot Island, it nested in the most exposed areas of uplands that were almost devoid of vegetation. Territories were on hilltops, ridges, old beaches, or frost-heaved areas where most of the surface was gravel. All nests were in the first places that were free of snow in spring. Even in these habitats, it often prefers disturbed areas, nesting near roads through tundra which are used for dusting, roosting, singing, and establishment of territorial boundaries (Bent 1942; Cannings and Threlfall 1981; Drury 1961; Jehl and Smith 1970; Maher 1980; Manning 1952, 1981; Manning and MacPherson 1952; Parmelee et al. 1967; Pelletier in Gauthier and Aubry 1996; Sinclair et al. 2003).

At night, the Horned Lark may dig roost holes and rest in them. In California, this appeared to be a response to cold by desert-nesting birds, with roosts dug at temperatures as high as 10°C. Roosts were often behind vegetation protecting birds from prevailing winds. Roost holes are just large enough (8 x 5 x 4 cm) for a lark to sit with its back almost level with the ground. In areas of soft soil, a new roost may be dug every night but roosts may be used for longer periods in harder soil. Small groups may occasionally roost within a 10-m circle; in 1 instance, there were 5 holes in a 20-cm wide depression (McAtee 1905; Trost 1972).

Ontario nests were on the ground in bare areas, stubble, or short grasses. They were in well-drained, flat areas or on slight slopes or elevations. Most were in depressions dug by the adult, but one was in a horse hoof-track and another was in the centre of a cow chip. Most nests are unconcealed; one was at the base of a tuft of grass, another had a clump of dead grass hanging over it. Some nests were beside a plant, grass clump, shrub, a boulder, driftwood, a person's cap, or a clod of earth. One nest was on a railroad and passed over by a train at least twice a day (Peck and James 1987, 1997).

Other North American nests were similar to those reported in Ontario. The female digs a depression for the nest, usually where the soil is very dry. Occasionally nests are in natural depressions such as cattle hoof-prints, cart ruts, and holes made by dislodged stones. Excavated dirt may be thrown out on 1 side and is often covered with mud pellets, small stones, wheat stubble, cornstalks, corncobs, cow dung, and plant rootlets, apparently in an effort to disguise the diggings. Most nests are protected from the prevailing wind by a tuft of grass, rock, earthen clod, or piece of dead wood. Nests have also been built under stones, large tin cans, boards, and pieces of tarred paper. In Colorado, vegetation offered no protection from wind at many nests and they were almost completely exposed to the sun 55% of the day. Forty percent were adjacent to cow pats and wind velocity within the nest was an order of magnitude less than ambient conditions. High exposure to sun may be beneficial early in the nesting season. At low latitudes, the need for shade results in a preference for northward orientation, mid-latitude nests are oriented predominantly eastward to obtain morning sun and shade in the afternoon, and high altitude nests tend to be oriented southward for maximum warmth all day (Beason 2020; Beason and Franks 1974; Bent 1942; Bowles 1900; Burton 2007; Campbell et al. 1997; Cannings and Threlfall 1981; de Zwaan and Martin 2018; DuBois 1935; Mousley 1916b; Sutton 1927; Verbeek 1967; With and Webb 1993).

Males establish territories upon arrival in spring and defend them until young leave the nest, including the time required to raise more than 1 brood. Birds may occasionally fly outside the territory to feed in neutral areas. Early territories are large then decrease in size as additional birds arrive. When a territorial male disappears and is replaced, territorial disputes heighten for about a week until the newcomer becomes established; final boundaries in these areas are usually similar to initial boundaries. Territory sizes vary depending on habitat type and quality and density of breeding birds. Territory sizes were 0.6-3.1 ha (average 1.6 ha) in Midwest agricultural areas, 0.3-1.4 ha in Colorado shortgrass prairie, 2.3-5.1 ha in heath habitat in Newfoundland (average 3.5 ha), l.5 ha in Wyoming, 0.6-0.8 ha in very disturbed upland tundra at Rankin Inlet and 1.2-2.4 ha in undisturbed tundra, 1.3-2.7 ha in Oregon, 4.9 ha in Kansas, 0.4-1.2 ha on Victoria Island, 0.8 ha in burned grassland in Illinois, and 0.8-6.0 ha in a grain field in New York (Beason 2020; Beason and Franks 1974; Cannings and Threlfall 1981; Fitch 1958; Maher 1980; Parmelee et al. 1967; Pelletier in Gauthier and Aubry 1996; Pickwell in Bent 1942; Verbeek 1967; Wiens et al. 1986).

Camfield et al. (2007) reported that 25% of nestlings banded in British Columbia returned the following year. In Colorado, 6 of 136 juveniles (4.4%) returned to breed (Dinkins et al. 2002).

Adults exhibit strong site tenacity. In Colorado, 65% of a population returned to the same territory, half to the same mate. In British Columbia, 80% of adults returned the following year. Birds on an Illinois golf course continued to nest after it was converted into house lots. They first nested on the stripped lots, then on streetways, then on old sand hazards, and finally on adjacent vegetable gardens until succession crowded them out. A Pennsylvania pair used the same territory several years in a row although road construction for urban expansion reduced its territory to less than 0.4 ha (Beason 2020; Camfield et al. 2007; Pelletier in Gauthier and Aubry 1996; Pickwell in Bent 1942).

Limiting Factors

Eggs have been found in Ontario nests from the last week of March until mid-July, with most present from mid-April until the end of May (Peck and James 1997). Nesting may be initiated when the mean temperature rises above 4.4°C. It takes 1 or 2 days to dig the nest cavity and another 2-4 days to build the nest. The first egg may be laid almost as soon as the nest is complete, or as long as 10-16 days may elapse before the first egg is laid. One female built 2 nests simultaneously. She used one, then finished the other nest and raised her second brood in it. One egg is laid per day, but on Victoria Island, the fifth egg was laid 3 or more days after the fourth. Incubation begins with laying of the last, but occasionally penultimate, egg. The incubation period of Ontario nests was 10-13 days, with 10-14 days reported elsewhere; 11 days appears typical. In most nests, all young hatch in the same day, but hatching may extend over 2 or rarely 3 days when incubation starts with the penultimate egg. Young leave the nest before they can fly at age 8-12 days, mostly 10 or 11 days (Beason 1984; Beason and Franks 1973, 1974; Campbell et al. 1997; Cannings and Threlfall 1981; Drury 1961; DuBois 1935; Maher 1980; Parmelee et al. 1967; Peck and James 1987; Pickwell in Bent 1942; Verbeek 1967; With and Webb 1993).

Egg dates in Ontario and Quebec suggest double brooding, but this has yet to be confirmed. In most locations, the Horned Lark raises 2 broods annually, and possibly 3 in southern areas. Only 1 brood is laid at high altitudes in Wyoming in the north. On Victoria Island, egg dates suggested some double broods; double broods have been documented in the more northern areas of British

Columbia. Renesting is common if a clutch is lost, often within 2 days in the south and in 4-8 days in Newfoundland. In Quebec, the cavity for a second nest was excavated the day after the first clutch was collected. Second clutches are initiated 4-7 days after successful nests. Clutches of 2-6 eggs have been reported in Ontario, mostly 3 or 4 eggs. Clutch sizes may increase northward, with mean clutch size of 2.5 eggs in British Columbia, 3.3 in Newfoundland, and 3.5 in the Northwest Territories. On Victoria Island, almost all clutches had 5 eggs, occasionally 4 or 6. In Washington, almost all clutches contained 2 or 3 eggs, with 4-egg clutches rare. There is 1 record of an 8-egg clutch. Later clutches tend to be larger. In Washington, most early nests contained 2 eggs compared with 3 for later nests. In Newfoundland, mean clutch was 3.0 eggs in nests initiated prior to mid-June and 3.5 for later nests. Of birds that made more than 1 nesting attempt, the first clutch was typically 3 eggs and the second 4 eggs. In Illinois, successive clutches of 1 female contained 3, 3, and 4 eggs. Saskatchewan clutch sizes decreased nonsignificantly as the season progressed (Beason 2020; Beason and Franks 1974; Bent 1942; Bowles 1900; Camfield et al. 2007; Campbell et al. 1997; Cannings and Threlfall 1981; DuBois 1935; Gaudet et al. 2020; Maher 1980; Mousley 1916b; Parmelee et al. 1967; Peck and James 1987, 1997; Pelletier in Gauthier and Aubry 1996; Sutton 1927; Verbeek 1967; With and Webb 1993).

The age at first breeding is 1 year, with nestlings and juveniles returning to breed in British Columbia and Colorado (Camfield et al. 2007; Dinkins et al. 2002). Once a bird has initiated breeding, it nests every year. The Horned Lark is at least seasonally monogamous, and some pairs may reunite in subsequent years. If a mate dies or disappears, a new mate is accepted. If a male dies, the neighbouring male may increase his territory and mate with the widow as well (Beason 2020; Beason and Franks 1974). Camfield et al. (2007) reported a case of a female pairing with a male she had raised the previous year.

The Horned Lark obtains almost all its food by walking in bare agricultural fields and short vegetation. In spring and winter, it may frequent roadsides when fields are snow-covered. Almost 95% of foraging time is in snow-free areas, especially in dry areas (63.7%). In Washington alpine communities, it foraged mostly in snow-free areas that were sparsely vegetated. Occasionally, updrafts from lower elevations deposited arthropods on snow where they were more conspicuous and possibly partially immobilized by colder temperatures. In these circumstances, larks foraged on snow, but usually briefly in the afternoon. It gleans most food from the ground, but may dig up larvae and worms with its beak and pry cutworms out of weed clumps or bases of corn stalks. Occasionally, it perches on a short plant to eat seeds. Adults are skilled at chasing and catching insects as they are flushed in front of the walking bird. Occasionally, it flies after moths and other insects in a manner similar to a flycatcher (Beason 2020; Cannings and Threlfall 1981; McAtee 1905; Norvell and Creighton 1990).

Very early in the season, nestlings may be fed some weed seeds, but most food brought is animal material. The diet of nestlings typically consists of about 80% animals. By May, virtually all food brought to the young is animal matter. Vegetation eaten by nestlings included wheat and seeds of green foxtail, amaranth, and wood-sorrel. Animal foods included beetles (weevils, scarab, leaf, June, and pill beetles, and click and ground beetle larvae), grasshoppers, lepidopteran larvae and pupae, leaf bugs, spiders, ant-lions, and centipedes. About half of nestlings' food in May in

Saskatchewan consisted of lepidopterans, and 77% of these were caterpillars. Later in the nesting season, grasshoppers are the dominant food item. Fledglings are largely vegetarian and eat little animal food (about 10%) August through October when it is most abundant. At the same time, adults feed predominantly on insects. It is probable that fledglings are not sufficiently skilled to catch many insects (Beason 2020; Cannings and Threlfall 1981; McAtee 1905; Pickwell in Bent 1942; Verbeek 1967).

McAtee (1905) examined 1,154 stomachs taken in all seasons, including birds from Ontario. He also reviewed a study that looked at 59 stomachs in 1892. These 2 studies were undertaken in agricultural areas and are not representative of the diet of the Northern Horned Lark. The diet consisted of 20% animal food and 80% vegetable matter, compared with 11% and 90% respectively in 1892. In January and February, animal foods comprised only 1.7% and 31% of the diet, mostly weevils and moth cocoons. Animal food increased to 15.7% and 27.3% in March and April, with increasing numbers of weevils, caterpillars, and bugs consumed, as well as some beetle larvae and leaf beetles. By May, animal food totalled 43.4% with important groups being weevils, June beetles, caterpillars, and grasshoppers. Adult consumption of insects increased from June through August due to the abundance of weevils and grasshoppers but, after August, animal food use declined rapidly to about 1% by December. The animal food was entirely invertebrates and mostly insects. It included beetles, butterflies, moths, grasshoppers, ants, spiders, flies, wasps, millipedes, mites, centipedes, snails, earthworms, termites, bugs, and ant-lions. The stomachs contained 105 plant species, including more than 90 species of grass and weed seeds. Grain comprised 12.2% of food, mainly oats, corn, and wheat. Corn was eaten almost exclusively in winter. The Horned Lark cannot eat entire kernels so depends on livestock or vehicle tires to crush them. Most grains consumed were waste in stubble fields and eaten from September to January. Other grain seeds eaten included those of buckwheat, sorghum, and millet. Weed seeds comprised 63.9% of food items with dominant species being foxtails, smartweeds, amaranths, purslane, ragweed, crabgrass, barnyard grass, and sedges. Grass and sedge seeds comprised 26.2% of the diet. It also consumed seeds of black mustard, wild radish, chickweeds, knapweeds, sunflowers, dandelions, hoary vervain, nightshade, corn cockle, pokeweed, and lamb's-quarters. Miscellaneous plant foods included bits of grass roots and stems, a few flowers, and algae. Fruit constituted only 0.2% of the diet and larks may have consumed only the seeds: blackberries, pears, and cherries. A considerable amount of gravel was consumed, probably to enhance digestion. Beal and McAtee (1912) reported similar findings. In Colorado, it pulled up and ate sprouting crops such as lettuce, wheat, milo, and oats (Beason 2020).

Wiens and Rotenberry (1979) and Rotenberry (1980) determined that the Horned Lark and other grassland species (Upland Sandpiper, Grasshopper Sparrow, Dickcissel, and Eastern and Western meadowlarks) ate much the same things at the same time. The same species collected at different times ate different things. There were no significant differences in the size of food items consumed by the species. The Horned Lark had the broadest diet composition niche of all the species. Food resources were not limiting to these species and individuals and populations exploited the food resources opportunistically without competition. Except in August, all Horned Lark samples collected during the breeding season contained at least 70% arthropods. In autumn, seeds constituted 60-70% of the diet and this proportion increased to 80-100% in winter. Grass seeds

increased in abundance in the diet between February and March and remained at a high level through October. In January, forb seeds constituted almost all the diet. The shift in seeds appeared to be related directly to availability. The major arthropod prey, beetles and especially weevils, were common spring through summer and grasshoppers became abundant in the environment and diet from the warmer parts of the summer into autumn. At some sites, ground beetles and caterpillars were important in the diet. The most important seeds in the diet were those of grasses, followed by those in the goosefoot and mustard families. Hymenopterans, bugs, flies, and neuropterans were also consumed.

Fewer data are available on the diet of northern adults. In Newfoundland, the Horned Lark ate more seeds, berries, and small leaves than nestlings early in the season. Food included small cranberries, crowberries, large ants, moth caterpillars and adults, beetles, crane flies, and spiders (Cannings and Threlfall 1981). In Labrador, the diet consisted of 52% animal matter. Adult and larvae geometer and owlet moths comprised 27.3% of the diet; large ants 7.0%; other hymenopterans, including ichneumonid wasps 5.7%; flies 4.3%; spiders 3.3%; leafhoppers, aphids, and other bugs 2.7%; and 1.7% small molluscs. Of the 48% vegetable diet, fruits and seeds of blueberries totalled 31.7%; the rest was sedge seeds and vegetable debris (Bent 1942). The latter 2 studies are probably characteristic of the diet of birds nesting along the Ontario Hudson and James Bay coasts; the other studies are probably representative of southern Ontario breeders.

The Horned Lark is rarely parasitized by the Brown-headed Cowbird. First clutches are laid well before cowbirds initiate egg laying. Lark eggs hatch as soon or sooner than cowbird eggs and larks develop quicker so that young cowbirds are often left behind in the nest. Successful parasitism does occur. The highest rate of parasitism was in the central prairies where nests may fledge 2 cowbirds. In Kansas, an average of 0.5 cowbird young fledged per parasitized nest. Lark fledging success was 0.7 per nest in parasitized nests compared with 1.4 in unparasitized nests. In Ontario, 4 of 185 nests (2.2%) were parasitized. In North Dakota, 5 of 25 nests (20.0%) were parasitized; in Wyoming, 0 of 140 nests were parasitized; in British Columbia, 0 of 115 nests were parasitized; and 0 of 163 Saskatchewan nests were parasitized. In North Dakota, 50 of 84 nests (59.5%) found after 15 May were parasitized; no nests found before 15 May were parasitized (Beason 2020; Campbell et al. 1997; Dinkins et al. 2002; Igl and Johnson 2007; Leighton et al. 2002; Lowther 1985, 1991, 1997; Mahoney and Chalfoun 2016; Peck and James 1997; Pickwell in Bent 1942).

Habitat loss and degradation is not a problem for birds along the northern coast. Prior to conversion of forested lands to agriculture, the Horned Lark was absent in southern Ontario. Habitat for it is currently declining in the south due to abandonment of farmland and conversion to residential areas. Some agricultural practices may also be detrimental. Modern machinery is able to get on the land earlier in spring so that first nests may be lost. It has been estimated that 138,000 young are killed annually across Canada due to direct effects of agriculture, including approximately 12,000 in Ontario. Mortality rates for the Horned Lark were lower than for other species because it completes its nesting cycle before crops are harvested. Most mortality is associated with tilling and seeding. Until the early 1900s, wheat was sown by broadcasting and larks often ate a high proportion of the seed. In some areas, poisoned wheat was sown first to kill the larks before sowing the final crop. Once seed drilling was initiated, birds could not access the seeds and poisoning was

terminated. Modern-day use of insecticides may reduce food availability and there are isolated reports of it being killed by carbofuran and fenthion (Beason 2020; Beason and Franks 1974; Hussell in Cadman et al. 1987; McAtee 1905; Pelletier in Gauthier and Aubry 1996; Tews et al. 2013).

In Alberta, the Horned Lark was the only species that used cultivated land to any degree. It occurred on cultivated and grazed plots only and was absent in undisturbed grasslands and mowed areas. On roadside counts, it occurred at all land uses and its occurrence was significantly higher at cultivated and grazed stops than at undisturbed sites. It benefits from agricultural activities that create its preferred barren conditions (Owens and Myers 1973). In Saskatchewan, it was more abundant in nonnative crested wheat grass than in native grasslands. Crested wheat grass cover can have twice as much bare ground as native mixed-grass prairie, thereby enhancing habitat conditions (Sutter and Brigham 1998).

Density in eastern Colorado was higher in a drought year than a wet year and similar results were reported for 4 prairie states. Densities declined during a severe drought in North Dakota. Niemuth et al. (2008) analyzed Horned Lark density in relation to the number of ponds present in a North Dakota study area over a 25-year period with extremes from severe drought to very wet conditions. It was more abundant in drier than wetter conditions. In North and South Dakota, Montana, and Wyoming, its abundance was not significant correlated with the amount of precipitation received in the current or previous year (Gorzo et al. 2016). In Colorado, survival was lower on very hot days (35°C or higher), following storm events, and on dry days with a lag period of 1 day. Survival rates were lower during warmer and drier breeding seasons. Projected climate changes may exacerbate these effects (Conrey et al. 2016). Nest survival rates tended to decline with increasing temperatures in Saskatchewan; nests are almost fully exposed to the sun at midday (Gaudet et al. 2020).

The Horned Lark responds positively to grazing. Heavily grazed areas are preferred to those that are lightly or moderately grazed (Dinkins et al. 2002). Grazing reduces the height and density of grass cover, making habitat more favourable.

Applications of toxaphene can be lethal to nestlings and density of the Horned Lark may decrease after spraying this chemical. Malathion and carbaryl do not appear to cause adverse effects. It may be adversely affected by fenitrothian, diazinon, fenthion, and chloropyrfos. In Ontario cornfields, numbers did not change after spraying with fonofos and terbofos to control rootworms (Dinkins et al. 2002).

The Horned Lark appeared to exhibit an aversion to roads and interstate highways in Illinois. Densities increased with distance from roads or highways (Dinkins et al. 2002). In Saskatchewan, it was equally abundant along roads and trails, although it tended to be more abundant along trails (Sutter et al. 2000).

In Wyoming, reproductive success was not lower at wind farms than at reference sites as measured by clutch size, number of fledglings, nestling mass, or daily nest survival rate. There was weak evidence of a higher average number of fledglings per successful nest at wind farms than reference sites. Within wind farms, clutch size and number of fledglings were not related to any development, nest-site habitat, or neighbourhood habitat characteristics. Horned Larks did not

avoid turbines, nesting an average of 185 m from them (range 4-490 m). Nestling mass was weakly negatively related to turbine density within 5 km and, in 1 of 2 years, nest survival decreased as turbine density increased. Turbine densities at scales of 1-5 km were the most informative models suggesting that intensity of development may have a greater influence on productivity than proximity to turbines (Mahoney and Chalfoun 2016).

The Horned Lark usually responds well to fire, especially if it reduces coverage of shrubs and grasses (Earnst et al. 2009). In Arizona, it increased in both native and nonnative grasslands after a wildfire and was more common on burned than unburned plots for 2-3 years after the fire (Bock and Bock 1992). Fire probably has the most important effect in western shrubsteppe communities and may not be particularly important in Ontario.

Spring snowstorms or heavy rainfall may result in nest loss. In Newfoundland, a severe mid-June storm destroyed all 3 nests with young and 4 of 5 nests with eggs were deserted (Cannings and Threlfall 1981). Pickwell (in Bent 1942) reported that late March snows disrupted all territories in 1 area. A period of deep snow resulted in abandonment of all nests. Renesting occurred 3 weeks later when conditions became suitable again. Seven cm or more of snow lasting 2 or more days would destroy a nest. MacDonald et al. (2013) determined that females occasionally took extended recesses from incubation of 59-387 minutes duration during inclement weather, compared with an average of 10.9 minutes for normal recesses. Extended recesses appeared to affect embryo viability. Hatching rate was 91% for nests where females did not take extended recesses and 81% where they did. Extended recesses may be an important mechanism that allows females to breed successfully under adverse weather conditions. In alpine areas of British Columbia, daily nest survival rates were not influenced by temperature alone or by single or cumulative days with more than 1 mm of precipitation. An interaction between temperature and precipitation resulted in much higher nest failure during cold storms than during storms with warmer temperatures (Martin et al. 2017).

The response of nesting females to human intruders varies. Birds that elect to nest near human activity become habituated and may be approached to within 40 cm before they leave the nest. Away from activity, birds may walk or fly from the nest when a human is 25 m to more than 100 m distant. In 1 case, an observer stood between a female and her nest. The female laid an egg on the ground rather than risk exposing the nest by returning to it (Beason 2020; Beason and Franks 1974; Pickwell in Bent 1942; Wackenhut et al. 1983).

The Horned Lark is vulnerable to being struck by aircraft at airports, and it is the most commonly reported aviation bird strike victim in the United States (Beauchesne et al. 2007). It nested in the gravel and grasses immediately adjacent to runways at Lester B. Pearson International Airport in Toronto (personal observation), and its habit of making high courtship flights may increase the risk of being struck by aircraft (Beauchesne et al. 2007).

Dinkins et al. (2002) offered management recommendations for the Horned Lark. These included burning in the spring to reduce woody species; burning, mowing, or grazing to create short sparse vegetation; controlling shrub growth by mowing or grazing; and using only rapidly degrading chemicals of low toxicity and applying them at the lowest possible rate.

Price (2004) predicted that the range of the Horned Lake might expand in southern Ontario if the average summer temperature increased by 2°C. The area of suitable climate in Alberta was anticipated to increase due to a northward expansion and no losses in the south (Nixon et al. 2016).

Status

McIlwraith (1894) stated the Northern Horned Lark was an abundant breeder around Hudson Bay and James (1991) considered it a common breeder along the northern coast. The Prairie Horned Lark was absent in Ontario and North America east of the Mississippi Valley prior to forest clearing by European settlers. Historically, it bred in tallgrass prairies of Illinois, Wisconsin, Minnesota, Iowa, Missouri, Kansas, the Dakotas, Nebraska, and Manitoba. Clearing for agriculture created ideal habitat and it rapidly spread eastward starting in the 1870s. McIlwraith (1894) reported its first occurrence in the province in 1868, stating that it increased annually and was well established as a breeder. By the turn of the 20th century, it appeared as a breeding bird in the Kingston area and spread as far east as Montreal about the same time. By the mid-1930s, it was a common breeder in agricultural areas north to southern Kenora and Sudbury districts and the Ottawa area. It was also common along the western coast of James Bay north to Cape Henrietta Maria and northwestward to the Manitoba border. It has never been very common on the Clay Belt (Baillie and Harrington 1937; Hurley and Franks 1976; Pelletier in Gauthier and Aubry 1996; Pickwell in Bent 1946; Smith 1957). James (1991) considered the Horned Lark a common breeder along the northern coast and in the agricultural south, but rare and local in the Canadian Shield in southern Ontario, in agricultural areas from Sudbury to North Bay and north to the Clay Belt, and in western Rainy River District. It was apparently an abundant breeder in Muskoka and Parry Sound districts in the early 1900s, but there are now only scattered records from this area, probably due to forest regeneration (Hussell in Cadman et al. 2007).

The breeding range of the Horned Lark did not change significantly between atlases, but its probability of observation declined significantly. Declines were significant province-wide, south of the Shield, and in the Great Lakes–St. Lawrence Forest Region in the Shield. The greatest decline was in the southern Shield, and its distribution was greatly reduced on Manitoulin Island. Declines are similar to the trends observed during the first atlas and are probably related to habitat loss due to natural succession and reforestation of marginal farmlands. The northern population along the Hudson and James bay coasts, as well as scattered populations in the Clay Belt and Rainy River District, remained unchanged between atlases. It was most abundant in the agricultural areas of Huron, Lambton, Middlesex, Chatham-Kent, and Essex counties. Another area of high concentration was at Cape Henrietta Maria (Hussell in Cadman et al. 2007).

Population increases in eastern North America were dramatic in the late 19th century until at least the mid-20th century or possibly to almost the end of the 20th century. The only quantitative data are from studies in the first and sixth decades of the 20th century in Illinois. No other bird species increased as dramatically in the state during this period. In June 1909, the Illinois population was estimated at 842,000 birds compared with 5.6 million in 1957 and 4.8 million in 1958. In the last quarter of the 20th century, populations appeared stable, but began to decline in the early 21st century. The increase in the mid-1950s was attributed to the Horned Lark's adaptability to nest within corn and soybean fields. Occupancy in these crops is still 100% in that state, but numbers

nesting in fields have declined. Early planting of crops is thought to be contributing to the decline (Beason 2020; Graber and Graber 1963; Walk et al. 2011).

The long-term (1970-2021) population trends determined by the Breeding Bird Survey (BBS) were annual decreases of 4.33% in Canada and 3.04% in Ontario; the short-term (2011-21) trends were annual decreases of 5.84% in Canada and 6.07% in Ontario. The long-term results were highly reliable; the short-term results were of medium reliability (A.C. Smith et al. 2023). The BBS does not sample the population of Horned Larks that breeds in the Hudson Bay Lowland and the Tundra Region.

POSTFLEDGING PERIOD

Young are fed for a week or more in the territory after leaving the nest and can usually fly when they are about 2 weeks old. They are independent at age 3 or 4 weeks, when juveniles start to flock together. These flocks continue to grow through summer and autumn and adults join the juvenile flocks in August and September (Beason 2020; Pickwell in Bent 1942; Sutton 1924).

MIGRATION

Birds along the northern coast and further north are migratory; most of Ontario's wintering birds belong to this population, although a few Prairie Horned Larks may remain all winter. Southern Ontario breeders tend to move southward for December and January (Beason 2020; Pickwell in Bent 1942).

The Horned Lark is a very early spring migrant, returning in February or early March in the south and late April in Algonquin Park. Males usually return a few to 12 days before females and establish a territory; occasionally birds arrive paired. Pairing occurs immediately upon arrival of the females. At the same time, unpaired northern birds are arriving and continuing northward (Beason 2020; Curry 2006; Tozer 2012). Manning (1952) thought that most birds he saw feeding in flocks along the shores of western James Bay and the southern Hudson Bay coast in May and June were migrants.

On Victoria Island and the Twin Islands, autumn migration starts by September (Manning 1981; Parmelee et al. 1967). Manning (1952) stated that the Horned Lark arrived in numbers in the Moose River estuary on 1 October and it is common to abundant by early September throughout the Hudson Bay Lowland (Wilson and McRae 1993). In the south, migration may extend until late October and November (Curry 2006; Weir 2008).

When the Horned Lark first arrives in spring, it is most common in agricultural fields and along roads. It may concentrate along roads until snow melts from fields. In the south, it inhabits areas similar to those used during the breeding season while it is migrating, but may make greater use of areas such as beaches, sand dunes, airfields, grassy meadows, and overgrazed meadows (Beason 2020; Campbell et al. 1997; Pickwell in Bent 1942; Weir 2008). While staging for autumn migration on the Twin Islands, it was common inland where vegetation was short and dry, but more numerous near the shore at the edge of tundra and on sand beaches (Manning 1981). In the Yukon, open habitats are used during migration, particularly sparsely vegetated areas such as mudflats, open fields, dry tundra, and roadsides (Sinclair et al. 2003).

On Victoria Island, Parmelee et al. (1967) banded a male in September 1962 and recovered it at the same spot in May 1966. It is uncertain if this is an example of breeding site fidelity or migration site fidelity.

Manning (1952) considered the Horned Lark an abundant autumn migrant along the James and Hudson bay coasts of Ontario. James (1991) termed it a common to abundant migrant in the province.

WINTER

Winter habitat is similar to that of other seasons, although the Horned Lark may rely on agricultural fields even more in winter. Roadsides are important habitat when fields are snow-covered. It is nonterritorial in winter, so large flocks may occur. On the prairies, it is most abundant where winter wheat and sorghum are grown. Other anthropogenic areas may be used when there is no snow cover, such as golf courses, airports, and pastures. In Illinois, habitats in order of preference in 1906 and 1907 were corn stubble, pasture, small grain stubble, and wheat. Fifty years later, preferred habitats were bean stubble, alfalfa, and mechanically picked cornfields. During the earlier period, most corn was hand-picked and stalks were left standing; this habitat was unused (Beason 2020; Graber and Graber 1963; Root 1988; Sutton 1927). In New York, it was more likely to be detected in fields with soybean and corn stubble than those with grass cover. It was also more likely to occur in larger fields, with its probability of occurrence increasing with field size for all 3 cover types. Probability of detection in corn and soybean fields was 15-20% in 3.2-ha fields and gradually increased to 75-80% in 17.4-ha fields. In grassy fields, the probability of detection was 5% in 3.2-ha fields and 40% in 17.4-ha fields. Larks were absent in fields smaller than 3.2 ha. Its probability of occurrence increased with increasing amounts of open habitat within 500 m (Rosenblatt and Bonter 2018).

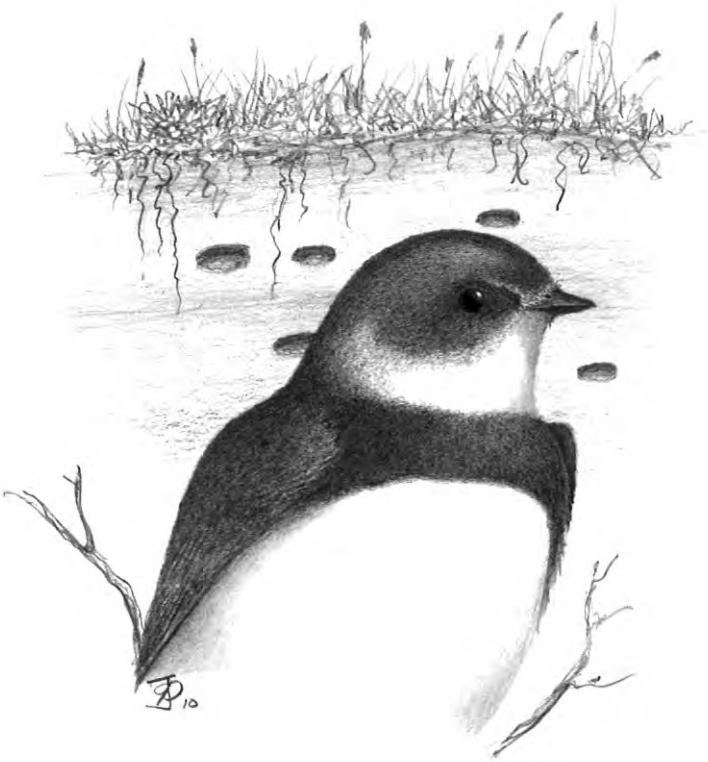
In winter, almost all food is plant material. The Horned Lark consumes waste grain and seeds of forage plants in fields, sedges, grasses, mallows, ragweed, witch grass, foxtails, amaranths, and numerous other weeds. Some dried fruits or berries may be eaten and possibly some insects in dormant phases. It feeds in farmyards and feedlots and, when horses were more common, fed on oats in their droppings along roads (Bent 1942; Pickwell in Bent 1942). It will come to winter bird feeders situated near agricultural fields where it feeds on the ground on mixed seeds (personal observation).

Prior to forest clearing, the Horned Lark was undoubtedly rare or even absent in winter. When McIlwraith (1894) first observed it circa 1869, it was a rare winter visitor. James (1991) considered it an uncommon winter resident in the south, north to Manitoulin Island.

On southern Ontario Christmas Bird Counts (CBC), Freedman and Riley (1980) noted a pronounced but erratic increase since 1959, prior to which it was rarely documented. From 1970-2021, CBC results indicate that the Ontario population was stable, increasing at an annual rate of 0.06%; from 2009-21, it decreased 8.67% annually (National Audubon Society 2022).

Bank Swallow

Riparia riparia



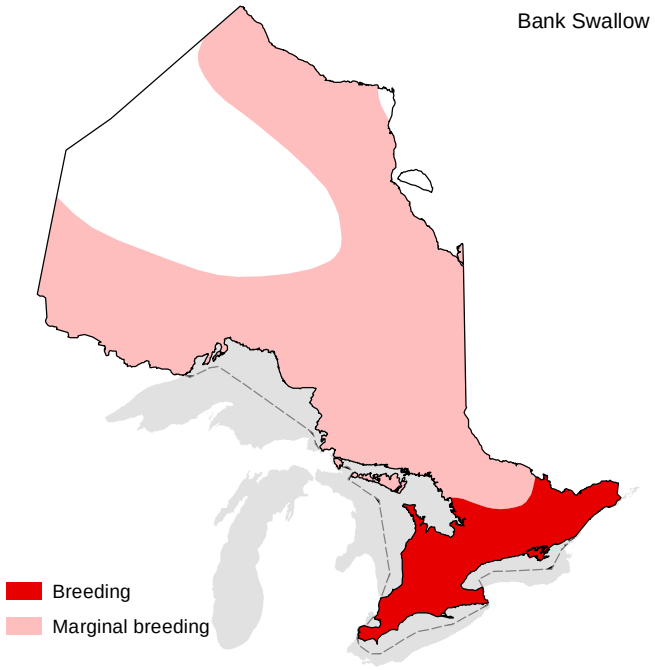
BREEDING SEASON

Habitat Requirements

Breeding habitats of Ontario Bank Swallows were roadside banks (24.8% of records); banks of rivers, streams, lakes, and lagoons (23.6%); farm pastures and fields (20.4%); wooded areas (14.7%); dunes, bluffs, and eskers (8.1%); earth, sand, and gravel cuts, piles, and pits (3.9%); rural and suburban sawmills and parking lots (2.2%); small islands (1.6%); and marsh and swamp edges (0.8%). Some of the descriptions are not a true reflection of the nesting area (Peck and James 1987).

Occupancy rates of lakeshore bluffs (63.0%) and aggregate pits (60.0%) by Bank Swallows were similar in southern Ontario. Colonies in pits were smaller (112 burrows) than those in lakeshores (560 burrows). Bluffs averaged 50.5-73.0% sand in lakeshores and pits. Colony size was not a significant predictor of burrow occupancy in lakeshores. Height of burrows and colony size had no effects on burrow occupancy in gravel pits, but burrow occupancy increased in medium and high burrows as colony size increased. Lakeshore colonies had a 100% persistence rate over 5 years but only 32% of aggregate colonies persisted during all 3 years. Colonies in pits were ephemeral, but new colonies were often established in other locations within the same pit. The probability of a pit

colony being used in consecutive years increased with colony size and the size of the available face (Burke et al. 2021).



The Bank Swallow relies on vertical banks for nesting and therefore has a patchy breeding distribution. It is most common in glaciated areas where there are deposits of unconsolidated soils. In these areas, erosion by water and wind may create steep banks that provide suitable nest sites. It is most common in glaciated areas with higher human populations because road and railway cuts, sand and gravel pits and other construction activities provide nesting opportunities. In the Clay Belt, it may nest where glaciation left deltas, raised beaches, kames, and eskers. In the Canadian Shield, it is restricted to shorelines of lakes, streams, and rivers, and where human activities have created steep banks. Natural nest sites include sand dunes and vertical banks along rivers, streams, lakes, and oceans. Anthropogenic sites include sand and gravel pits, road cuts, and piles of soil or other unconsolidated material. Rarely used natural sites include crevices in cliffs; 1 nest was in a dug hole in the ground that measured approximately 3 by 4 m and 3 m deep. Approximately 35% of Ontario and Quebec nests were in natural sites, the lowest for the country. This was attributed to the high human population, but it may be biased because most records are from areas of high human population. Data from 2001-17 indicate that the proportion of Ontario and Quebec nests in natural habitats increased to 50%, with 60.9% of Ontario nests in natural habitat. The increase in use of natural habitats may be due to policies that require slopes to be gentle in pits and road cuts, or to better coverage of natural habitat in more recent studies. A high proportion of nests are near water because waves or flowing water create suitable nesting substrate. Some colonies in human-made habitat are a considerable distance from water. It requires open areas for foraging, so colonies in extensively forested landscapes are associated with large rivers or lakes (Campbell et al. 1997; Champoux and Bombardier in Gauthier and Aubry 1996; Erskine 1979; Garrison and Taylor 2020; Leighton et al. 2002; Pelletier et al. 2022).

Along the Connecticut River, bank length, slope, vegetation cover, and soil type differed between active colony sites and random sites. Banks with colonies were longer, steeper, less vegetated, and had deeper, better-drained soil with fewer coarse fragments than random sites. Vegetation was the best predictor of swallows nesting at a site, but slope and vegetative cover were highly correlated. Banks that had 0-11% vegetative cover had a mean slope of 79°; banks with more than 11% vegetative cover had a mean slope of 56°. Mean slope at colonies was 89° compared with 55° at random sites. The probability of swallows nesting increased with increasing bank length; 82% of swallows nested in banks longer than 150 m. Potential but unused banks were consistently

shorter with more vegetative cover than used banks. Approximately 50% of banks were occupied, suggesting that nest sites may be limited, and this may explain the high persistence rate of colonies in this area (Silver and Griffin 2009).

In southern Ontario, the Bank Swallow was equally abundant on organic and conventional farms. Its presence was significantly associated with pasture and it was also associated with large, isolated trees and grassy strips between fields that often contained fences, but these relationships were not significant. It was significantly negatively associated with habitat heterogeneity. It was also negatively correlated with hay, streams, use of herbicides, and road, railway, and hydro rights-of-way (Kirk et al. 2011). This study was probably recording foraging Bank Swallows rather than nesting birds.

From the start of nest building until the beginning of egg laying, both members of a pair usually roost in the nest burrow. During incubation and brooding, the female roosts in the nest burrow while the male roosts nearby in another burrow or on trees and shrubs until the young are about 12 days old. Birds nesting near Port Burwell routinely flew to marshes at the base of Long Point to roost for the night. Distances between nest sites and nocturnal roosts were as far as 35 km. Some nestlings were as young as 9 days old when 1 or both parents went to roost in the marsh. Some males left the colony every night during the nestling period. Females tended to spend more nights back in the nest roosting. Marsh-roosting birds travelled quickly between the colony and roost sites and did not appear to forage in the vicinity of the marsh (Falconer 2013). Falconer et al. (2016a) radiotagged 11 males and 11 females in the Port Burwell area at 2 nesting colonies 29 and 33.5 km from the Old Cut Marsh at Long Point. Nineteen (86.4%) spent at least 1 night roosting more than 4.5 km from the nest site and 13 (59.1%) spent at least 1 night roosting near Old Cut or further east while their nests were active. The nocturnal roosts appeared to be within marsh habitat. Some males roosted away from the nesting colony every night; others never did. After the nestlings fledged, most adults did not roost overnight at the colony. Females spent more nights at the colony than males, possibly because females brooded the young at night. New Brunswick swallows frequently changed the roosts that they used. Females were less likely to roost communally during the incubation and brooding periods. Both sexes were less likely to roost communally when the nestlings were young and during inclement weather when young need assistance thermoregulating. After nestlings fledged, adults were less likely to roost communally during adverse weather, with the nest cavity providing better protection (Saldanha et al. 2019). Bank Swallows have also been reported roosting at night in agricultural fields as far as 6 km from the nesting colony.

Most Ontario nests were in burrows excavated by the birds. A high proportion of nests were in banks of sand, clay, or earth (60.6%); 37.5% were in sand, gravel, and earth pits; 1.3% were in sand dunes, and 0.7% were in human-made piles of gravel, sand, and sawdust. Three nests were in plastic tubes inserted into banks. Most nests were near the top of banks. Distances below the top of bank at 31 colonies were 0.2-3.0 m, mostly 0.6-0.9 m. Nest heights above water or land were 0.6-45.7 m, mostly 2-4.6 m. Nests were flat platforms in depressions at the end of burrows. Burrow depths of 297 nests ranged from 0.2 to 1.5 m, with most 0.5-0.6 m deep (Peck and James 1987).

Nests tend to be in near-vertical banks with slopes ranging from 76 to 105°. Soil consistency is important in defining nest-site suitability, and it also affects the depths of burrows. Near Ottawa, the Bank Swallow nested only in banks that had sufficient stability to maintain a 3-m vertical face; unused faces had only a 1-1.5-m vertical area above talus. John (1991) conducted soil penetrability tests and found that most nests were in soils with penetrability readings of 8-9 kg compared with less than 6 kg for unused sites. Preferred soils were mostly good quality construction-grade sands. Soils with lower penetrability may result in instability and erosion of the bank. Outside Ontario, nests have been reported in loess, till, clay, sand, and gravel. In California, most colonies were in soft banks: 22.1% in fine sandy loam, 38.4% in loam, and 8.1% in silt loam. The rest were in sand (3.5%), sandy loam (7.0%), clay loam (2.3%), clay (9.3%), and aggregated clay (9.3%). In Atlantic Canada, the Bank Swallow selected sandstone cliffs and, to a lesser extent, till cliffs; it avoided sand dunes for nesting. At a Wisconsin site, all burrows were in sand or sandy loam. Saskatchewan nests were in sand or fine gravels; most British Columbia nests were in silt, clay, or sand. Elsewhere, nests have been in natural cavities in rock cliffs, in sawdust and manure piles, rarely in drain pipes in concrete walls, in coal piles, in iron ore tailings, in granite dust, and once 5 m underground in an abandoned well (Campbell et al. 1997; Champoux and Bombardier in Gauthier and Aubry 1996; Falconer and Badzinski 2013; Garrison et al. 1987; Graber et al. 1972; Greenlaw 1972; Gross in Bent 1942; Knapton 1988a; Petersen 1955; Power et al. 2020).

Height of burrow entrances above ground of 0-38 m were reported from British Columbia, which represent the extremes reported from anywhere; most were 3-8 m above ground. Nest height is highly dependent on the height of available banks. Burrows are typically in the top third of the bank, and burrow density decreases from top to bottom of the slope. In lower banks, colonies may consist of a single row of burrows 30-40 cm from the top of the bank. In Saskatchewan, height and length of vertical banks affected usage by Bank Swallows. The average height of banks with nesting swallows was higher (1.8 m) than banks without swallows (1.4 m). Banks with colonies were significantly longer (30.9 m) than unused banks (21.9 m). Average heights of banks at nesting colonies were 3.2 m in Pennsylvania and Vermont and 3.3 m in California (Campbell et al. 1997; Garrison and Taylor 2020; Greenlaw 1972; Hjertaas et al. 1988).

The Bank Swallow prefers to nest in colonies. It may occasionally nest solitarily, but most nest in colonies. In Ontario, 48 isolated nestings and 200 colonies were reported for a total of about 9,600 nests; 99.5% were in colonies. Ontario colonies contained 2-1,500 pairs; the average size of 99 colonies was 45 nests. A more recent estimate indicated that the mean size of Ontario colonies was 130 nests and the median was 50 nests. Not all burrows in a colony are occupied. Along the Lake Erie shoreline, 57% of burrows were occupied in 2010 and 53% were occupied in 2011. On the Lake Erie bluffs, colonies are nearly continuous and consist of several thousand nests. In British Columbia, colonies contained 3-3,055 burrows; 52% of colonies had 15-75 burrows. In Michigan, 60% of colonies were small with 50 or fewer nests, but 71% of swallows nested in colonies with more than 100 nests, and 47% were in colonies of 200 or more. In Saskatchewan, colonies averaged 7.7 nests with a maximum of 48, but 68% of nests were in colonies of 10 or more nests. One of the largest colonies of 6,000 nests was reported from Illinois. Burrow site selection is affected by the presence of other burrows. Swallows are most likely to burrow in areas that already have high burrow density.

Large portions of uniformly suitable banks may be unused, with nests clustered in 1 area and densities of burrows greater higher up on the bank. Largest colonies are associated with the highest and longest banks (Campbell et al. 1997; Falconer and Badzinski 2013; Falconer et al. 2016b; Garrison and Taylor 2020; Garrison et al. 1987; Graber et al. 1972; Hjertaas et al. 1988; Hoogland and Sherman 1976; Peck and James 1987, 1997; Petersen 1955).

Although it is colonial, the Bank Swallow is territorial. Shortly after arrival, males start digging a burrow to attract a female. Other birds that approach too closely are threatened vocally or physically attacked. Birds burrowing high up in the bank are dominant and spend much less time in defence than those lower on the bank. Once pair formation occurs, both sexes defend the burrow and its immediate vicinity. The territory size is defined by the area that a bird is capable of defending around the burrow. Near Sundridge, tunnel entrances were consistently in a regular pattern supporting the hypothesis that the distance between burrows was determined by territorial disputes. The regular spacing allowed a greater density of nests within a given area, which may be an advantage of nesting colonially (Ghent 2001). In Wisconsin, the minimum distance between burrows was 10 cm, mostly 12.7-17.8 cm apart. In Pennsylvania, burrows were 17.8-43.2 cm apart; mean distance between burrows was 13.2 cm in California (range 1-59 cm). If a male is unsuccessful in attracting a mate to a burrow, he digs another. Consequently as many as 45% of burrows in a colony may be unoccupied. At active nests, the pair defends the burrow and a small area around it early in the nesting season but only the burrow is defended after the eggs hatch (Garrison and Taylor 2020; Garrison et al. 1987; Petersen 1955).

No information on home range size is available, but it is large. In New York, most flights were within 0.8 km of a colony (Garrison and Taylor 2020). It is likely that longer flights occur regularly in some areas, particularly if colonies in sand and gravel pits are distant from good foraging areas.

Many colony sites are short-lived due to slumping or other factors making them unsuitable. Colonies where massive reproductive failure occurred are seldom repopulated and, if they are, it is usually by different birds. Long-term colonies are associated with long, tall banks with regular erosion to maintain the vertical face, and where most birds in the colony have good nesting success. A large colony on the shoreline of Amherst Island in Lake Ontario was used for at least 2 decades and some British Columbia colonies are 18-25 years old. A Virginia colony was used over 30 years and one in Illinois was over 50 years old. In Saskatchewan, where nest banks and colonies are small, only 32% of colonies were used both years of a 2-year study (Blem and Blem 1990; Campbell et al. 1997; Freer 1979; Garrison and Taylor 2020; Graber et al. 1972; Hjertaas et al. 1988; Weir 2008).

Natal philopatry and adult site tenacity rates are variable, due in part to the ephemeral nature of colonies. In New York, return rates were 8.1% for juveniles, 13.4% for adult males, and 13.0% for adult females, for an overall return rate of 12.3%. The lower rate of return for juveniles is probably related to their higher mortality (80% in the first year). Of returning juveniles, 15 returned to the same colony and 18 moved to a nearby colony. Only 3% of females returned to or near their natal site compared with 12.5% for males. Site fidelity increases with age. In New York, 67% of birds captured on their first return were in the colony where they were first captured, 73% of those captured twice were in the same location where they were last trapped, and all birds returning for the third and fourth time returned to the same location. There was no difference in return rates of adult males

and females. Two-year return rates at a colony where most nests were successful were 19% and 15% compared with 3% and 1% at less successful colonies. In Virginia, 10 of 262 adults (3.8%) returned to the same colony. when this site became unsuitable, 1 bird nested at a nearby site. Return rates documented in other areas are: 50% of yearlings in Wisconsin, 46% of yearlings in New York, 4.4% of adults and 1.1% of young in Iowa and New York, 4.6% of adults in Illinois, 12.5% of adults and 4.8% of young in Connecticut, and 50% of adults and 2.0% of young in Wisconsin. Maximum distances that birds moved when they changed colonies in subsequent years were 15 km in Illinois, 114 km in Wisconsin, and 403 km in Michigan (Blem and Blem 1990; Campbell et al. 1997; Freer 1979; Garrison and Taylor 2020; Graber et al. 1972; Hjertaas et al. 1988; Petersen and Mueller 1979).

In Illinois, 2 of 898 adults (0.2%) were captured at different breeding colonies in the same breeding season. At 7 colonies within a distance of 15 km, 44% of birds changed colonies between years. In Illinois, a colony at a roadside cut was destroyed before any young fledged. None of the adults that nested within this colony were recovered at the nearby 6 colonies, suggesting that they did not attempt to renest. The following year, a new colony was established at the same site. Petersen and Mueller (1979) suggested that the 7 colonies they studied were acting as a regional colony with birds often moving between colonies within the group.

Limiting Factors

Eggs have been reported in Ontario nests from early May until the third week of July, with most present in the first 3 weeks of June. Young were being fed on 13 August in a Grey County nest (Peck and James 1987, 1997). If the weather is favourable upon spring arrival, males initiate tunnel digging almost immediately. In cold or wet springs, burrow construction is delayed until conditions improve. As soon as pairing occurs, both sexes dig using their bills, feet, and wings. It usually takes 4-5 days to complete a burrow, but occasionally as long as 14 days. Burrows at the top of a bank are usually completed in 4-6 days; lower burrows take 6-10 days. Birds lower in the colony must spend considerable time in nest-site defence. Daily excavation rates vary in different substrates: 2.7 cm in gravel, 10.0 cm in coarse compact soil, 8.3 cm in fine compact soil, 12.8 cm in coarse soil with gravel, and 9.4 cm in fine soil. Excavation of the nest chamber requires several days after the burrow reaches its maximum length. The female builds the nest as soon as the chamber is complete, typically taking 1-3 days. Eggs are laid at the rate of 1 a day. Incubation may start with the laying of the third last, penultimate, or last egg. Incubation periods at Ontario nests were 13-16 days, consistent with other reports. It is likely that individual eggs require about 15 days of incubation before they hatch. Hatching of the brood may take place over 2-3 days. Young fledge when they are 18-20 days old; most fledge by mid-July. In Saskatchewan, nesting took an average of 39 days once the burrow and nest were completed: 5 days for laying, 14 days for incubation, and 20 days for the nestling period (Beyer 1938; Falconer et al. 2016b; Garrison and Taylor 2020; Hjertaas et al. 1988; Peck and James 1987; Petersen 1955).

One brood is raised; earlier records of 2 broods appear to be erroneous. Renesting birds occasionally nest in the burrow of a pair that previously fledged young, giving the impression that a pair has raised 2 broods. One instance of 2 broods being produced in a burrow has been documented in Ontario, but it was unknown if the same or different pairs were involved. Replacement clutches are laid if the first clutch is lost in early or mid-season. This may occur in the

same burrow or one recently vacated by another pair. Clutches of 2-7 eggs have been reported in Ontario, with most containing 4-5 eggs. A single clutch of 9 eggs may have been produced by 2 females. Mean clutch size in Ontario was 4.44 eggs compared with 4.09 in Alaska (range 2-6 eggs), 4.87 in Saskatchewan (range 2-7 eggs), 4.98 in Michigan (range 3-8 eggs), and 4.38 in New York (range 2-7 eggs). Nests initiated prior to mid-June have larger clutches and better success rates than later nests. In Saskatchewan, early nests had a mean clutch size of 5.2 eggs compared with 4.3 eggs for later nests; late nests fledged fewer young. Almost all 2-egg clutches and most 3-egg clutches are associated with renesting attempts or late nests (Beyer 1938; Blem and Blem 1990; Campbell et al. 1997; Garrison and Taylor 2020; Gross in Bent 1942; Hjertaas et al. 1988; Hoogland and Sherman 1976; Imlay et al. 2019; Peck and James 1987; Petersen 1955).

Both sexes can breed when they are 1 year old, and they breed every year thereafter. The mating system is monogamous (Garrison and Taylor 2020). Mate guarding is performed by Bank Swallows. For a 7-10-day period after pair formation, the male closely pursues his mate in every flight from the burrow, and this may be as many as 100 times a day. During these flights, the pair is typically chased by 1-5 males seeking extra-pair copulations. Mate guarding appears to be effective because extra-pair copulations are rare (Beecher and Beecher 1979).

Typical foraging habitat during the breeding season is over open meadows and grasslands, but open water and wetlands are used during other periods of the year. During August in Ontario, consistently high numbers foraged in apple orchards but corn and soybean fields were avoided. Forested habitat is avoided while foraging. Grassland is preferred foraging habitat and colonies distant from grasslands are more likely to become extirpated. In California, foraging habitat also included riparian and upland woodlands but these habitats do not appear to be used in Ontario. The Bank Swallow forages almost entirely on flying insects that it captures in the air. Occasionally it may pick dead or moribund insects from the surface of water while it is flying. Rarely, it may land to feed on terrestrial invertebrates when there is a large, localized concentration. At Great Salt Lake in Utah, ground foraging on brine flies was the most commonly observed feeding behaviour. Typically, it forages within 200-500 m of the colony, but may forage several kilometres away on inclement days in spring before egg laying. Birds breeding near Port Burwell foraged less than a few kilometers (usually only a few hundred metres) from the colony, although they occasionally made longer trips. Birds spent most of their time near the breeding colony and were 4 times more likely to be encountered at the colony than 500 m distant from it. Probability of occurrence was approximately 13% 1,000 m from the colony and approximately 5% at 2,000 m. Foraging usually occurs over water, meadows, fields, and pastures, often at heights of 15-33 m, but often very low during inclement weather. Foraging heights may be higher in summer when temperatures are warmer (Anderson-Abbs and Bradbury 2013; Cohen and Dymerski 1986; Falconer 2013; Falconer and Badzinski 2013; Falconer et al. 2016b; Garrison and Taylor 2020; Graber et al. 1972; Paton and Fellows 1994; Petersen 1955; Sinclair et al. 2003).

In Pennsylvania, young were fed small flies, caddisflies, and mayflies almost exclusively by the time they were 6 days old and this continued throughout the nestling period. The diet of nestlings is almost entirely soft-bodied insects that are easy to digest. The diet of 43 young in New York by weight consisted of 33.6% flies, 29.5% beetles, 29.0% bugs, 6.8% hymenopterans, and 1.1%

vegetation. Other insects occurred in insignificant weights in 10.5% of stomachs. Soft-bodied flies comprised about 50% of nestlings' diet when they were young and about 20% later. Hard-bodied beetles comprised about 20% of the nestling diet in June and 40% later. Midges may be important in the diet of Ontario birds. Adults continue to feed young until 3-5 days after they fledge (Beal 1918; Beyer 1938; Falconer 2013; Garrison and Taylor 2020; Petersen 1955).

The diet of more than 300 adults from throughout North America consisted entirely of animal matter, except for 3 seeds found in 3 stomachs that were probably ingested incidentally. With the exception of a few spiders, the diet was comprised of insects. Flies were most important in the diet at 26.6%; these were mostly house flies and crane flies. Beetles constituted 17.9% of the diet, including 5.5% scarab beetles and 5.8% weevils. Ants appeared to be a favourite food, comprising 13.4% of the diet, and the Bank Swallow also ate other hymenopterans, especially parasitic wasps. Leafhoppers, aphids, and treehoppers comprised 8.0% of the diet, and other bugs were also consumed. Dragonflies comprised 2.1% of the diet, lepidopterans 1.2%; grasshoppers were rarely consumed. Other insects constituted 10.5% of the diet, predominantly mayflies. Mayflies were usually eaten early in the season and were important in April when they comprised 43.4% of all food. Consumption of mayflies declined with the season until they were absent in the diet by August. In New York, 21 adults ate 49.8% beetles by weight, 27.6% flies, 13.6% bugs, 3.3% hymenopterans, 4.5% stoneflies, 0.4% spiders, 8.4% other insects, and 0.8% vegetation (Beal 1918; Garrison and Taylor 2020). Those breeding along the bluffs of Lake Erie appear to feed on the abundant emergent midges for at least part of the breeding season; they also prey upon flying ants (Falconer et al. 2016b). The diet of this swallow consists of a relatively low diversity of prey. Nancekivell and Nocera (2025) used DNA to analyze the adult diet in New Brunswick and compared the diet of the Bank Swallow to those of the Alder and Least flycatchers and the Tree, Barn, and Cliff swallows. All species differed in their dietary breadth and prey preferences. The Bank, Tree, and Cliff Swallows ate more aquatic taxa than the other species, which consumed more terrestrial flies. The Bank and Cliff swallows had more restricted diets whereas the other species had broader generalist diets. The approximate frequencies of occurrence of invertebrate groups in the diet of the Bank Swallow were 90% aquatic flies, 10% terrestrial flies, and less than 5% each for lepidopterans, aquatic and terrestrial beetles, and bugs. The approximate frequencies of invertebrate families in the Bank Swallow diet were 60% mosquitoes, 40% midges, 30% limoniid crane flies, 10% long-legged flies, and less than 5% each for marsh beetles and weevils.

There is 1 record outside Ontario of the Bank Swallow being parasitized by the Brown-headed Cowbird. This occurred under unusual circumstances when bank slumping exposed the nest (Garrison and Taylor 2020).

The distribution and abundance of the Bank Swallow is highly dependent on availability of suitable nesting areas. In natural habitats, it requires a combination of complex processes such as hydrology, erosion, sediment deposition, and river migration to provide suitable breeding habitat. Its distribution is very local and sporadic within its general range due to its dependence on sheer banks and the instability of this habitat. It has benefited from human activities that created road cuts and sand and gravel pits. These habitats eventually become unsuitable due to slumping or rehabilitation, or nests may be destroyed in pits due to extraction. New policies on road cuts require

removal of vertical banks and no colonies have been reported in this habitat in Ontario since the 1980s. Human-made slopes and steep banks along watercourses become unsuitable nesting habitat over time. Slopes eventually erode and slump and gradually a talus slope is formed that stabilizes the bank at a gentler slope. When sand and gravel pits are depleted, government agencies typically require that banks be graded to a gentle slope, thereby rendering the site unsuitable for nesting. In many studies, the main cause of breeding failure has been slumping and nest destruction due to erosion or excavation. After a major landslide along the South Nation River in eastern Ontario, 152 burrows were dug in the newly created bank within 8 days. This was on 28 June, late in the breeding season, suggesting that suitable nest sites were limited. Bank stabilization projects along watercourses and the Great Lakes shorelines may permanently eliminate nesting areas, and this has the potential to affect a significant proportion of the breeding population. Many of northern Ontario's rivers have been dammed for hydroelectric generation. These convert flowing water to a series of impoundments that do not provide Bank Swallow habitat. Water-level fluctuations below dams may flood nests or cause erosion during critical periods of the nesting cycle (Bank Swallow Technical Advisory Committee 2013; Blem and Blem 1990; Byer 1938; Campbell et al. 1997; Czerwinski 1996; Falconer 2013; Falconer and Badzinski 2013; Garrison and Taylor 2020; Garrison et al. 1987; Graber et al. 1972; Petersen 1955).

The European Starling and House Sparrow may occasionally appropriate burrows (Garrison and Taylor 2020; Leighton et al. 2002).

Changes in agricultural practices may have been detrimental to the Bank Swallow. Large areas of pasture and hayfields have been converted to row crops or other land uses. Pastures and hayfields provide excellent foraging habitat whereas corn and soybean fields are avoided. There are concerns that it may be affected directly by pesticides or indirectly through a reduction in prey populations, but the actual effects have not been determined (Falconer et al. 2016b).

The Bank Swallow may be parasitized by a number of fleas, mites, and blow flies and these have the potential to reduce productivity. Sites with high flea frequencies are usually not reused in subsequent years (Falconer et al. 2016b).

The Bank Swallow is adversely affected by cold spring weather. Birds may die directly from exposure or indirectly due to low insect availability. In Saskatchewan, 39 were found huddled together but dead during cold weather (Garrison and Taylor 2020).

Bank Swallows frequently dust, often in large numbers, on unpaved roads and roadsides and other areas of exposed soils. This often occurs during the hottest days of summer, suggesting that they are attracted by the heat. Groups may also congregate on paved roads (Graber et al. 1972; Gross in Bent 1942; Petersen 1955). Due to this behaviour, it is frequently killed by vehicles (Gross in Bent 1942). Other Bank Swallows are often attracted to those that have been road-killed, thereby increasing its vulnerability. Dead birds are often found in clusters and flocks may be struck by vehicles (Falconer and Badzinski 2013).

Climate change has the potential to result in a mismatch of timing of insect emergence with the period when nestlings area being fed by the adults (Falconer and Badzinski 2013). Climate change has the potential to result in more frequent and more severe storms. These, coupled with

increased urbanization, lead to higher peak flows in streams during storms thereby increasing the risk of erosion in breeding colonies.

Price (2004) predicted that the Bank Swallow might no longer breed in southern Ontario if the average summer temperature increased by 2°C.

Status

The Bank Swallow appears to have increased in Ontario since European settlement. It was not recorded in the Kingston area in the mid-1800s, but was very common by the turn of the 20th century (Weir 2008). McIlwraith (1894) considered it a common summer resident, breeding throughout the province, and very abundant in the Hamilton area. Sheppard et al. (1936) considered it a very abundant breeder in Niagara Region, nesting in cliffs along the shorelines of Lakes Erie and Ontario and at several locations near Niagara Falls. Baillie and Harrington (1937) stated that it was common but sporadically distributed as a breeding species in the province. Breeding distribution was from the southern border north to Hudson Bay and west to Lake of the Woods, essentially the entire province where suitable nesting areas were present. It was uncommon and not well distributed in the Clay Belt (Smith 1957). During the first atlas, 5,500 pairs were estimated in more than 200 colonies. James (1991) considered the Bank Swallow a locally common breeder in southern agricultural areas and rare in the Canadian Shield and forested areas north to the Hudson Bay coast. In Elgin County, it is an abundant nester in the cliffs along the Lake Erie shoreline. Lancaster et al. (2004) concluded that there were at least tens of thousands nesting along the lake and possibly hundreds of thousands. In 2010 and 2011, Bird Studies Canada surveyed 121 km of the Lake Erie shoreline between Turkey Point and Rondeau Provincial Park and estimated 121,450 individuals in 2010 and 102,250 in 2011 (Anonymous 2011; Falconer and Badzinski 2013). In the 260-km reach between Turkey Point and Point Pelee, the breeding population consisted of more than 100,000 breeding pairs in all 3 years from 2010 to 2012. During this period, numbers fluctuated annually by as much as 30% (Falconer 2013), but from 2010 to 2015 the trend appeared to be stable (Falconer et al. 2016b). Near Port Stanley, almost 100,000 burrows were recorded in 2010 but only 50,000 were present in 2024 (Barlow 2025). Cadman and Lebrun-Southcott (2013) surveyed Bank Swallows along a 14.9-km reach of the Saugeen River near Walkerton from 2009 to 2013. The average number of burrows counted annually was 2,195. There was no significant change in numbers over this period, although there were annual variations as high as 16%. Small colonies appeared and disappeared depending upon the annual suitability of the site, but large colonies were occupied every year. In 2010, 20,500 burrows were reported along the north shore of Lake Ontario, mostly between Ajax and Port Hope. In 27 aggregate pits in Wellington County, 5,300 individuals were counted in 2010; breeding in that county occurred exclusively in pits (Falconer and Badzinski 2013).

The second atlas indicated that the Bank Swallow had declined significantly since the first atlas province-wide and in all regions except the Hudson Bay Lowland. It was most abundant along the Lake Erie shoreline and the Lake Ontario shoreline east of Toronto. Other areas supporting large colonies were the Saugeen and Albany rivers (Sandilands in Cadman et al. 2007). Along the Lake Erie shoreline, the highest breeding density was along the shore of the Norfolk Sand Plain, which includes Long Point westward to Port Stanley (Falconer 2013).

Populations of the Bank Swallow initially increased significantly due to forest clearing and creation of aggregate pits and road cuts, but current trends are uncertain. Most information on trends comes from the Breeding Bird Survey (BBS). BBS results are not very reliable due to the ephemeral nature of colonies and the fact that the BBS samples mostly foraging birds, which may be considerable distances from the nesting colony, and rarely samples actual nesting areas. Long-term (1970-2021) trends determined by the BBS indicate annual decreases of 4.94% in Canada and 6.88% in Ontario. The short-term (2011-21) trends were annual decreases of 0.109% in Canada and 5.97% in Ontario. All trends were of medium reliability except that the Canadian short-term trend was of low reliability (A.C. Smith et al. 2023). Falconer et al. (2016b) acknowledged that the BBS was not well suited to adequately sample colonial birds such as the Bank Swallow.

Cadman and Lebrun-Southcott (2013) noted the disparity in the results of surveys along the Saugeen River and results of the BBS. The Saugeen River population was stable whereas the BBS indicated a precipitous decline. They suggested that removal of steep roadside banks due to changes in highway standards and increased use of berms around aggregate pits might make it more difficult to observe Bank Swallows from roadsides. This would result in a decline in numbers detected by the BBS survey methods. Another possible explanation is the loss of pasturelands and hayfields due to their conversion to row crops. Seeds of row-crop plants are treated with insecticides, so insect biomass in the vicinity of row-crop fields is lower than in most areas. Swallows may be foraging more frequently now in habitats that are infrequently sampled by the BBS. Despite the weaknesses of the BBS in sampling the Bank Swallow, the decline may be real. In Illinois, BBS results indicate an increase in this species (Walk et al. 2011).

More accurate information on the Ontario status of the Bank Swallow is available from surveys of Bank Swallow burrows conducted on Lake Erie, Lake Ontario, along the Saugeen River and other rivers, and in aggregate pits from 2009 to 2014. These data suggest approximately 110,000 individuals along Lake Erie, 20,000 along Lake Ontario, 20,000 along the Saugeen River, and 277,000 in pits and quarries. A conservative estimate of the Ontario population is 409,000 birds, but this excludes estimates from rivers in the Hudson Bay Lowland and miscellaneous habitats such as construction sites. The Hudson Bay Lowland population may be substantial and of provincial significance. Breeding has been recorded along the Severn, Fawn, Winisk, Ekwan, and Moose rivers (Falconer et al. 2016b).

The Bank Swallow is designated threatened in Canada and Ontario. The goal of the recovery strategy for Ontario is to maintain a stable, self-sustaining population of at least 330,000 breeding pairs across the breeding range by 2035. This will require reducing the annual rate of decline by 0.5% for the next 10 years. In the north where there is no targeted monitoring, the short-term goal is to maintain a breeding population distribution across each block by the time of the third atlas in 2021-25 (Falconer et al. 2016b).

POSTFLEDGING PERIOD

After the young are 12 days old, both adults roost outside the nest burrow on trees or shrubs or in marshes. For about a week after fledging, young return to the colony at night and roost in either the nest burrow or other burrows. Shortly after fledging, young and adults roost together during the day on wires and also in trees, on exposed roots in banks, in shrubs, on logs, and on sandbars and

gravel bars. Telephone and hydro lines are used most frequently where they are available. Nocturnal roosts used at this time and until autumn migration are typically in marshes or in trees near water. These are usually large communal roosts of several swallow species. Four roosting areas have been described from Ontario. Historically, very large flocks roosted along the Niagara River, Welland River, and both waterfronts in Niagara District. In the Kingston area, the Bank Swallow has roosted in the Cataraqui and Little Cataraqui marshes, which are dominated by cattails. The Pembroke roost was on a point at the confluence of the Muskrat and Ottawa rivers, and it became an island during high water. Swallows roosted in the canopy of a 0.5-ha stand of black willows 10-15 m tall. This roost was occupied for about 15 years; prior to that swallows roosted in boathouses along the waterfront. In the cattail marshes in the Inner Bay of Long Point, as many as 45,000 Bank Swallows roost nocturnally during the postfledging and autumn migration periods. Most late-summer roosts are near major rivers, large lakes, or in large marshes. Elsewhere, the Bank Swallow has roosted in willows; in marshes along the Mississippi River in Illinois; in a marsh in a bay of Lake Ontario in New York; in a large marsh dominated by cattails, irises, arrowheads, and pickerelweed; in wild rice along a river in Connecticut; and in dense stands of rushes and cattails bordering British Columbia lakes (Beyer 1938; Campbell et al. 1997; Falconer and Badzinski 2013; Falconer et al. 2016b; Garrison and Taylor 2020; Graber et al. 1972; Gross in Bent 1942; Petersen 1955; Ross et al. 1984; Sheppard et al. 1936; Weir 2008).

Juveniles may disperse widely during the postfledging period and visit several nocturnal roost sites, presumably assessing the suitability of potential future breeding sites (Falconer et al. 2016b).

MIGRATION

The Bank Swallow is a diurnal migrant that usually arrives in Ontario in late April or early May, occasionally as early as mid-April or rarely by mid-March. The peak of migration occurs in the second week of May (Falconer et al. 2016b). Spring migration is more rapid and direct than autumn migration. Early arrivals spend most of their time foraging over water, often several kilometres from the eventual nest site. Some birds may be prospecting for suitable nest sites at this time. Adults arrive 2-3 weeks in advance of yearlings and settle in the best locations within the colony. Adults may be done nest construction before yearlings arrive (Garrison and Taylor 2020; Graber et al. 1972; Gross in Bent 1942; Petersen 1955). Autumn migration is much more leisurely and prolonged, and begins in late July shortly after the young fledge. Juveniles begin migration earlier than adults, but stay in the breeding range later. At the premigratory roost in Pembroke, swallows start arriving in July and numbers continue to increase until mid-August, after which there is a decline in numbers with every cold front until the roost is abandoned by early September. Large numbers appear at Prince Edward Point in late July. Most leave the province in early September, with stragglers remaining in the south until late October (Curry 2006; Garrison and Taylor 2020; Graber et al. 1972; Gross in Bent 1942; James 1991; Ross et al. 1984; Tozer 2012; Weir 2008).

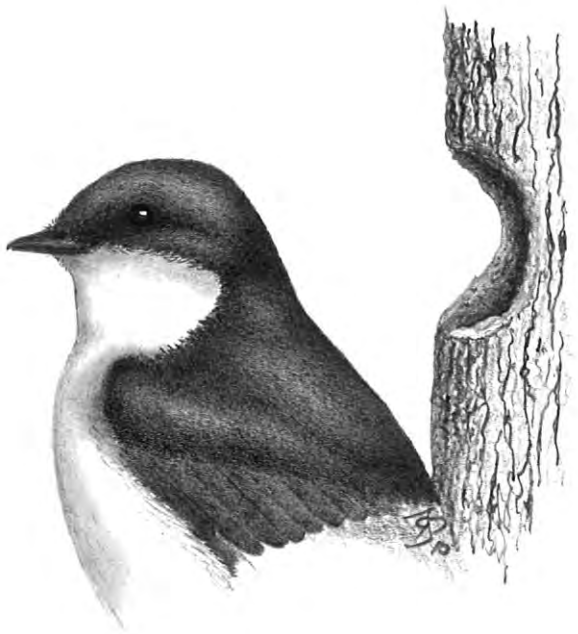
During migration, the Bank Swallow is strongly associated with large rivers and streams, although it may migrate on a wider front in spring. It may also occur over ponds, lakes, marshes, and muskegs and, to a lesser extent, fields and meadows, roadsides, farmsteads, and wooded areas. It often forages along ridges and cliff faces because the turbulent air currents at these sites bring flying insects up from lower levels. It appears to forage as it flies during migration rather than stopping at

specific sites to refuel. A variety of perches may be used during migration including dead trees, fences, hydro and telephone lines, tall plants, cattails, bulrushes, and a variety of human-made objects. During migration, it has roosted overnight in nest burrows and in marshes (Campbell et al. 1997; Graber et al. 1972; Gross in Bent 1942; Imlay et al. 2020; Paton and Fellows 1994).

The Bank Swallow is common to locally abundant during migration (James 1991). Flocks of 250 or less are typical throughout North America in spring. Autumn flocks are much larger, but there are few reliable estimates because of the mixed-species nature of the flocks. Flocks of 5,000 and 4,500 Bank Swallows were seen at Presqu'ile on 2 August 1978 and 11 August 1977, respectively. In the Hamilton area, 10,000 were noted on 10-12 July 1934 and 50,000 were estimated on utility wires near Cayuga on 19-20 July 1983 (Curry 2006; Garrison and Taylor 2020; Gross in Bent 1942; LaForest 1993; Ross et al. 1984; Weir 2008).

Tree Swallow

Tachycineta bicolor



BREEDING SEASON

Habitat Requirements

Ontario Tree Swallow nests were in a variety of habitats, but mostly in open areas. Although 58.9% were in forested areas, including swamps and burns, wooded areas that were used were usually open: 42.2% were in deciduous stands, 37.4% in mixed stands, and 20.4% in coniferous stands. Of the remaining nests, 10.8% were in wetlands (excluding treed swamps, but including cattail and sedge marshes, buttonbush thicket swamps, bogs, and wet meadows); 9.9% were on roadsides and shorelines of rivers and ponds; 7.1% on sand dunes and beaches; 5.5% in farmland, including pastures and fields; 4.1% in rural and urban populated areas, including gardens, cottage areas, lumber mills, streets, golf courses, and canals; and 3-7% on rocky islands and cliffs. More nests were reported from dry than wet areas. Many in wet habitats were where dead trees provided nest sites in open areas suitable for foraging. Nest-box locations were a major factor dictating habitat use (Peck and James 1987).

Natural nesting habitat consists of wetlands and beaver ponds where there are standing dead trees with cavities. Snags along streams, drainage ditches, and fencerows may be used for nesting provided that they are adjacent to open habitat. Substantial open areas are required around the nest for foraging. Nest boxes in open fields or near water are readily used. Near Kingston, Tree Swallows used nest boxes placed at all distances from forest (2-100 m). Boxes furthest from forest

edge were settled first, indicating a preference for nest sites distant from forest. Similar results were reported from Cape Cod, where no boxes under trees were used. In British Columbia, 59% of breeding records were from open habitats associated with humans, especially where nest boxes were available. These habitats included farmlands, rangelands, rural and suburban areas, orchards, golf courses, gardens, and pastures. Of these, 55% were in backyards or farmyards, 20% near water, and 6% in aspen parklands. Other nesting habitats included open fields and meadows, orchards, roadsides, young and mature forests, burns, bottomlands, and campgrounds. Natural habitats used in British Columbia included areas with dead trees for nesting and open spaces for foraging, such as swamps, bogs, beaver ponds, burns, river shorelines, and wet meadows. It tended to nest within 15 m of forest edge, possibly to reduce competition with European Starlings. In the Yukon, it breeds primarily in wetlands and on margins of lakes and rivers but also in open, shrubby areas; deciduous, mixed, and coniferous forests; and burns. In Illinois, nests were associated mostly with swamps or marshes with standing dead timber in or near water. In California, it was equally abundant in oak savannahs with grass or shrub cover, montane hardwoods, and oak woodlands (Aitken et al. 2002; Austin and Low 1932; Barber et al. 1996; Campbell et al. 1997; Graber et al. 1972; Rendell and Robertson 1990; Sinclair et al. 2003; Winkler et al. 2020; Wood et al. 2013).

In southern Ontario, the Tree Swallow was more abundant on organic than conventional farms but not significantly. It was significantly associated with farmsteads, streams, number of tillages, and road, railway, and hydro rights-of way. It was also associated with hay, grassy areas between fields that often contained a fence, and the number of large, isolated trees, but these relationships were not significant. It was significantly negatively correlated with habitat heterogeneity and usage of manure. Negative nonsignificant relationships were with pastures and use of biodynamic spray for weed control, or no weed control (Kirk et al. 2011).

In North Dakota, the Tree Swallow preferred areas with 2-28% tree cover (Cunningham and Johnson 2019).

In early spring, nest cavities may be used as communal roosts during prolonged periods of below-freezing weather. Near Kingston, Stutchbury and Robertson (1990) found 4 adults roosting in a box 1 morning and another morning there were 5-25 birds roosting in 5 boxes. This was after 4 days when the minimum temperature was below freezing, but roosting was not observed after a

single cold day. Roosting was not observed in warmer springs. Most roosting birds were females and only 16% remained to nest, suggesting that some were migrants.

Ontario nests were in bird boxes (84.6%); cavities in trees, snags, and roots (11.0%); cavities in fence posts, utility poles, and pipes (3.2%); holes in buildings and boats (0.5%); unspecified locations (0.4%); recesses and ledges of limestone cliffs (0.05%); mailboxes (0.05%); and cavities in street lights (0.05%). Single nests were reported in a howitzer barrel, a newspaper cylinder, a hole in a sandbank, a car tire, an unused pump, a flower pot, and a hole in a concrete wall. Bird boxes used include those made specifically for Tree Swallows as well as those designed for bluebirds, ducks, and Purple Martins. Most tree nests were in dead trees, but a few were in live trees. Single nests were reported in a floating stump and a floating tree log. Nests were both in old woodpecker nests and natural cavities. Over 80% of tree nests were in 8 species of deciduous trees; the rest were in 4 species of conifers. Preferred species, in descending order of preference, were birches, elms, poplars, willows, and pines. Height of nests in natural situations ranged from 0.2 to 23 m, with most 1.5-6 m up (Peck 1972; Peck and James 1987). Mills (1981) reported a nest in a steam boiler at a mill in Muskoka District.

Near Kingston, nest cavities were in snags from less than 2 m to more than 9 m above water, but 75% were in snags shorter than 6 m. Twenty-seven percent of nests were in tree stumps shorter than 2 m; 46% of cavities that were used were less than 2 m above the pond's surface. Cavities higher than 6 m were used infrequently, but the Tree Swallow occupied the 2 highest available cavities (8.3 and 10 m). Tree Swallow nest cavities differed significantly from the other cavity nesters (Northern Flicker, Great Crested Flycatcher, Eastern Bluebird, Eastern Starling, and Common Grackle), with other species nesting in thicker snags with larger cavity entrances and volumes. Although Tree Swallows usually occupied the lowest cavities with the smallest entrances and volumes, they also used the highest cavities with the largest volumes. The mean distance of nests from pond shorelines was 38.8 m; 77% of nests were within 55 m of shore (Rendell and Robertson 1989). Nests averaged higher in snags (3.4 m) than in boxes (1.5 m); entrance holes were larger in snags, averaging 7.6 cm high and 5.3 cm wide compared with 3.7 cm in diameter for nest boxes (Robertson and Rendell 1990).

Of 4,370 nests reported to Canadian nest record schemes, only 14% were in tree holes, typically created by woodpeckers. The Tree Swallow may also use boxes designed for bluebirds, Purple Martins, Prothonotary Warblers, Wood Ducks, and goldeneyes. In Iowa, the Tree Swallow usurped 1.5% of 534 Prothonotary Warbler nests and apparently killed 2 adult warblers. The Tree Swallow may use any nest box with a cavity entrance larger than 3.3 cm. Two Ontario studies, one of a population using natural cavities and the other in nest boxes, found that entrance cavities facing south or southeast were preferred. This may provide a warmer microhabitat. Some studies demonstrated a preference for south-facing cavities; others have found no significant differences in orientation. Adults require an unobstructed flight path to the cavity; nests may be abandoned if grass grows up in front of the cavity entrance. A number of unusual nests and nest sites have been reported: in eaves of buildings, in a Bufflehead nest, in steel drums containing Mallard nests, in old Cliff Swallow nests, in a fire hydrant, on an active ferry, in holes in the ground, an active Barn Swallow nest on the outside of a building was usurped, in a hole in a railing, in pipes, in a newspaper box, and in a small cavity in the side of an abandoned Bonaparte's Gull nest in a live spruce tree (Aitken

et al. 2002; Austin and Low 1932; Benton 1968; Butler and Campbell 1987; Campbell et al. 1997; Erskine 1979; Erskine and McLaren 1976; Graber et al. 1972; Holroyd 1975; Lumsden 1986, 1989; Munro and Rounds 1985; Rendell and Robertson 1994a; Scerbicke et al. 2024; Sinclair et al. 2003; Tyler in Bent 1942; Winkler et al. 2020).

Lumsden (1986, 1989) summarized Tree Swallow nest-box use in Ontario. It was indifferent to the interior colour of boxes, using both black and white, and had no preference for cavity entrance diameters of 3.5 cm or 4.4 cm. Large nest boxes were preferred, with an inside floor of 15.3 x 15.3 cm and a volume of 4,588 cm3 rather than a floor of 10 x 10 cm and 1,935 cm3 volume. Shallower nest boxes of 12 cm versus 16.5 cm were preferred. Once preferred nest boxes were all occupied, it occupied the other box types. Munro and Rounds (1985) described similar results from Manitoba, where it was indifferent to nest-box colour. It nested in shallow boxes near the ground, and preferred smaller cavity entrances than other species. It demonstrated great variability in nest sites and its habitat selection was the least-successfully classified by statistical analyses of the cavity-nesting species that they studied. Parren (1991) compared selection of nest boxes by Tree Swallows, Northern House Wrens, and Eastern Bluebirds in Vermont. Boxes used by swallows had fewer small woody stems under and around the box than unused sites. Used boxes provided a longer field of view and were further from high perches than those used by wrens. Bluebird and swallow nest sites did not differ significantly.

The Tree Swallow nests singly or colonially, with colonies usually associated with dead, flooded timber or clusters of nest boxes. Most apartment-type houses support only a single pair, but occasionally all compartments are occupied. Despite nesting in colonies, it defends a territory, although there are rare instances of active nests 1-3 m apart and of 2 females nesting in the same cavity. Territoriality is frequently intense against other cavity-nesting species such as Great Crested Flycatcher, Northern Flicker, Black-backed Woodpecker, Purple Martin, Northern House Wren, European Starling, and House Sparrow. Territory size may vary between natural habitats and nest-box populations. Birds nesting in a natural area near Kingston nested an average of 27.l m apart, with 62% of pairs nesting 15-35 m from the nearest pair. A few pairs nested more than 45 m apart; 2 pairs nested within 3.6 m of each other. Nests were evenly distributed and further away from each other than random. Many suitable nest sites were not used and some pairs defended multiple nest sites. Similar results were observed in natural cavities in Oregon, where the average nearest-neighbour distance was 39.4 m (range 17-70 m); 46% nested 17-35 m from their neighbour. Near Kingston, nest boxes were erected in distant clusters. The initial pattern of nest occupation was that 1 pair settled in each of the clusters before a second pair appeared in a cluster. Second pairs in a cluster typically selected the box furthest away from the occupied nest. Territorial defence declined during the nest-building stage so that birds could settle in without territorial dispute about 14 days after the early birds initiated nesting. Nest-box studies suggest defended areas of 6-8 m, but more typically 10-15 m. Territories may be smaller when food is abundant. Feeding territories are not defended (Barber et al. 1996; Harris 1979; Hussell 2012; Mitchell and Robertson 1996; Muldahl et al. 1985; Rendell and Robertson 1989, 1994b; Robertson and Gibbs 1982; Stutchbury and Robertson 1985; Winkler et al. 2020; Whittle 1926).

Home range sizes may be very large. In spring, birds may completely abandon a colony temporarily if the weather is adverse. On Kent Island, New Brunswick, the island was occasionally abandoned, and the nearest land was 10 km away. Adults may forage as far as 60 km from the nest site, with the distance travelled decreasing to 2-5 km during brood rearing (Paynter 1954; Stocek 1986; Winkler et al. 2020). Near Kingston, females tended to be detected further from the nest in the pre-laying period (average 661 m) than during the laying period (225 m). Two females roosted in or near their nest boxes and rarely moved more than 50 m from the nest, one was commonly found at intermediate distances from the nest, and one routinely roosted more than 2.5 km from the nest. Movements of Tree Swallows during the breeding season may be extensive and highly variable. Individuals do not return to the same nocturnal roost night after night (Stapleton and Robertson 2006).

Natal philopatry is low with nestlings dispersing so widely that few are recaptured in subsequent years. At Long Point, 5-10% of fledglings return to breed; of 417 young, 27 (6.5%) returned (De Steven 1980). In Saskatchewan, 0.8% of nestlings returned to a nest-box trail to nest. The nest-box trail was 77 km long and many returns were distant from the natal box (13-50 km). The average distance from the natal nest to the first breeding site was 19.2 km. Only 1 bird returned to nest in its natal box, one to a box across the road, and another returned to within 1.6 km. One nestling first nested in a box 254 km away (Houston and Houston 1987). Also in Saskatchewan, Shutler and Clark (2003) estimated that 4.9% of nestlings returned to breed, and that 23.3% of young that survived their first year returned to breed. Of natal returns, 84 were seen 1 year after hatching, 81 after 2 years, 34 after 3 years, and 1 after 7 years. Some Saskatchewan nestlings dispersed long distances, and dispersal directions were random. One was found nesting 1,965 km away in Wisconsin 4 years later and another first nested in North Dakota 1,125 km from its natal site (Stiles and Houston 1994). In New Brunswick, less than 2% of nestlings returned to nest (Wheelwright and Shultz 1994; Wheelwright et al. 1991). In Colorado, 23% of 611 nestlings returned to their natal 0.5 x 0.5-km nest-box group, but only one (0.16%) nested in its natal box. The remaining 77% that returned to the general area nested in a different 0.5 x 0.5-km grid. Another 15 birds nested about 30 km from their natal nest (Cohen et al. 1989). Natal return rates were 3.7% in Massachusetts, with some first nesting 6.4-145 km from the natal site (Chapman 1935, 1939, 1955). The low return rate may be because the later-returning yearlings may be forced to go elsewhere to secure a nest site or yearlings might disperse indiscriminately and return to the natal area only by chance. Hosner and Winkler (2007) examined North American banding records and found that prior to 1967 65-95% of juveniles returned to within 13.6 km of their banding site; recent data indicated about 25-35%. The change was attributed to changes in recapture-reporting rules. The number of long-distance (more than 100 km) recaptures increased dramatically in the 1970s, presumably due to higher effort and more banders. All datasets revealed that hatch-year birds dispersed significant further than adults. One bird banded as a fledgling in Washington State was recovered the following year in Michigan, a dispersal distance of 2,367 km. Overall, only 2.7% of juveniles dispersed further than 100 km from the natal site, and 85% dispersed less than 15 km.

Adult return rates are 13-60% with some returning to the same nest box but most to the same general area. Forty-one percent of males and 21% of females returned to the same nest box. In

Saskatchewan, the average distance between subsequent nest boxes of adult females was 37.8 km. In Colorado, 66% of returning males nested in the same box compared with 33% of females. In Massachusetts over a 15-year period, 39.6% of adults returned to breed at least once: 43.0% of males and 36.5% of females. In New Brunswick, the female return rate was 30.8%-53.8% (average 45%) and the male return rate was 8.6-50.0%. Some birds may use a nest box for as long as 5 consecutive years; others may move considerable distances between nests. One adult nested 592 km away the following year and another nested 1,085 km away (Chapman 1935, 1939, 1955; Houston and Houston 1987; Mason 1968; Shutler and Clark 2003; Stiles and Houston 1994; Wheelwright and Shultz 1994; Wheelwright et al. 1991; Winkler et al. 2020). Banding data for North America revealed that adults returned to the same banding block 96-98% of the time prior to 1967 compared with 84-89% of juveniles. Later data indicated that 50% of adults and 22% of juveniles returned. There was no difference in dispersal rates or distances between the sexes, but this may have been due to the difficulty of sexing this species (Hosner and Winkler 2007). Eight-seven percent of females that nested successfully at Long Point returned the following year, but only 4.4% of unsuccessful females returned (Bradstreet 1969). Clark et al. (2018) analyzed survival and return rates of Tree Swallows at 8 North American locations, including Long Point and Mud Creek in Ontario. Annual variations in survival were unique to each site and different at the 2 Ontario sites, although they were only 30 km apart. At Long Point, males had a higher return rate than females; the overall return rate was 77%. At Mud Creek, differences in return rates of the sexes were trivial with an overall return rate of 83%. Winter climate conditions were associated with only 9-13% of variation in survival rates at the 2 Ontario sites, but with as much as 66% in British Columbia. Severe cold weather in spring that depressed insect abundance was the greatest factor affecting survival rates in Ontario, particularly for females.

Limiting Factors

Eggs have been reported in Ontario nests from the third week of April until the first week of August, mostly in the last week of May and first week of June (Peck and James 1987). In Algonquin Park, nests are under construction from early to mid-May, eggs are present from late May to late June, nestlings are present from late May to late June, and dependent fledglings have been observed from late June to mid-July (Tozer 2012).

Early arriving pairs claim a nest cavity upon arrival, but nest construction may not start for 1-3 weeks. Late-nesting birds may build a nest in 4-8 days, but these nests are not as well constructed. Earlier-nesting birds may take 2 weeks to build a nest. In southern Ontario, nest construction usually begins in the last week of April and continues into early May. Most eggs are laid in southern Ontario 5-22 May (range 3 May-1 July). In the Kingston area, most clutches are initiated 11-16 May, with a few later clutches laid by yearlings. At Long Point, clutch initiation was 7-28 May. Near Sudbury, the first eggs were laid between 15 May and 2 June (mean 23 May). In Michigan, yearling females began laying an average of 7 days later than older females. Eggs are typically laid at the rate of 1 a day; longer intervals occasionally occur, usually in response to adverse weather. Females can rest 1-7 days between eggs without affecting viability. Incubation usually begins with laying of the penultimate egg, but it may rarely be delayed by as much as a week. Typical Ontario incubation periods were 10-17 days, averaging 13-14 days. The incubation period at 1 nest was 7 days indicating

that incubation was initiated early during the egg-laying phase. At 10 nests, incubation periods were 18-25 days indicating a delay in incubation. Elsewhere incubation periods of 11-19 days have been reported, with most eggs hatching in 14-15 days. The incubation period is strongly influenced by weather and takes longer in cold weather when clutches may be temporarily abandoned. Most clutches hatch in 1-2 days. Rarely, all eggs hatch on the same day, or hatching may occur over 3 days. At Port Rowan, 90% of nestlings from 6-egg clutches hatched on 31 May and 1 June. Fledging occurs at age 15-25 days, but mostly in 18-22 days. Larger broods tend to have longer nestling periods because food delivery rates do not vary according to brood size. Fledging is asynchronous. In Manitoba, only 13.8% of birds fledged from nests on the same day (Austin and Low 1932; Blancher and McNicol 1988; Campbell et al. 1997; Coe et al. 2015; Hussell 2003; Hussell and Quinney 1987; Leffelaar and Robertson 1986; Lombardo et al. 2024; Paynter 1954; Peck and James 1987; Quinney et al. 1986; Stutchbury and Robertson 1985; Tyler in Bent 1942; Wheelwright and Shultz 1994; Winkler et al. 2020; Zach 1982).

Normally 1 brood is raised per season with second broods rare, except perhaps in the southern portion of the Tree Swallow's range. Double broods have been reported in Ontario (Peck and James 1987), and Hussell (1983) reported 2 pairs raising 2 broods in a single season at Long Point. In the first case, eggs were laid in another nest box before the first young fledged. It was uncertain if any young fledged from the second brood. In the second case, eggs were laid in the same box starting 12 days after the last young fledged from the first brood. All young successfully fledged from both broods. Both double-brooded pairs were the earliest recorded breeders at the site. In Colorado, no second broods were documented in thousands of nestings. In Massachusetts, only 1 case of double brooding occurred in 22 years of study (Chapman 1955; Winkler et al. 2020). In Tennessee, 88 of 206 pairs (42.7%) were double brooded. Second broods contained about 1 egg less, fledged 1 less young, and had lower success than single and first broods. Females with second broods initiated clutches 5 days earlier than single-brooded females, a significant difference (Aborn 2020). In Virginia, Monroe et al. (2008) confirmed 18 cases of double brooding, 5% of birds that successfully raised first clutches. Most double-brooded females initiated their first clutches before the peak of clutch initiation. Females with earlier and smaller clutch sizes were most likely to breed twice within a season. Double-brooded females initiated their first clutch 5.4 days after the first egg of the season compared with 12.8 days for single-brooded females. Double-brooded females waited an average of 9.3 days after young from the first nest fledged before starting a second clutch. Renesting is common if the first clutch is lost; females may lay 3 clutches in an attempt to raise a brood. Renesting may occur either in the same or a different cavity. Clutches of 2-12 eggs have been reported in Ontario. Both a 9- and a 10-egg clutch were known to be produced by 2 females. Most clutches contained 5 or 6 eggs. Mean clutch sizes at Ontario study areas were 4.68, 5.60, 5.81, 5.92, and 6.20 eggs. Throughout its range, the clutch size is 2-8 eggs, but typically 4-7. Clutches larger than 8 eggs are probably due to the efforts of more than 1 female. The mean clutch size in 13 populations ranged from 4.7 to 6.2 eggs. There is a slight tendency for clutch size to increase with latitude, and clutch size declines with the season. Seasonal declines in clutch sizes are greater at higher latitudes. This appears to be related to food supply, with insect availability declining more rapidly with time at more northerly locations. Yearlings tend to nest later than adults and consequently have smaller clutches. Later clutches may be 1-3 eggs smaller than early clutches. In Wyoming, females nesting

at high altitudes began laying eggs an average of 10 days later than those nesting at lower elevations and laid an average of 0.4 fewer egg, a significant difference. This may have been a response to the later clutch initiation or the colder weather, or may have been an adaptive mechanism to ensure that there was adequate food to feed the nestlings. In New Brunswick, first nests had significantly larger clutches (5.86 eggs) than replacement nests (5.00 eggs). In Ontario, clutch size did not increase with female age after age 2 years. In New Brunswick, clutch size tended to increase with age until age 4 years, after which it declined (Austin and Low 1932; Blancher and McNicol 1988; Campbell et al. 1997; Chapman 1955; Dunn et al. 2000; Hussell and Quinney 1987; Johnson et al. 2018; Karagicheva et al. 2016; Lombardo 1983; Paynter 1954; Peck and James 1987; Rendell and Robertson 1989; Stutchbury and Robertson 1988; Tyler in Bent 1942; Wheelwright and Shultz 1994; Winkler et al. 2020).

Clutch size in Ontario is influenced by the physical characteristics of the nest cavity and food availability. Near Kingston, clutches were significantly smaller in small nest boxes and natural cavities than in large nest boxes. Clutch size was determined by the area of the floor of the cavity, but was not influenced by cavity volume. Near Long Point, insect biomass varied significantly at 3 study areas, and was significantly correlated with clutch size. The greatest effect was during egg laying when 85% of variation in clutch size was explained by insect biomass. At 1 site, 25% of swallows laid 7 eggs compared with 4% at a site with 90% less insect biomass (Blancher and McNicol 1988; Hussell and Quinney 1987; Quinney 1983; Rendell and Robertson 1989, 1993; Robertson and Rendell 1990). In Quebec, clutch size was negatively correlated with the amount of intensive agriculture, with birds in these landscapes laying fewer eggs than those in landscapes dominated by hayfields and pastures. Greater amounts of pesticides are used in intensive agricultural areas, which may affect swallows' physiology and reduce breeding success (Pellerin et al. 2016).

The Tree Swallow is typically monogamous, but some cases of male polygyny have been reported. In some cases, both females deposited eggs in the same nest and all 3 adults cooperated to raise the brood. More frequently, the second female nested a short distance from the first and the male helped provide food to both broods. Over 3 years, 7%, 8%, and 0% of males were polygynous in Alberta; the frequency of polygyny may be related to food abundance or scarcity of nest sites. Occasionally pairs remate for more than 1 year. This may be more site tenacity rather than prolonged attraction to the same mate. Near Kingston, 50% of broods contained young sired by extra-pair males, totalling 38% of young. Broods contained either 0 or many illegitimate young. Resident males sired only 20% of extra-pair young. In Oregon, 69% of young were fathered by extra-pair males; 44% of broods were entirely extra-pair young and 40% consisted of both extra-pair and within-pair young. One young was fathered by the male but was not related to the female. There was no significant difference in rates of extra-pair paternity between nest boxes and natural cavities. In 93 Wisconsin broods with mixed paternity, 33% of young were sired by the social mate and 67% were sired by an extra-pair male. Successful extra-pair sires were more experienced breeders and were larger and in better condition (Barber and Robertson 1999; Barber et al. 1996; Chapman 1935, 1955; Dunn and Hannon 1991, 1992; Farber 1972; Leffelaar and Robertson 1985; Lifjeld et al. 1993; C.A. Long and Long 1990; Pinkowski 1975a; Quinney 1983, 1986a; Simmons 1985; Stutchbury and Robertson 1985; Whittingham and Dunn 2014; Winkler et al. 2020). Intraspecific nest parasitism

occurred at 5.8% of nests in New York, with 2 eggs appearing in a nest in a day. This was considered an underestimate; the revised estimate was that 9.2% of nests were intraspecifically parasitized. At another 6.7% of nests, eggs disappeared during egg laying. They may have been removed by a parasitic female (Lombardo 1988; Winkler et al. 2020).

Both sexes are capable of breeding at age 1 year. In some populations, few yearlings breed because they are unable to secure a nest site. Yearlings are further disadvantaged because they arrive on the breeding grounds later and have a different plumage than older birds. The proportion of yearling females breeding in a population varies from 10% to 80%; in newly established populations, 70-80% of yearlings breed compared with 6-35% in well-established populations. Essentially all 2-year-olds breed. Nonbreeding birds constitute a floater population which was estimated to be 23-27% of the total population near Kingston. Floaters frequently visit active nests. Originally it was thought that they were helping at the nest but it appears as though they are prospecting for a future nest site. When nest boxes were erected later in the nesting season near Kingston, floaters defended them within a few hours (Chapman 1955; Lombardo 1985; Stutchbury and Robertson 1985, 1987; Winkler et al. 2020).

De Steven (1978) compared the breeding biology of yearling females with that of adults at Long Point. Yearlings had a significantly smaller clutch size (5.1 eggs compared with 5.9), lighter eggs, and laid first eggs an average of 2.6 days later than adults. The percentage of hatched young that fledged was significantly lower for yearlings (92.7%) than for older birds (99.4%), and older birds raised more young.

Almost all the Tree Swallow's food is obtained by aerially foraging on insects. In New York, most foraging occurred within 100-200 m of the nest at heights of less than 12 m. Less than 20% of the time was spent foraging at heights greater than 12 m. In Saskatchewan, it foraged at a mean distance of 182 m from the nest over an area of 1.3 km2. It spent a disproportionate amount of time foraging in and near wetlands and avoided crop fields. Occasionally it lands on the ground to forage, often in flocks. This is typically in response to high concentrations of food such as emerging midges and stoneflies. It may take insects from the surface of water and has taken seeds out of ice in a pond while in flight. In New York mixed swallow flocks, the Tree Swallow foraged much lower than Cliff Swallows. It either foraged in different strata or habitats than Barn Swallows, or the 2 species captured different prey. In northwestern Ontario, 87.9% of foraging time was over water during egg laying, but only 31.6-56.8% during incubation (Cohen and Dymeraki 1986; Erpino 1984; Harris et al. 2024; Hobson and Sealy 1987a; McCarty and Winkler 1999a; Paton and Fellows 1994; Ramstock et al. 1998; St. Louis et al. 1990; Tyler in Bent 1942). Curry (2006) reported Tree Swallows foraging on the ground in yards in Caledonia during a period of unusually cold weather.

Nestlings are brought a variety of flying insects. Young have been fed leafhoppers, aphids, snails, clams, crayfish parts, fish bones, and a variety of fly species, particularly midges. An Ontario study determined the nestling diet to be 46% flies, 26% bugs, 11% mayflies, 5% dragonflies and damselflies, 4% beetles, 4% molluscs, 2% spiders, 1% book lice, 1% hymenopterans, and traces of lacewings, caddisflies, and lepidopterans. At Wahnapitea, snails, clams, and crayfish parts were fed as a calcium supplement to nestlings. In this area, the most important nestling foods by mass were horse flies (14.4%) and burrowing mayflies (13.4%). Non-living, high-calcium foods (mollusc shells

and fish bones) constituted 3.5% of nestlings' food. The nestling diet was 6.4% aquatic compared with 32.3% terrestrial items, and 2.8% semiaquatic animals. Midges comprised 22% of trap biomass but only 5% of the nestling diet. Mayflies were less than 1% of trap biomass but 21% of the nestling diet. Other items fed to nestlings near Sudbury were house flies, hump-backed flies, aphids, leaf bugs, and dragonflies. Midges were 44-92% of items fed to nestlings in different studies in the Long Point–Port Rowan area (Blancher and McNicol 1988, 1991; Chapman 1955; Hussell 1988; Pinkowski 1975a; Winkler et al. 2020). In southern Ontario, the diet of nestling Tree Swallows was predominantly aquatic emergent insects. Barn Swallow nestlings were fed mostly terrestrial insects; the diet of Cliff Swallows was intermediate (Bumelis et al. 2022). Tree Swallow nestlings also fed more on aquatic-emergent prey than Barn Swallow nestlings in Saskatchewan (Diaz Bohorquez et al. 2025).

Near Port Rowan, 74% of the adult diet consisted of flies, mostly nematocerans such as midges. The Tree Swallow also ate other flies, bugs, and dragonflies. The largest insect eaten was a 42-mm dragonfly. It preferentially fed on medium-sized (4-6 mm) insects. At 1 site, 45% of the diet consisted of medium-sized insects compared with 13% availability; at another site, medium-sized insects were 43% of available prey and 61% of food. Small (1-3 mm) and large (7-10 mm) prey were taken significantly less than their availability. Only 18 of 3,318 insects (0.7%) in the diet sample were larger than 10 mm (Quinney and Ankney 1985). Blancher and McNicol (1988, 1991) reported a greater variation in diet near Sudbury. It was affected by the acidity of the lakes that swallows nested beside. They fed on emergent insects such as midges, mayflies, dragonflies, damselflies, and caddisflies. Egg-laying females ate snails, fish bones, and calcareous grit to obtain calcium. Midges and house flies are small, but were important in the diet due to their abundance. Large prey species were eaten much less frequently, but were important to the diet in terms of mass: giant casemaker caddisflies (7.0%), lappet moths (6.2%), crimson-ringed whiteface (a dragonfly, 4.6%), and soldier flies (3.9%). Flies comprised 70-75% of the adult diet. Egg-laying females also preyed on mayflies (15%) as well as midges and black flies. Later in the season, adults ate more dragonflies and damselflies (10%) and a variety of smaller terrestrial prey. Midges and black flies were consumed primarily in the morning. Horse flies were most likely to be eaten in wetlands with extensive littoral areas. Terrestrial species were eaten mostly late in the season. It preferentially selected mayflies, particularly burrowing mayflies. Prey 1-35 mm long contributed significantly to the diet. With the exception of 5 families of large moths with mean lengths of 13-19 mm, almost all terrestrial prey was less than 10 mm. Several aquatic food items were longer than this including all odonates and several mayfly, caddisfly, and fly species. At Vermilion Bay, St. Louis et al. (1990) found that midges less than 8 mm long were the dominant insect and assumed that this was the major food item. Swallows appeared to respond to emerging midges and fed on concentrations of them. There was no apparent preference for species of midges. Nancekivell and Nocera (2025) used DNA to analyze the adult diet in New Brunswick and compared the diet of the Tree Swallow to those of the Alder and Least flycatchers and the Bank, Barn, and Cliff swallows. All species differed in their dietary breadth and prey preferences. The Tree, Bank, and Cliff swallows ate more aquatic flies and other taxa than the other species, which consumed more terrestrial flies. The 2 flycatcher species and the Tree and Barn swallow had broader generalist diets than Bank and Cliff Swallows, which had more restricted diets. The approximate frequencies of occurrence of invertebrate groups in the diet of the Tree Swallow were 90% aquatic

flies, 15% terrestrial flies, 10% lepidopterans, 10% aquatic beetles, 10% terrestrial beetles, and 5% or less for bugs, hymenopterans, caddisflies, mayflies, and odonates. The approximate frequencies of occurrence of invertebrate families in the Tree Swallow diet were 60% limoniid crane flies, 35% mosquitoes, 35% midges, 10% marsh beetles, 10% ground beetles, and 5% or less for long-legged flies, bristle flies, flower flies, snipe flies, and leafroller moths.

Beal (1918) examined 343 Tree Swallow stomachs, including some from Ontario. It was the only swallow that ate an appreciable amount of vegetable matter: 80 stomachs contained vegetable matter, and 35% contained nothing else. The diet consisted of 80.5% animal and 19.5% vegetable matter. Vegetable matter eaten was predominantly bayberries (16.9% of the diet); they were eaten all summer. Other seeds and fruits eaten were those of red cedar, dogwoods, Virginia creeper, grasses, and lady's-thumb. Flies constituted 40.5% of food items, but only of 5 families: crane flies, horse flies, robber flies, flower flies, and house flies. Beetles comprised 14.4% of the diet including 5.9% scarab beetles and 1.9% weevils. Other invertebrates eaten included ants (6.4%), other hymenopterans (7.6%), stink bugs, treehoppers, aphids, chinch bugs, lepidopterans (1.1% annually, mostly adults but some caterpillars), dragonflies, mayflies, and spiders. Almost 2% of the diet in August and September consisted of grasshoppers, with an annual rate of 0.4% of the diet; grasshoppers were not actively selected. These results differ significantly from Ontario studies. Midges are important in the Ontario diet, and the Tree Swallow has not been reported eating any vegetable matter. In New York, it ate a wide range of insects from at least 11 orders, but flies were most frequently consumed. Bugs, odonates, and other taxa were equally important some years. Dragonflies, damselflies, and brachyceran flies were actively selected. Bugs were eaten in proportion to their availability. It ate food 1-50 mm long, but insects 3-5 mm long formed the greatest proportion of the diet. Insects 0-3 mm were selected (McCarty and Winkler 1999a). In Saskatchewan, aquatic flies and odonates comprised most of the diet of adults and nestlings. The nestling diet contained higher proportions of terrestrial flies and a wider dietary niche than adults, indicating a seasonal change in adult feeding habits (Michelson et al. 2018). When feeding over running water, the diet may change to stoneflies, mayflies, and caddisflies; the latter 2 orders are also consumed when feeding over ponds or lakes. It has fed on crustaceans, water boatmen, bulrush and other sedge seeds, fragments of rose thorns, and flying ants (Tyler in Bent 1942; Winkler et al. 2020).

In Ontario, 1 of 4,585 (0.02%) Tree Swallow nests was parasitized by cowbirds (Peck and James 1997). Winkler et al. (2020) knew of only 1 other definite record of cowbird parasitism and concluded that cavity nesting probably limited parasitism. In British Columbia, 0 of 3,329 nests were parasitized (Campbell et al. 1997). Mills (1988) experimentally parasitized 15 Ontario nests with a cowbird egg. One egg disappeared the day before swallows hatched; only 7 of the 14 remaining eggs hatched. All 7 cowbird young died 3-12 days after hatching. Six of the 7 nests fledged all swallow nestlings, but the other failed completely. He concluded that the Tree Swallow was a poor host for the cowbird, in part due to cavity nesting, but also because adults are often off the nest foraging for prolonged periods. Hauber (1998) artificially parasitized a nest in New York by putting a young cowbird in it. The cowbird nestling was accepted and it appeared to fledge successfully. It was concluded that the cowbird does not typically parasitize the Tree Swallow because the 2 species

were historically separated and the cowbird may not recognize it as a potential host, and nest defence in swallow colonies may deter cowbirds.

Food availability can be a significant limiting factor that may affect reproductive success. Prey abundance may be affected by weather, nutrient levels in wetlands used for foraging, lake acidity, and whether a lake supports fish. Food availability may affect the ability of single parents to raise a brood. In the Kingston area, both adults appear to be necessary for young to fledge, but in the Long Point area and Alberta, where insects are more abundant, single parents successfully fledged most, if not all, young (Dunn and Hannon 1992; Leffelaar and Robertson 1985, 1986; Quinney 1986b; Winkler et al. 2020). At Port Rowan, insect abundance significantly affected nestling growth rates and survival. Of females attempting to raise 6 young, the average number of fledglings was 6.0 where insects were abundant and 5.5 where insects were less abundant. All young that died appeared to have starved (Quinney et al. 1986). Nest-box occupancy was always 98% or higher at sites with high insect abundance but varied between 75% and 96% at sites with relatively low insect abundance (Hussell 2012).

In New Brunswick, weather conditions significantly affected swallow foraging behaviour. Birds were completely absent when the weather was unsuitable, presumably due to a lack of flying insects, but all were present when conditions were suitable. Swallows were never seen at the colony when the temperature dropped below 13°C. The mean temperature was 19.7°C when birds were present and 11.2°C when they were absent. When temperatures were 13-20°C, birds were more likely to be present if the sun was shining. Birds were often, but not always, absent during rain. Stocek (1986) concluded that temperature was an important influence on swallow movement to 15°C. Between 15 and 20°C, the presence of sunshine and duration of rain had a significant effect on whether swallows remained in the area. Other studies demonstrated that nest success is significantly lower in colder years, particularly when there is accompanying precipitation. In Saskatchewan, where productivity declines have been demonstrated in cold, wet years, egg mortality was high 1 year with very hot temperatures. In the same area, a heavy snowfall early in the season resulted in swallows abandoning their nests and renesting (Austin and Low 1932; Chapman 1935, 1939, 1955; Houston 1982; Houston and Houston 1998; McCarty and Winkler 1999b). During cold weather birds may succumb to starvation or directly to cold. In New York, over 85% of birds found dead in nest boxes during a cold spell were yearlings. Yearlings are more susceptible to cold because of inexperience in using plant food when insects are scarce, finding and capturing insects, and finding a safe refuge during inclement weather. Almost complete nest failure may occur in populations during cold, rainy weather in spring (Lombardo 1986; Shutler and Clark 2003; Stiles 1998; Tyler in Bent 1942). Later nesting birds are less successful in raising young with the condition of offspring explained by weather conditions, emphasizing the importance that delays due to inclement weather may have (Dawson 2008). Cold springs that depressed insect abundance were the most significant factor affecting survival of females at Long Point and Mud Creek (Clark et al. 2018). In British Columbia, clutch size, number of eggs hatched, and number of young fledged were lower in years with high amounts of early season snowfall and cooler temperatures (McArthur et al. 2017).

In New York, foraging Tree Swallows focused on ponds with higher nutrient levels and no fish. In spring, when they are vulnerable to cold weather and food shortages, they selected feeding areas that produced the greatest number of insects. Later in summer, when insects were abundant everywhere, no preference for ponds was exhibited (McCarty 1997).

Near Sudbury, lake acidity explained 31.5% of variation in clutch size. Nestling growth increased with increasing water alkalinity but decreased if fish were present. Fledging success increased as wetland or lake pH increased. At acidic sites, clutches averaged 0.8 egg less per clutch, and 1.3 fewer nestlings fledged per successful nest. Fledglings on acidic sites were significantly smaller. Midges are unaffected by acidity; at wetlands with pH greater than 6.0, nestlings were fed 30% mayflies compared with 11% at acidic sites. Caddisflies were important foods at pH 5.0-6.0, but were seldom eaten elsewhere. Calcium-rich foods are important to developing nestlings and egg-laying females. These were obtained locally in wetlands that were not acid stressed; adults nesting at acidic wetlands travelled as far as 2 km to obtain mollusc shells. More dragonflies and damselflies were eaten at acidic wetlands and where there were no fish. Emergence traps indicated fewer insects at acidic areas. The diversity of food that was available and fed to nestlings was also a function of pH. Thirteen of 14 mollusc species fed regularly to nestlings occurred only where the pH was higher than 6.0. Thirteen of 18 mayfly genera occurred only where the pH was higher than 6.0 and none were observed at a pH of less than 5.0. The important mayfly in the diet, a burrowing mayfly, occurred only in lakes larger than 12 ha with a pH above 6.0. Increasing acidity resulted in a switch in diet from acid-sensitive mayflies to more tolerant flies (midges), a decline in the diversity of foods eaten, a change in the size and type of calcium-rich food fed to nestlings, and a decline in number of young fledged (Blancher and McNicol 1988, 1991). At Vermilion Bay, more acidic lakes had lower densities and levels of emergence of midges. Tree Swallows foraged at their nest-site lakes when emerging insects were abundant, but foraged elsewhere when prey was scarce (St. Louis et al. 1990).

In Saskatchewan, males nesting at croplands spent 14% of their time near the nest box compared with 62% for males in grasslands; agricultural females spent 19% of their time at the nest box compared with 35% for grassland females. Reduced insect availability in agricultural areas increased the time spent away from the nest to forage. Wetlands in agricultural sites had higher concentrations and frequencies of detections of neonicotinoid insecticides than wetlands in grasslands. Heavier pesticide use in agricultural areas may reduce prey biomass and availability. Birds at agricultural sites may reduce parental care in response to lower food availability and focus more on satisfying their own energy demands. Nestlings raised in grasslands were in better condition than those raised in cropland (Stanton et al. 2016). In Saskatchewan, Michelson et al. (2018) compared the diet of the Tree Swallow in grassland and row-crop agricultural landscapes with similar densities of wetlands. More than 75% of the adult and nestling diets were composed of aquatic invertebrates at all sites and in all years. Nestlings consistently had a higher proportion of terrestrial flies in their diet and a broader diet than adults. The proportions of all prey sources (aquatic and terrestrial) were similar in croplands and grasslands indicating that wetlands provide essential habitat that may buffer some of the effects of agriculture. Small patches of seminatural habitat such as roadside ditches with grasses and herbaceous vegetation, trees, and shrubs may provide adequate insect prey even in areas dominated by row-crops. Bellavance et al. (2018) studied the effects of agricultural

intensification on prey availability and nestling diet in Quebec. In crop-field landscapes, arthropod abundance was highest early in the season, increased to a small peak in mid-June and then decreased strongly. In non-agricultural landscapes, arthropod abundance increased at an increasing rate throughout the sampling period, with greatest abundance occurring in early July. Landscapes that were 50% cultivated showed only a slight increase in arthropod abundance throughout the sampling period. Associations between fly subgroups and landscape composition differed between trap and nestling diet samples suggesting that prey selection was altered by agricultural intensification. Results suggested that agriculture can alter the availability of preferred prey for the Tree Swallow.

Because the Tree Swallow is a cavity nester, nest-site availability is one of the greatest limiting factors. The provision of nest boxes may result in establishment of a population in an area where it was formerly rare or absent. At Long Point, it was traditionally absent most years. The first year that nest boxes were erected, 2 pairs nested in the 6 boxes. A decade later, 152 pairs nested in the 171 available boxes. The scenario of populations being created as a result of nest-box programs is common throughout its range (Austin and Low 1932; Holroyd 1975; Houston and Houston 1998; Winkler et al. 2020). In the Kingston area, significantly more nests in boxes were successful than those in natural cavities. Adults appeared to prefer boxes to natural cavities. Similar results were observed in Oregon. Near Kingston, higher nests in natural cavities were significantly more successful, with nests less than 4 m from the ground suffering highest predation rates. Nest height was the primary factor affecting nest success (Barber et al. 1996; Rendell and Robertson 1989; Robertson and Rendell 1990).

The Tree Swallow experiences competition for nesting cavities even where cavities are relatively common. Near Kingston, it had 5 competitors for natural cavities: Northern Flicker, Great Crested Flycatcher, Eastern Bluebird, European Starling, and Common Grackle. In nest boxes, the only competitors were bluebirds and Northern House Wrens. Great Crested Flycatchers were usually successful in evicting swallows; in some cases swallows were triumphant over flickers, but occasionally flickers took over swallow nests and they may remove swallow eggs. Northern House Wrens may be significant competitors for nest sites, but usually only within 20-30 m of a forest edge. Wrens may puncture eggs or kill young, or fill the cavity with twigs, which typically results in desertion. The most significant competitors appear to be House Sparrows and starlings. Most Tree Swallows were evicted from villages and towns once the House Sparrow arrived. The Tree Swallow may take over Purple Martin and bluebird nests and it also may be evicted by them. It may compete successfully with the Prothonotary Warbler for nest sites. Other species that have been documented taking over Tree Swallow nests include Buffleheads, red squirrels, and northern flying squirrels (Austin and Low 1932; Erskine and McLaren 1976; Graber et al. 1972; Holroyd 1975; Lumsden 1989; McIlwraith 1894; Rendell and Robertson 1990, 1991; Robertson and Rendell 1990; Tyler in Bent 1942; Winkler et al. 2020).

At Fox River and Green Bay, Wisconsin, PCB concentrations in eggs, newly hatched young, and 12-day-old nestlings were significantly higher at contaminated sites than control areas. This is one of the highest contaminated areas in North America, but PCBs did not appear to affect nesting success. Birds nesting around other areas of the Great Lakes had lower PCB burdens, except for the

Cornwall area which had similar levels (Custer et al. 1998). McCarty and Secord (1999) concluded that PCBs were a hormone disruptor that may affect its behaviour. In Atlantic Canada, Burgess et al. (2001) documented increased levels of PCBs, DDE, dioxin, and selenium in Tree Swallows nesting near known contaminated areas. All sites were less contaminated than polluted areas in the Great Lakes and St. Lawrence and Hudson rivers. In southern Ontario, Bishop et al. (2000) studied the effects of pesticides used in apple orchards on the Tree Swallow. It experienced significant declines in reproduction with increased pesticide exposure and toxicity. Pesticides resulted in declines in egg fertility and daily egg and chick survival. Organochlorine concentrations in eggs did not correlate with reproductive outcomes, but cumulative toxicity scores and organochlorine concentrations were significantly correlated suggesting a combined effect of residual organochlorine concentrations and current-use pesticides. Organochlorine compounds, particularly DDE, are likely to affect egg survival in some orchards and other compounds such as oils and sulphur appear to be potentially toxic. Although the fungicides applied in the apple orchards appeared to have low toxicity to birds, they are applied repeatedly at high rates and often in combination with other chemicals and contributed to the overall toxicity score of nests. Swallows that nested in orchards in British Columbia had 7.7 times more DDT, 2.8 times more DDE, and 4 times more DDD than swallows nesting in other habitats. Despite the high contaminant burden, there was no apparent effect on reproductive success. Contaminants were accumulated locally rather than on the wintering grounds (Elliott et al. 1994). Bouland et al. (2012) examined the sex ratio of broods of Tree Swallows nesting in the floodplain of a river in Virginia that was contaminated with mercury. Broods in contaminated sites contained a mean of 31% males compared with 46% in uncontaminated areas. The bias toward female-dominated broods in contaminated areas may be due to endocrine disruption. The Tree Swallow is vulnerable to polycyclic aromatic hydrocarbons which are highly correlated with egg failure. Nestlings of birds nesting near wastewater treatment facilities in southern Ontario are exposed to brominated flame retardants and stain repellents. Due to the predominance of aquatic prey in its diet, the Tree Swallow is an important bioindicator of environmental contaminants. Many colonies have been established in the Great Lakes Basin to monitor pollutants (Hopkins et al. 2024).

In Quebec, Pigeon et al. (2013) determined that intensive agriculture can lower the fitness of adults, but females are able to buffer these impacts so that they do not affect nestlings.

The reproductive success of Tree Swallows nesting under 765 kV and 69 kV transmission lines in Ohio was compared with control areas. Significant reductions in breeding success under power lines occurred at all sites. The mean number of young fledged was 3.53 under power lines compared with 4.54 at control sites. Areas under high-voltage lines may be suboptimal breeding habitat (Doherty and Grubb 1998). In Manitoba, it avoided nesting in areas of high radiation. Nest boxes that were selected had a mean exposure of 9.3 µC per kg per day compared with highs of 38.7 µC per kg per day. Zach and Mayoh (1982) concluded that birds may be forced to use nesting boxes in higher radiation areas when breeding densities are higher, and this may reduce breeding success or growth of nestlings.

In New Brunswick over a 24-year period, the breeding population on an island decreased over 90%. The major reason for the decline was low immigration rates to the island, followed by survival

rates of males and females. Natal philopatry rates were less than 6%, so local recruitment and reproduction rates had little effect on population trends (Taylor et al. 2018). Near Kingston, Cox et al. (2018) determined that population trends depended upon juvenile recruitment, adult return rates, and fledging success. The number of nesting attempts, clutch size, and hatching rate had little effect.

In Montana, salvage logging after a forest fire significantly decreased the number of breeding Tree Swallows (Hutto and Gallo 2006). In Quebec boreal black spruce forests, it occurred only in recent burns and was absent in clear-cuts and all forest stages (Imbeau et al. 1999).

Tree Swallows nesting in boxes exposed to playback of natural gas compressor noise spent less time incubating, had fewer eggs hatch, and produced fewer young than neighbours in quiet boxes (Williams et al. 2021).

Price (2004) predicted that the breeding range of the Tree Swallow might contract in southern Ontario if the average summer temperature increased by 2°C. Bradley (2015) summarized results from across Canada that examined its adaptability to changing temperatures. Birds at Long Point were much more flexible in their timing of initiation of egg laying and thus better adapted to changing temperatures than birds nesting further north. In Michigan, the first egg dates of older females got earlier with warmer April and May temperatures but yearling female first egg dates did not change with increasing temperatures (Lombardo et al. 2024).

Status

Ontario's Tree Swallow population increased after deforestation due to European settlement, and again when nest-box programs were initiated. McIlwraith (1894) considered it a common summer resident. Sheppard et al. (1936) stated that it was rare in Niagara Region. Baillie and Harrington (1937) concluded it was probably the most common swallow in the province, nesting throughout the south and commonly to southern James Bay and the Manitoba border. They thought that it probably nested throughout the province. Smith (1957) considered it very common in the Clay Belt. The first atlas confirmed that it was common throughout the province, with highest concentrations in the Kawartha Lakes area. Populations appeared to be lower in the extreme southwestern portion of the province (Quinney and Dunn in Cadman et al. 1987). James (1991) termed it a common to locally abundant breeder throughout the province, except in the Hudson Bay Lowland where it is rare.

The second atlas demonstrated that there had been no change in the range of the Tree Swallow since the first atlas. Breeding evidence was obtained in virtually every square south of the Shield. Its probability of observation declined significantly in the province between the 2 atlases. Declines were experienced in the Canadian Shield with populations remaining stable in other regions. It was most abundant south of the Shield. This was to be expected given the open habitat in this area and the numerous nest boxes that are present. In the Shield, it is restricted mostly to wetlands and areas of human populations. It is less common in the Hudson Bay Lowland, probably due to a scarcity of trees with cavities suitable for nesting (Lepage in Cadman et al. 2007).

Michel et al. (2016) used Breeding Bird Survey (BBS) data to analyze population trends of the Tree Swallow over broad geographic areas. In the east, Tree Swallow trends were declining in New

England and the Maritimes, but increasing throughout the mid-Atlantic and southern Great Lakes regions, and were stable in interior Quebec and Ontario. There was little concordance among the trends of avian species of aerial insectivores. The strongest relationship was observed in the Great Lakes area where declining trends of the Barn Swallow were positively correlated with those of the Purple Martin and Tree Swallow, which showed a slight but nonsignificant decline. Overall, the Tree Swallow exhibited the most stable and increasing population trajectory. Although the aerial insectivores are often considered to be a guild that is declining, only the Chimney Swift exhibited significant declines in over half its population trajectories. The lack of concordance among the species suggests that they are not showing similar responses to local ecological processes. Results indicated that declining population trends among aerial insectivores are not universal either within or across species. There was limited evidence that declines are concentrated in any single region of North America.

Long-term (1970-2021) population trends determined by the BBS were annual decreases of 1.05% in Canada and 2.42% in Ontario. The short-term (2011-21) trends were annual decreases of 1.11% in Canada and 1.08% in Ontario. All results were highly reliable except that the short-term Ontario trend was of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Shortly after fledging, young and adults leave the nesting area and gather in good foraging areas such as meadows bordering marshes or rivers (Tyler in Bent 1942). In large areas of its Ontario breeding range, the Tree Swallow may be absent by mid-July, but remains common at roosts. The Pembroke roost is at the confluence of the Muskrat and Ottawa rivers on a small point that becomes an island during high water. It is a 0.5-ha stand of black willow 10-15 m tall. Swallows roost in the canopy, starting in early July. This roost had been used for about 15 years by 1984 with swallows roosting in boathouses prior to that. In Kingston, birds start flocking in early July and gather on utility wires and trees, usually near marshes. The major roost there is in the cattail marsh along the Cataraqui River. This roost has been used traditionally for at least 32 years. Major roosts are used throughout autumn migration, with new birds arriving from the north and flocks leaving constantly after mid-August (Ross et al. 1984; Weir 2008).

MIGRATION

The Tree Swallow is a diurnal migrant that flies low to very high, often in loose flocks. It typically arrives in the province in mid-April, rarely in late February (James 1991). There are indications that it now arrives earlier than historically; McIlwraith (1894) reported that it did not arrive until early May. Males usually arrive several days before females and start defending a nest cavity, but occasionally the sexes arrive together. Older birds of both sexes tend to arrive earlier than younger birds, at least until age 4 years (Winkler et al. 2020). Southward migration begins soon after the young fledge. Many breeding areas are devoid of birds by late July, with almost all breeding areas vacated by late August. Migrants have been observed flying south over Lake Ontario in late July and early August. Many of the early flocks there disappear by late August, but are replaced continuously by flocks arriving and departing throughout September. Large numbers leave the Kingston area in mid-October when the first frosts occur. At communal roosts, there were significant numbers of swallows present at the end of July, with a peak in mid-August; the roost was abandoned in late August. Large

exoduses from the roost coincided with colder weather. Occupation of the Pembroke roost occurs in early July with numbers peaking in the second week of August. Thereafter, numbers drop with each cold front until the roost is abandoned in early September. Although large areas of its range may be devoid of birds by late July, the Tree Swallow is typically present in the province until mid-October, with some records into November or early December (Ross et al. 1984; Weir 2008).

During spring migration, watercourses, especially major rivers that flow north-south, are very important habitat. In southern Ontario, the Grand River is a spring migration corridor. There may still be snow on the ground and ice on ponds when the Tree Swallow arrives. Ice-free watercourses and marshes are often essential as a source of early emerging insects. It may be some time after spring arrival before it spreads over the general landscape. Even then, it prefers areas with water and abundant insects such as beaver ponds, lakes, streams, rivers, damp meadows, sewage lagoons, and ditches. During autumn migration, it is still strongly associated with north-south flowing rivers and watercourses as well as water bodies, but these habitats are not as critical as in spring (Campbell et al. 1997; Curry 2006; Graber et al. 1972; Tyler in Bent 1942).

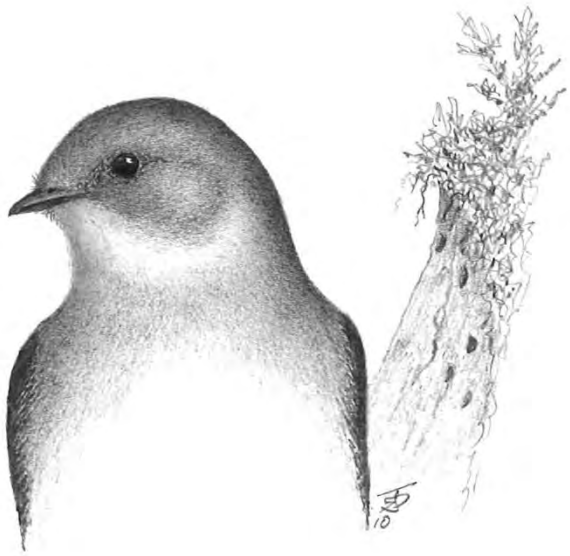
Premigratory roosts are critical habitats that support significant numbers of swallows. Roosts typically support more than 1 species of swallow, so that it is frequently difficult to estimate Tree Swallow populations. On 10 August 1983, it was estimated that 115,000 swallows entered the Pembroke roost, and Tree Swallows vastly dominated the numbers. Ross et al. (1984) reported 250,000 Tree Swallows in a roost at Matchedash Bay, and flocks of 20,000 at Lake Chemung near Peterborough and in Holland Marsh. At the Kingston area roost, it was estimated that 80-90% of the swallows were Tree Swallows. Numbers fluctuated from about 125,000 swallows in late July to 221,000 in mid-August down to 462 on 24 August in 1986 (Weir 2008). In the United States, the Tree Swallow may gather in roosts numbering in the tens or hundreds of thousands, or even millions (Tyler in Bent 1942). Doppler weather radar has revealed fairly regular spacing (100-150 km) of migratory roost sites through North America (Winkler et al. 2020).

In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season for 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming during the second period. The Tree Swallow arrived significantly earlier in spring during the second period, but there were no differences in its autumn departure dates or length of breeding season.

The Tree Swallow is common to locally abundant during migration (James 1991). Flocks of 1,000-5,000 have been observed in spring. Autumn flocks of 4,000-10,000 occur frequently in staging areas, with a maximum of 25,000 (Curry 2006; LaForest 1993; Weir 2008).

Northern Rough-winged Swallow

Stelgidopteryx serripennis

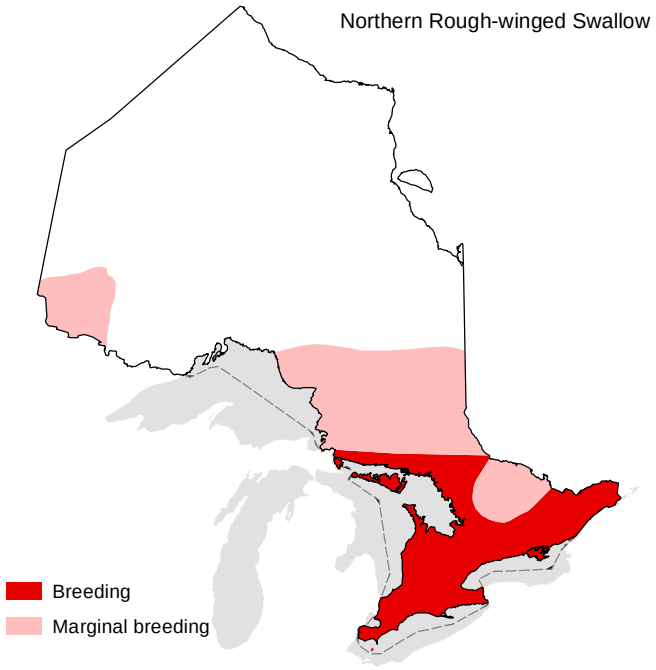


BREEDING SEASON

Habitat Requirements

Northern Rough-winged Swallow breeding habitats in Ontario include farmland fields and pastures (30.7% of nests); river and stream banks and floodplains (25.3%); wooded areas (22.6%); rocky bluffs and cliffs (7.8%); gravel pits, quarries, and road cuts (7.4%); artificial structures such as bridges, planing mills, canals, and dykes (3.5%); islands (1.2%); urban parks (0.8%); and sand dunes (0.8%). Approximately 44% of nests were in human-influenced habitat (Peck and James 1987). De Jong (2020) stated that 30-60% of Canadian nests were in altered habitats; Messely (in Gauthier and Aubry 1996) concluded that only 25% of Canadian nests were in altered areas. In British Columbia, 54% of nests were in human-influenced habitats compared with 25% 14 years earlier. Thirty-five percent of nests were near water; other studies have reported a majority of nests near water. The most frequently used habitats are earthen banks along watercourses, roads, railway lines, and in gravel pits and stockpiled soil piles. Similar habitats are used for nesting throughout its range (Beal 1918; Campbell et al. 1997; De Jong 2020; Dingle in Bent 1942; Graber et al. 1972; Lunk 1962; Messely in Gauthier and Aubry 1996; Sheppard et al. 1936).

Males rarely spend the night in the burrow and the female does so only during laying, incubation, and brooding. Night roosting in the burrow does not occur prior to laying. During the



breeding season, swallows roosted at night in small willows and aspens around a pond and in cattails. Lunk (1962) surmised that groups of males gathered nightly throughout the breeding season and that they were joined by females not on the nest and possibly later by newly fledged young.

Ontario nests were in tunnels in sand or clay banks of rivers, creeks, and roads (48.4% of nests); in drainage holes in concrete bridges and culverts (33.5%); in crevices in rock and shale cliffs and rock road cuts (5.5%); in drainage and ventilation pipes (2.6%); in tunnels in sawdust piles and sand dunes (1.3%); in holes in trees (0.6%); in a hole in a concrete wall (0.3%); in a crevice in a stone wall (0.3%); in a hole in a boathouse wall (0.3%); and on a ledge beneath a concrete wall (0.3%). One tree nest was in an old woodpecker cavity; another was in a natural cavity. One cliff nest was in a cave with an entrance measuring 0.6 by 1.1 m. There were 19 records of it nesting in Bank Swallow colonies and it often used old Belted Kingfisher burrows. One nest under a bridge was in a broken Cliff Swallow nest. Nests were 0.2-18 m above ground or water, with most 0.9-2.4 m up (Peck and James 1987).

Of nests reported to Canadian nest records schemes, 68% were in natural sites and 32% were in gravel pits and road cuts, plus in Ontario nests were in holes in cement, brick, or stone walls. In Ontario and Quebec, 50% of nests were in human-made sites, the highest percentage in the country. A high proportion of nests were in sand and clay banks, frequently in burrows abandoned by Bank Swallows, Belted Kingfishers, or small mammals. Unusual nest sites include semi-trailers and a barrel. The rough-winged swallow nests in any available crevice, including eavestrough gutters and wharves. It frequently uses pipes, crevices in cliffs, and human-made structures for nesting. In British Columbia, 89% of nests were in burrows excavated by Bank Swallows and Belted Kingfishers as well as artificial burrows, drainage pipes, and blasting holes drilled into rock faces; 11% were in crevices in cliffs. One British Columbia and 1 Ontario nest were in a nest box. In Michigan, artificial burrows placed into the face of gravel pits were readily accepted, often within seconds of installation. In British Columbia, nests were 0.3-30.0 over ground or water, with most 2.2-4.5 m up. Burrow length was 15-123 cm (average 60 cm). In Pennsylvania, it nested in drainage pipes 122 cm long with a diameter of 10.2 cm. Average distance from the entrance to the centre of the nest was 82.4 cm (range 53-117 cm). Only 6.8% of nests were built at the inner ends of pipes. In British Columbia, nests were 25-90 cm from the entrance (average 60 cm). In Illinois, nests were 25-90 cm from the entrance, mostly 45-50 cm. There is no correlation between the burrow entrance and its exposure to the elements or compass direction. Some unusual nest sites were inside a garage where

the nest was accessible only when the door was open, and on a steamship that made daily round trips of 77 km along a river. The adults followed the ship to tend to the nest and feed young (Blake 1953; Campbell et al. 1997; De Jong 2020; Dingle in Bent 1942; Erskine 1979; Fleming 1907; Graber et al. 1972; Hill 1988a; Lunk 1962; Nickell 1949; Stedman and Sinbeck 1988). Over 4 years in Michigan, Lunk (1962) found no evidence of its excavating cavities, although it very rarely threw some sand out of existing cavities. He concluded that it depended almost entirely upon existing cavities constructed by Bank Swallows or Belted Kingfishers. Hill (1988a) stated that it rarely, if ever, excavated its own nest burrow and De Jong (2020) concurred. Bergstrom (1953) reported it completing a nest excavation in Connecticut. Solitary nests in piles of fill suggest that it may occasionally excavate its own burrow. Use of burrows dug by other species is most frequent.

The rough-winged swallow is not strongly territorial. Pairs may occasionally nest in the same cliff suggesting that it may be loosely colonial. During nest-site selection and nest construction, the pair spends considerable time perched near the nest. A close approach by an intruder may provoke vocalizations and the intruder may be chased for several seconds. Both sexes share defence of the nest. Once the nest nears completion, tolerance of neighbours increases until no aggression occurs. Perches near the nest are used as a vantage point for maintaining the territory, but perches are not defended. Members of 2-3 pairs may use these perches at different times without conflict. Colonies are typically small, 2-65 pairs, but usually under 10 pairs. In Michigan, the closest that pairs nested was 4.4 m. It frequently nests within 30 cm of Bank Swallows with no aggression and the 2 species appear to be indifferent to each other. There are usually only 1 or 2 rough-winged swallow nests within a Bank Swallow colony. In British Columbia, a large Bank Swallow colony was usurped by rough-winged swallows. Seventy-five pairs of rough-winged swallows nested among 356 burrows. The local sites that had previously been used for nesting were abandoned. The following year, Bank Swallows reclaimed their original colony. In Ontario, 313 isolated nests have been reported plus 68 colonies totalling approximately 259 nests, an average of about 4 nests per colony. In Canada, the average colony size is 4 pairs, except in British Columbia where colonies average 10 pairs (Campbell et al. 1997; De Jong 2020; Graber et al. 1972; Lunk 1962; Messely in Gauthier and Aubry 1996; Peck and James 1997). No information is available on the breeding season home range, but the rough-winged swallow may fly hundreds of metres to obtain food for nestlings (De Jong 2020).

Natal philopatry is very low. In Michigan, a first-year bird nested within 600 m of where it was hatched. No other young returned, indicating considerable dispersion. There are no other records of young returning to breed near their natal site. Adults may use a site for more than 1 season. Burrows are frequently reused, but not necessarily by the same birds. In some cases, burrows were used in as many as 5 consecutive years, all by different females, but evidence suggested that the same male returned. In Michigan, 1 female nested in the same site in 2 years, and it appeared as though the same males returned frequently (Blake 1953; De Jong 2020; Lunk 1962).

Limiting Factors

Eggs have been found in Ontario nests from early May until the third week of July; most are present in the first 3 weeks of June (Peck and James 1987). In Algonquin Park, nests are under construction from early to late May, eggs are present from late May to mid-June, and dependent fledglings have been observed from late June to mid-July (Tozer 2012).

Once a pair selects a nest site, a few pieces of nesting material may be placed in it, but actual nest construction may be delayed a week or more. In Michigan, the mean time taken to build a nest was 6.2 and 7.0 days over 2 years (range 3-20 days). The minimum time occurred during a second nesting when there was no lag time during construction, and maximum times occurred during adverse weather. Usually another 3-4 days elapse between nest completion and initiation of egg laying. This interval may be as long as 13 days under adverse weather conditions, or may not occur in replacement nests. An egg is laid daily, but a day was skipped in 16.4% of Michigan clutches. Of 17 Michigan nests, continuous incubation began in 2 nests with the third-to-last egg, 12 with the penultimate egg, and 3 with the last egg. The mean incubation period of last-laid eggs was 16 days (range 15.5-16.5 days). Two Ontario clutches had incubation periods of 15 days. Hatching of the brood occurs over 0.5-3.5 days. The nestling period is 17-22 days, with most young leaving the nest at age 18-21 days (mean 19-19.5 days). Younger members of a brood tend to leave at an earlier age than older chicks. Young may all leave the nest on the same day, or fledging may be spread over 2 days. The complete nest cycle from nest building to fledging is a minimum of 45 days (De Jong 2020; Dingle in Bent 1942; Lunk 1962; Peck and James 1987).

One brood is raised per year; 1 attempt at renesting may occur if the loss is early in the breeding season. After 10 June, females may be physiologically incapable of laying another clutch. Replacement nests may occur either in the same or a different burrow. If another burrow is used, it is typically very close to the first one, occasionally as far away as 80 m. The interval between the initial loss and initiation of laying of the second clutch is 10-11 days. Clutches of 2-8 eggs have been reported in Ontario, with most nests containing 4-6 eggs. The normal clutch size is 4-8 eggs, mostly 5-7 eggs. In Michigan, the mean clutch size was 6.25 eggs. There appears to be a general increase in clutch size with latitude, but differences are not substantial (Blake 1953; De Jong 2020; Dingle in Bent 1942; Campbell et al. 1997; Graber et al. 1972; Lunk 1962).

The rough-winged swallow is monogamous and capable of breeding at age 1 year. Breeding continues every year thereafter provided it is successful in finding a suitable nest site. There may be a considerable population of floaters that are unable to find a nest site (De Jong 2020; Lunk 1962).

The rough-winged swallow is predominantly an aerial forager. It tends to feed more over open water and at lower heights than other swallows. During inclement weather, it may forage very close to ground or water. It has eaten cracked corn beneath a bird feeder during the breeding season, taken floating insects from the surface of water, fed on the ground on dead midges washed up on a lake shore, and eaten larvae on dead fish and flies on waterfowl scat. Spring foraging is usually in the vicinity of the nesting area, but it may desert the breeding area during inclement weather to find more profitable feeding sites (De Jong 2020; Lunk 1962; Screws 1993; Sealy 1982).

Food brought to the young appears to be predominantly flower flies, other flies, and hymenopterans, and possibly crane flies and mayflies (Lunk 1962). Beal (1918) examined 136 stomachs, including some from Ontario. All food was animal material except for some unknown woody material in 1 stomach, a piece of root in another, and 2 currant seeds in a third stomach. Vegetable material amounted to 0.21% of food. Food was predominantly insects as well as a few spiders and a single snail. Flies were favoured, comprising 32.9% of the diet. Hymenopterans were next in importance at 30.9% and were eaten regularly. Of the hymenopterans, ants comprised 12.0%

of the total diet, but were 35.5% of prey in July and 22.9% in September. Beetles constituted 14.8% of the diet, especially scarab and leaf beetles and weevils. Bugs comprised 14.9% of food items and were eaten regularly May through September, but not in April. Eighty percent of bugs were consumed in August and September, with the most common in the diet being stink bugs, treehoppers, leafhoppers, and ebony bugs. Other insects eaten in small amounts included moths, grasshoppers, dragonflies, and mayflies.

Nest-site availability may be the most significant limiting factor to rough-winged swallows. Only 10% may find suitable burrows when they arrive in spring. Occupancy of artificial burrows is high and almost immediate, even in deliberately selected suboptimal habitat. Fresh digging of any kind immediately attracts birds. At Bank Swallow colonies, 1 or more pairs are almost always present, and they usually eventually find a nest site. Swallows also investigate fresh Belted Kingfisher burrows. Some birds may remain in the general area of Bank Swallow colonies for as long as 3 weeks; after this, they may lose the urge to initiate nesting. As a result, there may be a considerable population of floating nonbreeders, reinforcing the contention that the rough-winged swallow rarely digs its own burrow. Local populations may greatly benefit from proper management and rehabilitation of pits and quarries and installation of artificial burrows (De Jong 2020; Lunk 1962).

The rough-winged swallow may be affected by cold, wet weather in spring. Prior to egg laying, adults may completely abandon nesting areas during inclement weather. Young nestlings may die of hypothermia during cold springs, and nestlings and young fledglings are vulnerable to starvation when it is cold and wet and there are few insects flying. In Michigan during a period of very cold, wet weather a female and 3 males were found in a burrow and 3 females and 1 male were in another burrow. An adult found dead in a burrow was presumed to have died during this period (De Jong 2020; Lunk 1962).

Nests in streambanks are vulnerable to flooding during heavy rain events. Streambank erosion may also result in slumping and loss of nests. Even nests in sand and gravel pits may be lost due to erosion in heavy rainstorms (De Jong 2020; Lunk 1962).

Status

The rough-winged swallow has increased significantly in Ontario and eastern North America, and probably throughout its range. McIlwraith (1894) knew of only a single record from London, where it had been found breeding the previous 1-2 years. In the Toronto area, Fleming (1907) thought that it was probably a rare summer resident. Baillie and Harrington (1937) stated that it was not particularly numerous, but found in some numbers in certain areas. At this time, the breeding range was known to be from the southern border of the province north to Ottawa and southern Georgian Bay, and probably to Manitoulin Island. It was assumed that it bred near Lake of the Woods. The first Kingston record was 2 pairs in 1925 (Weir 2008). During the first atlas, it was common and widespread south of the Canadian Shield, but uncommon in the southern portion of the Shield (Taylor in Cadman et al. 1987). James (1991) considered it a locally uncommon breeder north to Sault Ste. Marie and North Bay and locally rare north to Kenora, Thunder Bay, and Chapleau.

The second atlas demonstrated that the distribution of the Northern Rough-winged Swallow had not changed significantly since the first atlas. It was not detected in many squares in the

southern portion of the Canadian Shield where it had been observed previously. Its probability of observation declined significantly province-wide and in all regions except the Hudson Bay Lowland. It was most abundant in southwestern Ontario, particularly near Great Lakes shorelines. It was most abundant in western Lambton County, Essex County, near Rondeau, east of Long Point, in Niagara Region, and all areas near large rivers or the Great Lakes. Higher densities were also associated with the Grand River in Waterloo and Brant (Sandilands in Cadman et al. 2007).

The rough-winged swallow benefitted from the growth of human populations, which resulted in an increase in nest sites. It was scarce in the northeastern United States until the last third of the 19th century and was first documented in New York in 1870. A major northward expansion occurred between 1950 and 1970 (De Jong 2020; Lunk 1962; Messely in Gauthier and Aubry 1996).

Long-term (1970-2021) trends determined by the Breeding Bird Survey (BBS) indicated annual decreases of 1.24% in Canada and 2.21% in Ontario. The short-term (2011-21) trends were an annual increase of 1.21% in Canada and an annual decrease of 2.93% in Ontario. The long-term trends were highly reliable but the short-term trends were of medium reliability (A.C. Smith et al. 2023). The BBS is not well suited to monitoring rough-winged swallow populations because it typically detects it when it is foraging away from the breeding area.

Michel et al. (2016) used BBS data to analyze population trends of the Northern Rough-winged Swallow over broad geographical areas and to compare its trends with those of other aerial insectivores. Populations were stable in the Great Lakes, New England, and the coastal southeast areas or increasing throughout North America east of the Rocky Mountains. It exhibited the lowest probability of decline of the species that were studied. Although the aerial insectivores are often considered to be a guild that is described as having a negative trend, only one of the 5 species examined, the Chimney Swift, exhibited significant declines in over half its populations trajectories. Results indicated that declining population trends among aerial insectivores are not universal either within or across species.

POSTFLEDGING PERIOD

Broods stay together for a short period after fledging, usually accompanied by 1 or both parents. Adults feed the young during this period, but it is uncertain for how long (De Jong 2020). After fledging, broods move freely over a wide area, but spend considerable time in groups on suitable wires, fences, and trees. In Michigan, 1 brood roosted along a broken-down fence sheltered by shrubs and woods. Broods leave the nesting area shortly after fledging and accompany other swallows in areas more suitable for foraging and roosting, such as near larger lakes and rivers. Some rough-winged swallows use the roost in the cattails at the Cataraqui Marsh near Kingston (Lunk 1962; Weir 2008).

MIGRATION

The rough-winged swallow appears to be a strictly diurnal migrant. Both migrations are prolonged and not particularly noticeable. Spring arrival is 1-2 weeks in advance of Bank Swallows. In the south, it typically arrives in mid-April, with some appearing in early April. In Algonquin Park, arrival is in early May with some arriving in late April. Autumn migration appears to begin shortly after the young fledge, and adults move southward in advance of juveniles. Migrants have been observed flying

south over Lake Ontario in late July. Most leave Algonquin Park before the end of August. In the south, most leave by the end of September with late records in November and December (Black and Roy 2010; Campbell et al. 1997; Curry 2006; De Jong 2020; Graber et al. 1972; Tozer 2012; Weir 2008).

During migration, the rough-winged swallow is most common near water. In spring, rivers and lakes that are ice free and provide a source of flying insects are important foraging areas. It may also feed over shallow ponds, open creeks, sewage lagoons, meltwater areas, and anywhere with open water. Foraging may also occur over open woodlands, especially during autumn migration. When insects are abundant in autumn, it feeds over ponds, streams, and meadows. It occurs most frequently in natural habitats, but is occasionally found around suburban gardens and farmsteads during autumn migration. In addition to occasionally using traditional swallow roosts, it may roost singly or in small numbers on open perches such as dead trees or shrubs, or roots projecting out of stream banks (Campbell et al. 1997; De Jong 2020; Graber et al. 1972).

James (1991) considered the rough-winged swallow an uncommon to locally common migrant. In spring, it migrates singly or in very loose flocks, usually of fewer than 10-20 birds. In spring and especially autumn, it may occur in small numbers in larger aggregations of swallows. In autumn, larger numbers (100-800) may congregate (Curry 2006; La Forest 1993; Weir 2008).

Purple Martin

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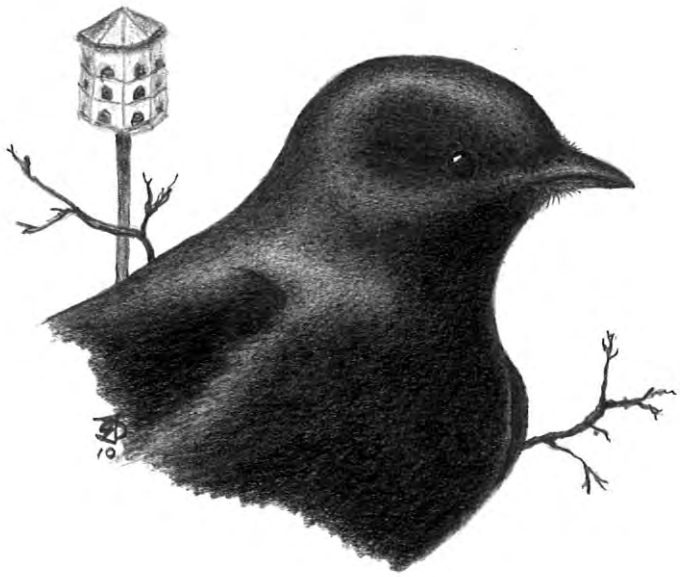


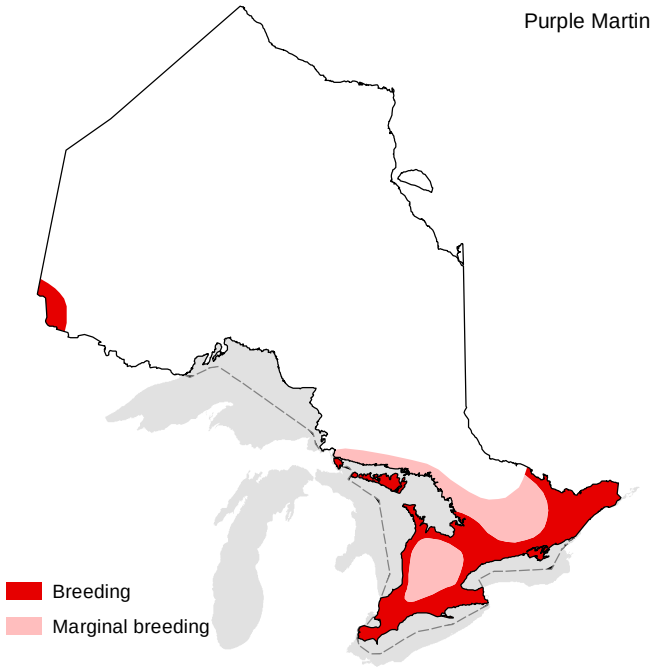
BREEDING SEASON

Habitat Requirements

In Ontario, the Purple Martin has nested in urban gardens and commercial areas, parks, and cottage areas (62.7%); on rocky shorelines and islands (14.8%); in wooded areas and clearings (7.7%); on treed sand-dune/marsh areas (7.7%); in farmland, including pastures (6.5%); and in a limestone cliff (0.6%). Many nests were at the edge of water and most were close to permanent water (Peck and James 1987). It formerly nested in the Gothic architecture of buildings in Hamilton (McIlwraith 1894).

Throughout its range, the Purple Martin is strongly associated with water. Historically, prior to erection of nest boxes, it was probably associated with riparian areas, wooded ponds, and beaver ponds with snags containing old woodpecker nests. Now that it is dependent upon nest boxes, it is found almost exclusively in cities, towns, and other human settlements, although close proximity of water appears essential. In the Kingston area, all martins were associated with human habitation and human-made martin houses. None were found in heavily forested areas without human habitation. In British Columbia, it originally nested in cavities of old buildings in Vancouver, a habitat that has since been abandoned. Now it nests in sheltered estuaries and harbours where abandoned pilings provide nest sites. It also inhabits deciduous second growth near water, mudflats, power line rights-of-way, and farmland where snags are present for nesting. Almost all British Columbia nests were

close to water in forested or urban habitat (Brown et al. 2021; Campbell et al. 1997; Jackson and Tate 1974; Weir 2008).



In Ontario, the Purple Martin breeds mostly in colonies of 2-40 pairs, averaging 8, with colony size dictated by martin house size. Forty-seven single nests were reported. Most nests were in elevated, human-made boxes, mostly apartment-type houses but also some single-unit houses. Other artificial nesting sites included holes in walls, roofs, and eaves of buildings, and behind awnings; in town towers and church belfries at heights of 7.6 to 15 m; behind metal siding on buildings; inside a building under a ledge at 7.6 m; in the bottom of a tire on a post at 1.7 m; in a hole in a fencepost at 1.2 m; in an electric light standard; in pipe holes of a wrecked boat's engine boiler, just above water; in the swing bridge at Huntsville (Mills 1981); and in a half-sunken dredge. Natural nest sites included a colony in holes in a limestone cliff at 30 m and a single nest in a tree cavity at 4.6 m. Nests in martin houses were 2.1-12 m from ground (Peck and James 1987). In 1955, a pair nested in a natural tree cavity at Long Point (Holroyd 1975). Sheppard et al. (1936) reported a large colony on the main street of St. Catharines, where it nested in the upper portions of old stores.

In eastern North America, the Purple Martin now nests almost exclusively in nest boxes, but western populations still frequently nest in natural cavities or in other human-made features. Early Alberta naturalists reported it nesting in small cavities in burnt-over forests. Nesting in trees adjacent to lakes continued at least until 1955 in Alberta. As early as 1910, it started using nest boxes and does so almost exclusively there now. In the west, it continues to nest mostly solitarily in natural or woodpecker cavities in trees or cacti. Of about 3,000 nests reported to Canadian nest record schemes, only 7 were in trees or stubs. In Illinois, it rarely nested in natural situations even historically but in 1966, birds were found nesting in tree stumps standing in water of the Mississippi River. A colony was reported on islands in the Gulf of California where it nested in crevices under ledges and boulders on steep slopes and in chimney-like columns of rock. A Wisconsin nest was in a natural cavity in a tree at ground level. It has nested among large boulders in Lac des Milles Lac, Minnesota, and in a tall, dead pine perforated with woodpecker cavities in Florida. It appears to prefer dead trees when nesting under natural conditions, but occasionally nests in live trees if they have woodpecker holes. Nests have been reported 0-40 m from ground, with most 2.4-5.5 m up (Banks and Orr 1965; Brown et al. 2021; Erskine 1979; Finlay 1971, 1975; Graber et al. 1972; Pistorius 1975; Sprunt in Bent 1942).

Now most nests are in artificial nest boxes built especially for martins. It prefers larger and deeper compartments than are generally available in commercially sold apartments; deeper cavities increase nesting success. Aluminum houses are preferred to wooden ones in some areas and vice versa in others. Wooden houses buffer temperatures better, but are more likely to attract starlings. There is no difference in percentage of occupied houses in city and rural areas, but suburban areas support significantly fewer martins than urban and rural houses. Breeding success was higher in houses that were near water. Occupancy rates were higher in houses closer than 30 m to a building. In Ohio, some sites became unsuitable due to gradual overshadowing of the nest house by trees and buildings. Occupancy rates are not affected by density of trees or shrubs in the area, but there are fewer martins as vegetation height increases. Excessive noise or smell may result in nest-site abandonment. A site may also be unattractive if there are no nearby wires for perching (Brown et al. 2021; Jackson and Tate 1974; Mayfield 1964; Perry and Bloch 1987). Numerous other artificial structures have been used for nesting. Native Americans erected hollowed-out gourds for nesting martins as early as 1712. Each gourd is a single cavity. Gourds are often preferred to nest boxes because the cavity is larger and deeper. Gourds are still frequently put out for nesting martins in the southeastern United States, but much less frequently elsewhere. Martins also nest in many types of structures not specifically designed for them. Most commonly used are cracks and crevices in buildings, but the incidence of this is declining due to more modern building design. The older Gothic architecture provided numerous nest sites, and older towns near rivers were most likely to support colonies. Occasionally, it nests in traffic light or street light standards that have crevices. It has also nested in cracks and cavities in civil defence sirens, a flag pole, aviation warning balls on hydro transmission lines, bridge superstructures, and portholes of decommissioned ships. It also nests in nest boxes built for waterfowl. In Florida, 6 nests were found in 3 active oil rigs, which had a complete arc cycle of 5-6 m every 5-10 seconds. Another unusual nest was in a gourd attached to the mast of a moving ship (Brown et al. 2021; Campbell et al. 1997; Copley et al. 1999; Graber et al. 1972; Hofstead 1995; Leighton et al. 2002; Limoges and Bombardier in Gauthier and Aubry 1996; Maehr et al. 1988; McIlwraith 1894; Sprunt in Bent 1942; Weir 2008).

The Purple Martin is highly colonial, particularly in the east. Colonies larger than 35 pairs are rare, even where multiple apartment houses are available. The largest reported eastern colony was 300 pairs nesting under boulders and in rock crevices on islands in Minnesota. The largest natural colony of western birds had more than 100 pairs nesting in a sandstone cliff. Despite being colonial, it is territorial. Nests in natural situations in the west were at least 100 m apart, with median nearest-neighbour distances of 325 m and 238 m over 2 years. In apartment houses, a territory consists of 1 or more rooms of the apartment and the porches adjoining the rooms. Roofs of martin houses are not defended and defence does not occur away from the house. Males frequently defend several rooms at the beginning of the nesting season then relinquish some later on. The largest maximum territory size in Texas was 36 rooms, and the largest minimum territory size was 18 rooms. For 30.3% of males, the maximum and minimum territories were the same, averaging 4.1 rooms. Of males that initially defended multiple rooms, 21.5% defended only 1 room as their minimum territory size. Only 12.6% defended 1 room for both their maximum and minimum territory. Shrinking of the territory usually occurs when nestlings are being fed. Defence of multiple rooms early in the nest season may promote polygyny if another female moves into one of the rooms. Usually the male stops guarding

additional females allowing yearlings or floaters to take possession of a room. These birds consistently challenge the dominant male, who often gives up some of the rooms in his territory. Once established, neighbouring males rarely fight or trespass. They may even defend the neighbour's territory when he is absent (Brown 1979; Brown et al. 2021; Morton et al. 1990). In western populations nesting in natural cavities, larger territories of 20-30 m are defended (0.1-0.3 ha), and birds may control cavities as far as 115 m away (Brown et al. 2021).

Natal philopatry is low. In Maryland, less than 2% of young returned to breed (Morton and Patterson 1983). In Texas, less than 1% of birds banded as juveniles were recovered the following year in their natal colony. Only 8% returned to any colony within the 6 km2 where most colonies were located. Brown and Bitterbaum (1980) suspected that those that returned to the natal area did so coincidentally rather than homing. Of birds returning to within 8 km of the natal colony in Texas, 79% were males. Five percent of yearlings returned to breed in their natal colony in Ohio and Maryland. Of 46 yearling birds that were recaptured in the breeding season in Michigan, 28 (61%) were found at the natal site, 7 (15.2%) were within 12-35 km, 8 (17.4%) were within 45-93 km, and 3 were at distances of 160, 274, and 338 km (Allen and Nice 1952; Brown et al. 2021; Morton et al. 1990). In Alberta, 2 nestlings returned: one to the natal area and the other nested 37 km away (Finlay 1971). Tarof et al. (2011) recorded a return rate of 22% of fledglings in Pennsylvania. Some of these may have nested a considerable distance from their natal area. de Greef et al. (2012) reported average dispersal distances of juveniles of 63 km (range 0-2,644 km). Most (70.9%) dispersed 50 km or less from the natal site; 1.6% dispersed further than 500 km. Longitudinal dispersal averaged further (97 km) than latitudinal dispersal (54 km).

Adult nest-site tenacity is fairly high. In Pennsylvania, birds were studied at 2 breeding colonies 19 km apart, at other colonies within 50 km of the core colony area, and at a large premigratory roost that was known to attract Purple Martins from distances of 200 km or more. Of birds breeding at age 1 year, 84% of females and 87% of males returned the following year. Of birds that bred at a colony in their first and second years, 91% of females and 84% of males returned to breed again (Stutchbury et al. 2009). In Texas, approximately 35% of nesting mature birds returned to the same breeding area. In Maryland, 55% of adults nested at the same colony as in previous years, and many nested in the same apartment house. In Ohio, 1 bird nested 16 km from its previous nest site; another nested 160 km away (Brown and Bitterbaum 1980; Brown et al. 2021; Morton et al. 1990).

Limiting Factors

Eggs have been found in Ontario nests from the last week of May until the first week of August, with most present in the last half of June (Peck and James 1987). In the south, nest building may not be initiated for 6-8 weeks after arrival, but this interval may be 2-4 weeks in Ontario; 2-3 weeks elapse before nest building in Michigan. Adults arrive before yearlings and have a longer period between arrival and nest building; yearlings may begin nesting 1-2 days after claiming a nest site. In Alberta, adults took an average of 13.6 days for nest construction compared with 7.6 days for yearlings; later-nesting birds built the nest quicker. When age groups were combined, time for nest construction averaged 11.8 days (range 5-27 days). More time may elapse between nest completion and egg laying. In Alberta, this interval averaged 3.2 days (range 0-9 days); the interval in Michigan was 4-5 days. Eggs are laid at the rate of 1 a day. Full incubation occurs by the time the penultimate egg is

laid. The incubation period has been reported as 12-20 days, but is typically 15-18 days. Estimates of less than 14 days may be errors. Incubation periods of 14-17 days have been reported in Ontario. Most eggs within a clutch hatch in 24-36 hours, rarely 4 days. Young fledge when they are 24-37 days old, but 28-29 days is probably typical. Nestlings leave one at a time and usually do not all leave on the same day. Broods of 6 may take 3 days to leave the nest; fledging of a brood may take as long as 8 days. If a nestling remains in the nest after the rest have left, adults continue to feed it until it fledges (Allen and Nice 1952; Brown et al. 2021; Campbell et al. 1997; Finlay 1971; Graber et al. 1972; Johnston and Hardy 1962; Morton and Derrickson 1990; Peck and James 1987; Sprunt in Bent 1942).

Typically 1 brood is raised a year; only 1 is raised in Ontario. Double broods have been confirmed only in Texas. Clutches of 2-7 eggs have been reported in Ontario, with most containing 4 or 5 eggs. Overall, clutches of 1-8 eggs have been reported, but 3-6 is typical. Clutch size declines with season, chiefly because later-nesting yearlings have smaller clutches. Yearlings produced fewer eggs than adults in Texas (4.11 compared with 4.97 eggs) and Alberta (4.29 compared with 5.00 eggs). Replacement clutches average 0.5-1.0 egg smaller than first clutches. In Alberta, all replacement clutches contained 4 or 5 eggs compared with 5 or 6 eggs for first nests (Allen and Nice 1952; Brown 1973; Brown and Bitterbaum 1980; Brown et al. 2021; Campbell et al. 1997; Finlay 1971; Graber et al. 1972; Peck and James 1987, 1997; Sprunt in Bent 1942).

The age at first breeding is 1 year; copulation has been observed by birds that were only 29 days old. Juveniles that have been fledged for as little as 6-7 weeks may start to defend nest sites. Although most yearlings breed, there is also a floating population of males and females. Stutchbury (1991) determined that male floaters without territories were present in an Arizona population. Floaters intruded on territory holders early in spring prior to egg laying but incursion decreased to almost zero during egg laying and incubation. Most floaters (21 of 41 adult males and 46 of 47 subadult males) obtained territories by gaining control over some of the cavities defended by a territorial male. In the other cases, floaters defended territories where the previous owner was no longer present. Most floaters eventually established a territory after 2-29 days. Brown (1978a) noted nonbreeding floaters in Texas that included males, females, adults, and first-year birds. These birds did not successfully acquire a nest and breed. Nest-site availability did not appear to be limiting in this population. Some yearling males are unsuccessful in defending a nest site, or they may be expelled from nest boxes by starlings or House Sparrows. In a Maryland colony, 12.9% of yearling males were unmated compared with 3.6% of adult males and 0.6% of females. This suggested that there was a shortage of females in the population. Birds breed every year if they can find a suitable nest site. Mate replacement may occur if 1 member is lost. When the male disappears, often no other males show interest in the widow, and she raises the brood herself. When a female is lost, the male usually finds a replacement in 2-4 days. The new females ignore the previous clutch; a new nest is built over it and another clutch is laid. The same individuals rarely remate in subsequent years even when both are present. Two of 15 (13%) pairs whose both mates were present remated in Maryland. The annual pair bond dissolves after young fledge (Brown 1978b, 1979, 1983; Brown and Bitterbaum 1980; Brown et al. 2021; Finlay 1971; Morton and Derrickson 1990).

The Purple Martin is typically monogamous, although polygyny occasionally occurs. In Texas, about 20% of males were polygynous early in the season, but only 5% continued as polygynists

throughout the season. Polygyny usually occurs when a female allows a second female to settle in a male's multi-compartment territory before he has relinquished part of it. The male provides parental assistance to both females, although generally more to the first female (Brown 1975, 1979; Brown et al. 2021; Southern 1959). Females are frequently subjected to forced extra-pair copulations so not all young in a nest may be related to the male. Older males father a high percentage of eggs in their nests but yearlings may not be related to any of the young in their nests (Morton 1987). Intraspecific nest parasitism may occur occasionally early in the laying period. In Oklahoma, 7 of 394 nests (1.8%) contained parasitic eggs; no cases of parasitism were reported from hundreds of nests in Texas (Davis 1988; Morton et al. 1990; Wagner et al. 1996).

Almost all food is captured aerially, frequently at altitudes of at least 50 m. The Purple Martin forages higher than other swallow species, often to heights of 150 m. When it is cool in the spring, it may feed low over ponds and lakes to take aquatic insects. Rare foraging techniques include gleaning insects off foliage, taking caterpillars or other insects while walking on the ground, and skimming insects off the surface of water or even diving into water. It may rarely converge on swarms or mass emergences of insects. It does not forage when temperatures are below 9°C due to the scarcity of flying insects and may require temperatures of at least 13°C to forage successfully and survive. Foraging does not occur during rain regardless of temperature. Food may be a limiting factor for nestlings because the number of feedings per nestling is negatively related to brood size. Chick starvation is common (Brown 1976: Brown et al. 2021; Wagner et al. 1996). In Illinois, it preferred to forage over fallow fields followed by, in order of frequency, shrubby areas, oat fields, soybean fields, alfalfa fields, and corn fields (Graber et al. 1972). In Quebec, 33 Purple Martins from 7 colonies had foraging ranges of 0.4-65.2 km2 (mean 8.28 km2). Their foraging habitat consisted of 25.4% developed land, 17.6% cropland, 16.0% forest, 13.5% water, and 2.4% wetlands (Dunoyer et al. 2024).

The Purple Martin feeds almost exclusively on insects, although it may consume a few spiders. The insects eaten appear to reflect local availability and vary seasonally and geographically. Young nestlings are fed mostly small crushed beetles, but older nestlings are fed larger prey including dragonflies, grasshoppers, butterflies, small snails, and eggshells. Favoured nestling foods included monarch butterflies and green darners (Brown 1978b; Brown et al. 2021; Finlay 1971; Sprunt in Bent 1942). Walsh (1978) studied the diet of nestlings in Alberta in 1970 and 1971. Darners (a family of dragonflies) constituted 22% and 27% of the weight of insects fed to young over the 2 years. Percentages of other insects fed to young were flower flies (29% and 17%), brush-footed butterflies (1% and 23%), midges (10% and 4%), horntails (5% and 5%), ants (4% and 6%), long-horned beetles (5% and 2%), skimmers (dragonflies) (1% and 4%), narrow-winged damselflies (4% and 1%), house flies (3% and 1%), bees (2% and 1%), caddisflies (2% and 1%), water boatmen (2% and 1%), and others (8% and 6%). Brush-footed butterflies were significantly more important in the diet in the second year because nesting was initiated later when these species were more abundant. The mourning cloak butterfly was taken most frequently; its adults do not emerge until later in the summer. In Quebec, the diet of 29 nestlings was comprised of 38.5% flies, 34.2% beetles, 11.1% lepidopterans, 7.3% mayflies, 3.1% caddisflies, 2.3% bugs, 2.0% hymenopterans, 1.0% odonates, and 0.5% neuropterans. As nestlings aged they were fed more beetles and mayflies and fewer flies. The

nestling diet was initially dominated by small soft-bodied prey. Older nestlings were fed larger, more chitinous prey such as beetles (Dunoyer et al. 2024).

Beal (1918) examined the contents of 205 adult stomachs. The food was entirely animal matter, predominantly insects with a few spiders and other arthropods. Hymenopterans were the most abundant food and constituted 23% of food items, including 3.5% ants. Flies were second in abundance at 16.1%. Important fly families were crane, house, and robber flies. Bugs comprised 14.6% of the diet, including stink and ebony bugs. Beetles totalled 12.5% of food, including weevils and ground, tiger, and scarab beetles. Adult moths and butterflies comprised 9.5% of the food. Dragonflies were a favoured food, comprising 15.1% of items consumed. This suggests that dragonflies are actively hunted and, since many were larger species, they are a significant component of the diet. Grasshoppers and crickets constituted 1.1% of the diet; miscellaneous insects and invertebrates were 8.1%. These included mayflies, spiders, isopods, mollusc shells, and fish vertebrae. Adults feed on a wide variety of insects, with 57 families of insects found in the diet in a Kansas study. The overall diet includes beetles, bugs, damselflies, dragonflies, leafhoppers, grasshoppers, crickets, butterflies and moths, wasps, bees, caddisflies, spiders, cicadas, winged termites, mayflies, tent caterpillars, scarab beetles, ground beetles, weevils, aphids, ebony bugs, ichneumonid wasps, crane flies, robber flies, and harvestmen. The diet varies seasonally based on insect availability. Flies and soft-winged bugs predominate early in the season with true bugs, butterflies and moths, hymenopterans, and dragonflies consumed later; beetles are eaten throughout the breeding season (Brown et al. 2021; C.D. Riggs 1947; Sprunt in Bent 1942). Johnston (1967) studied seasonal variation in the martin's diet in Kansas. Beetles were consistently a high proportion of the diet varying between 32% in June and 68% in April. Scarab and ground beetles and weevils were the most important beetles. True bugs comprised only 2% of the May diet but 28% of the June diet. Soft-winged bugs were unimportant most of the breeding season except in May when aphids comprised 17% of the diet. Flies formed 3-20% of the diet with the minimum in August and maximum in April. Crane flies were the most important of this group. Consumption of hymenopterans was low in April (2%) and May (8%), but was 35% in June and 32% in August. Ichneumonid wasps were the most important hymenopterans. Butterflies were important only in August when they comprised 14% of the diet. The variety and mass of insects eaten was greatest in August. DNA metabarcoding of Purple Martin fecal samples from 2 sites in the United States and one in Winnipeg determined that 71 species of 39 families in 10 orders of invertebrates were consumed. The most important orders were flies, lepidopterans, and odonates, with lesser numbers of beetles, mayflies, bugs, and hymenopterans. Ticks and orthopterans were least important; caddisflies were consumed only at Winnipeg but were fairly common in the diet (Forsman et al. 2022). In Quebec, the diet of 69 chick-rearing adults was comprised of 42.1% beetles, 25.6% flies, 9.6% lepidopterans, 9.5% bugs, 6.0% hymenopterans, 4.3% caddisflies, 1.2% mayflies, 1.1% fleas, 0.5% odonates, 0.08% neuropterans, and 0.08% orthopterans (Dunoyer et al. 2024). Wade (1966) stated that Purple Martins consumed 2,000 mosquitoes per day. He concluded that this was conservative, and that 10,000-12,000 might be eaten in a day. Kale (1968) concluded that mosquitoes are a negligible item in the diet. Behaviour patterns of mosquitoes and martins result in them seldom overlapping, and none of the literature reporting it eating large numbers of mosquitoes is

substantiated. Martins and mosquitoes very rarely occur together in the same place or at the same time. The claim that martins regularly consume 2,000 or more mosquitoes a day is incorrect.

Cowbird parasitism of the Purple Martin is rare, or perhaps non-existent. Campbell et al. (1997) reported an incident of cowbird parasitism in Michigan where the egg was rejected. Brown et al. (2021) concluded that reports of cowbird parasitism were not credible.

Adverse weather is a significant limiting factor to the Purple Martin. It is not well adapted to cold or rainy weather in spring and early summer. More northerly populations are small and ephemeral due to weather effects. Regional populations as far south as the mid-Atlantic states are periodically eliminated or reduced due to cold weather. During cold weather that lasts 3-4 days, eggs may become chilled as a result of adults' spending longer times foraging. These eggs do not hatch and are abandoned. When weather is cold, adults cannot find insects and they may perish as well. A hurricane in June 1972 eliminated populations from Virginia and Massachusetts west to the Great Lakes. It was estimated that 90-100% of nestlings and thousands of adults died, while survivors deserted colonies. After 3 days of temperatures below 6°C, territorial defence ceased and as many as 10 adults huddled together in a single compartment. When the cold snap extended another day, some adults died. After significant declines, it may take as long as a decade for populations to recover. Excessive summer heat coupled with parasites may cause death of nestlings; they may jump from the nest under these conditions (Brown 1976; Brown et al. 2021; Finlay 1976; Graber et al. 1972; Mayfield 1964; Sprunt in Bent 1942). Cold or wet weather may delay nesting and result in smaller clutch and brood sizes. Young that fledge later in the season have lower annual survival rates because of less foraging time and experience before migration (Tarof et al. 2011).

Availability of nesting cavities is another significant limiting factor. Existing colonies often increase in size if additional houses are provided, or new colonies may become established with provision of houses. Nest-site availability was the major limiting factor at Long Point, and populations started to recover in British Columbia when a nest-box program was initiated (Brown et al. 2021; Copley et al. 1999; Holroyd 1975). Raleigh et al. (2019) concluded that the use of artificial nesting houses was a significant component in the conservation of eastern populations of the Purple Martin. Nest success in artificial nesting structures was greater than 85%; clutch size and the number of fledglings produced was slightly higher in structures with entrances designed to exclude starlings.

There is intense competition for nest sites, particularly from starlings and House Sparrows. These 2 species take over nest cavities or make them unsuitable for nesting by stuffing them full of grass. Both species throw out martin eggs and young and usurp nests. Starlings may trap adults inside and enter and kill them. Population declines have been attributed to competition with House Sparrows and European Starlings; local extirpations of martin populations may occur without human intervention. Native species may also compete for nest cavities including Tree Swallow, Northern Rough-winged Swallow, Great Crested Flycatcher, Northern House Wren, Eastern Bluebird, House Finch, and Red-headed Woodpecker (Allen and Nice 1952; Brown 1981; Brown et al. 2021; Copley et al. 1999; Graber et al. 1972; Jackson and Tate 1974; Perry and Bloch 1987; Sheppard et al. 1936).

Price (2004) concluded that the range of the Purple Martin might increase in southern Ontario if the average summer temperature increased by 2°C.

Status

McIlwraith (1894) stated that the Purple Martin was generally distributed in Ontario, but common nowhere. At Toronto, Fleming (1907) reported that it was a regular summer resident, but local and declining in numbers. Sheppard et al. (1936) considered it common but very local in the former Welland County, where it nested only in houses erected for it. In the former County of Lincoln, it was less common and local in small colonies. Baillie and Harrington (1937) considered it a common breeder in the south, especially in and around towns, north to Manitoulin Island, northern Frontenac County, and Renfrew County. It also bred at Kenora, Lake of the Woods, and near Lake Superior wherever suitable breeding sites were available. Mills (1981) noted a general increase in the mid-1970s in Muskoka and Parry Sound districts. James (1991) termed it a locally common summer resident north to Georgian Bay and Ottawa, uncommon and local north to Sudbury, and an occasional straggler in the north to Kenora and Thunder Bay.

The second atlas showed that the range of the Purple Martin had contracted significantly since the first atlas. It was no longer present at Lake Temagami, Lake Nipissing, Thunder Bay, Dryden, or in the Sudbury area. It disappeared from much of the southern Canadian Shield and the inland areas of southwestern Ontario. South of the Shield, it was predominantly associated with the shorelines of Lakes Huron, Erie, and Ontario, and along the St. Lawrence and Ottawa rivers. Its probability of observation declined significantly province-wide and in every region where it occurred, except in the Boreal Forest Region where it is rare. It was most abundant in the Niagara Peninsula, Chatham-Kent, and Essex and Lambton counties, with areas of moderate density around Lake Simcoe, along the St. Lawrence and Ottawa rivers, and in Prince Edward County (Cadman in Cadman et al. 2007).

Purple Martin populations have fluctuated considerably historically. It was probably uncommon prior to European settlement, but prospered with forest clearing, construction of buildings, and provision of nest sites for it. It probably reached its peak population in the mid-19th century. Populations declined significantly in the late 19th century due to introduction of the European Starling and House Sparrow. In New York, the population declined 30-50% between 1860 and 1910 due to these 2 species. In 1911, the Purple Martin was the third most abundant bird in Montreal; by 1974, Quebec colonies were scattered and the largest known colony was 70 birds. The northern limit of its range shifted southward in the 20th century. It no longer occurs in the Northwest Territories and it does not occur as far north in British Columbia as previously. In April 1982, it suffered a serious decline in Ontario and New York and probably Quebec because of unusually cold temperatures (Brown et al. 2021; Limoges and Bombardier in Gauthier and Aubry 1996). Long-term (1970-2021) Breeding Bird Survey (BBS) data indicate an annual increase of 0.772% in Canada and an annual decrease of 3.5% in Ontario. The short-term (2011-21) trends were an annual increase of 5.92% in Canada and an annual decrease of 0.998% in Ontario. The long-term data were highly reliable; the short-term data were of low reliability (A.C. Smith et al. 2023).

Michel et al. (2016) used BBS data to analyze population trends of the Purple Martin over broad geographic areas and to compare its trends with those of other aerial insectivores. Purple Martin populations were stable in the extreme northeast but declined in the Great Lakes region, with

stronger declines in the north and west. Southern Ontario was one of the areas experiencing the greatest rate of decline. There was little concordance among the trends of the aerial insectivores. The strongest relationship was observed in the Great Lakes area, where declining trends of the Barn Swallow were positively correlated with those of the Purple Martin and Tree Swallow. The Purple Martin exhibited the second-highest probability of decline behind the Chimney Swift. Although the aerial insectivores are often considered a guild that is described as having a negative trends, only 1 of the 5 species examined, the Chimney Swift, exhibited significant declines in over half its population trajectories. Results indicated that declining population trends among aerial insectivores are not universal either within or across species.

POSTFLEDGING PERIOD

Young begin catching insects 4-5 days after fledging and are independent 7-10 days after fledging. When young fledge, they are immediately led away from the nesting colony by the adults to what have been termed grouping or gathering areas. Large numbers of broods assemble in these areas. Gathering areas may be in trees and on television aerials, but most frequently on utility wires. Birds congregate under concrete bridges in some places. Twenty-six broods assembled 90 m to 1.6 km from the nesting area and most were within 1 km of the nest; 15 broods were not found within a 1.6-km radius. Broods remain at the gathering area 2-3 days after the last young fledges then leave before they are completely independent. It is uncertain where they go, but they may join premigratory roosts. While at the gathering area, fledglings may return to roost at the nest at night or during daytime storms, but typically only until 7-10 days after fledging (Brown 1978b; Brown et al. 2021; Morton and Patterson 1983). In Maryland, a nesting colony of 3 apartments was used as a postbreeding roost. Young continued to use the colony for roosting until early August. Of juveniles using the colony, 74 (54%) had been raised in the colony and 63 (46%) were immigrants. Broods native to the site that had a parent present were most likely to have all brood members in the roost, even though they were scattered throughout the compartments and houses (Morton and Patterson 1983). During autumn in Streetsville, both young and adults congregated in spruce trees around houses, and adults were still fledging young (Mitchell 1947).

Flocking into premigratory roosts by adults occurs as soon as young fledge. In the southern portion of the Purple Martin's range, large late-summer roosts of 100,000-200,000 have been reported. Precise roosting locations may vary year to year, but the general location of large roosts appears to be traditional. Although roosts may occur in a variety of habitats, many are associated with water. In 1986, a swallow roost in cattails in the Kingston Cataraqui Marsh contained at least 600 martins in late July and over 2,400 in mid-August. In Pembroke, Purple Martins roosted on a point at the confluence of the Muskrat and Ottawa rivers in the canopy of a 0.5-ha stand of black willows 10-15 m tall. At the eastern end of Hamilton Harbour, 1,500 were present in a roost on 6 September 1959. In Illinois, dense willow stands 3-6 m tall along watercourses were particularly favoured for roosts. Roosts also occurred on city buildings, power lines, and sandbars in rivers. One large roost was in a 12-ha hawthorn thicket. In South Carolina, a roost of almost 2 million swallows was on an island in a lake. In Arizona, groves of cottonwoods were used as roosts. A roost in a New Jersey city was on the main street in a 1-ha grove of silver maples. Although there were hundreds of similar areas, only this area was ever used. In this area, there were only 150 breeding pairs, but at

least 15,000 martins came to the roost every night (Brown et al. 2021; Cater 1944; Curry 2006; Graber et al. 1972; Ross et al. 1984; Russell and Gauthreaux 1999; Sprunt in Bent 1942; Weir 2008).

Home range size during the postfledging season is unknown, but may be extremely large. In Arizona, it was thought that birds at a premigratory roost covered approximately 1,400 km2 during the day; at a South Carolina roost, some birds flew as far away as 100 km in a day (Cater 1944; Russell and Gauthreaux 1999).

MIGRATION

Migration is on a broad front, with most of the eastern population crossing the Gulf of Mexico. Autumn migration may begin when young fledge, so departure may be staggered within an area and vary year to year. Autumn migration may be nocturnal, at least in part (Brown et al. 2021; Graber et al. 1972).

In southern Ontario, most birds arrive in mid-April with early arrivals in late March. In the southern Shield, arrival extends through May, with a few arriving in mid-April. Autumn migration is underway in August, with most leaving the province in early to mid-September, but stragglers may occur until mid-October (Black and Roy 2010; Curry 2006; LaForest 1993; Mills 1981; Tozer 2012; Weir 2008).

The first spring arrivals are adult males followed closely by adult females, although both sexes of adults may arrive at nearly the same time. In Michigan, yearlings often arrive weeks after older birds. Yearling breeders return significantly later than all other age classes. Males returned earlier than females for all age classes (Allen and Nice 1952; Morton and Derrickson 1990).

In British Columbia, migrants occurred in open areas of coastal lowlands, where they often foraged over large lakes, harbours, estuaries, bays, marshes, agricultural fields, and intertidal areas (Campbell et al. 1997).

During migration, the Purple Martin may roost colonially in urban areas and towns, but it may also roost in areas associated with forests and water. Fournier et al. (2019) identified 48 migration roost sites and determined that forest islands (small forests surrounded by unsuitable habitat) were used for roosting more frequently than they occurred in the landscape and that martins roosted in areas further from water than availability. Seventy-five percent of roost locations were in forests, 13% were in agricultural areas, 8% were in urban areas, 2% were in wetlands, and 2% were in cut forests. Results suggested that it routinely uses forested habitat and that forested islands are preferred. These habitats may afford enhanced predator protection and the surrounding open spaces may provide suitable foraging habitat. Previous anecdotal information indicated that it roosted near human development, but this study demonstrated that it preferred more remote areas.

In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season for 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming during the second period. The Purple Martin arrived significantly earlier during the second period, but there were no differences in its autumn departure dates or length of breeding season.

James (1991) considered the Purple Martin a common to locally abundant migrant in Ontario.

Barn Swallow

Hirundo rustica

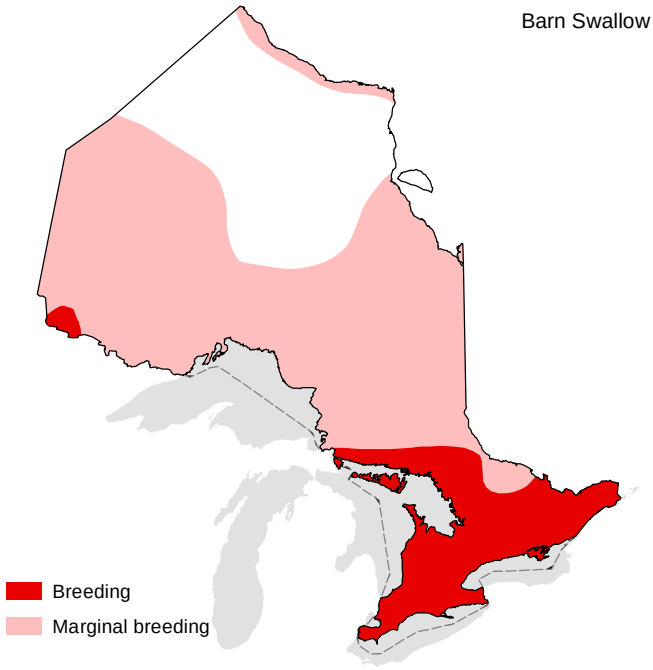
BREEDING SEASON

Habitat Requirements

In Ontario, the Barn Swallow breeds in a wide variety of habitats, but is essentially absent in extensively forested areas and muskeg. Breeding habitats were farmland, including crop fields, pastures, and coniferous plantations (36.0% of records); at lake and river shorelines and along road rights-of-way (30.5%); in wooded clearings, including cottage areas and parkland (25.6%); in urban areas, including residential and commercial land (17.2%); on rocky cliffs and islands (15.8%); in marshes, bogs, meadows, and floodplains (3.9%); in sand-dune areas (3.7%); and on tundra (3.2%). Nesting in wet habitats appeared to be due to presence of open areas for foraging. The primary influence on habitat selection was presence of human-made structures for nesting, such as bridges and buildings. More than 88% of nests were on artificial sites (Peck and James 1987).

The Barn Swallow was negatively correlated with organic farms and more abundant on conventional farms in southern Ontario. Field sizes were smaller on organic farms. Herbicides, insecticides, and chemical fertilizers were applied at conventional farms; biodynamic sprays were

used at organic farms only. It was significantly negatively correlated with the amount of hedgerows but was positively correlated with farmsteads (Kirk et al. 2011).



Breeding habitat typically contains open areas for foraging, a nest site with a vertical or horizontal substrate that is protected from the elements by a roof or overhang, and a source of mud. Historically, the Barn Swallow nested in caves and rock crevices and occasionally in hollow trees, but it now occurs mostly in agricultural areas, cities, suburbs, and along highways where there are buildings and culverts. In British Columbia, 80% of nests were in human-influenced habitats: 34% in rural areas, 21% in cultivated farmlands, and 20% in suburban and urban areas. Associated foraging areas included rural and urban backyards, farmyards, farmland, roadsides, weedy fields, near water (lakes, marshes, and streams), meadows, orchards, and vineyards (Brown and Brown 2020; Campbell et al. 1997; Fitch 1958; Samuel 1971).

Both members of a pair may roost together in the nest cup over night, but begin roosting elsewhere once the young are near fledging (Brown and Brown 2020).

Ontario nests were inside or outside buildings, on beams and posts, under eaves and awnings, under roof peaks, on walls, on verandahs, on light fixtures and wires, over windows and doors, and on pipes and ventilators (71.6% of records); under bridges and in road culverts (14.9%); on rock faces and in caves (12.2%); on dredgers and trucks (0.8%); on concrete walls (0.3%); and on a tree limb (0.2%). Occasionally, the Barn Swallow nested in unusual sites, including on hanging pieces of paper and cloth, a gear wheel, a pulley, a leaning plank, and a sunflower seedhead tacked to a barn beam. The only nest found in a tree was on a limb at a major fork in a white birch. Most nests were attached by mud to a vertical surface close to an overhead horizontal surface; many were on horizontal ledges or various substrates. Old nests were often reused and occasionally old Eastern Phoebe and American Robin nests were used. Nests in road culverts were 3-9 m from ground or water. Nest heights in other areas ranged from 0.3 to 10.7 m, with most 2-3 m up. Three exceptions were nests 15.2 m up on a bridge, 25.9 m up on a tower platform, and 45.7 m up on a rocky cliff (Peck and James 1987). The Barn Swallow has nested on rock faces and cliffs at 10 locations in Algonquin Park (Tozer 2012). Other unusual nest sites were reported in Ontario: on a ferry in the Kingston area (Weir 2008); a nest attached to a wire running between the peaks of a small barn (Rayner 1988b); and in a parking garage in Kingston. It had access to the garage only when a vehicle went in or out (Fairfield 2001). Artificial nesting structures are frequently built for Barn Swallows in Ontario. These are 2.1 x 1.8 m roofed wooden structures on 3.6-m poles with predator guards on them. Wooden artificial nest cups

are provided within the structure. Usage of these by swallows is very low, probably because they are too small. Larger structures measuring approximately 3 x 3 m are often successful in attracting nesting Barn Swallows (personal observation).

Erskine (1979) examined approximately 5,000 nest record cards across Canada. Only 48 nests (1%) were on cliffs or in caves, 54% were in buildings, 33% were on the outside of buildings, and 12% were on other structures. In Manitoba, Knapton (1988a) reported 6 nests on an 8-m high cliff face on an island in Lake Winnipegosis. Three nests were in natural cavities of the rock and the others were on the cliff face. Traditionally, the Barn Swallow nested predominantly in caves or in crevices in rock faces. It prefers to nest 1.2-7 m or more away from entrances to caves and buildings, and in the darkest portions of culverts that are typically avoided by Cliff Swallows. Most Quebec nests were on artificial substrates, but some were under rock outcroppings on cliff tops, on trees, and inside caves. In British Columbia, 1% of nests were in caves, cliffs, or banks of sand or rock, and in tree cavities. The rest were on artificial structures: 92% in or on buildings, and 4% on other structures such as wharfs or bridges. All Illinois nests were in or on buildings or under cement or metal bridges and culverts. In the Yukon, picnic shelters at campgrounds are regular nesting sites. There are numerous reports of it nesting on boats and ferries that travelled daily distances of 20 km or more. It has nested on moving oil pumps in Saskatchewan, on a train in British Columbia that carried passengers over a 3-km portage, and in wells and abandoned mine shafts. An Ohio nest was suspended from a wire, and nests have been built on top of coils of wire and in a willow tree overhanging a river. Height of British Columbia nests was 0.3-30 m, with most 2.4-3.5 m up (Bent 1942; Brown and Brown 2020; Campbell et al. 1997; Graber et al. 1972; Landry and Bombardier in Gauthier and Aubry 1996; Lesher 1988; Murray 1962; Radford 1971; Redmond and Murphy 2007; Samuel 1971; Sinclair et al. 2003; Stewart 1954). In North Carolina, Barn Swallows readily used artificial nest cups attached to concrete girders under a pier (Mercadonte and Stanback 2011). In Mississippi, it nested exclusively on bridges. No bridges without water under them were used. Bridges constructed primarily of wood and that did not have utility wires nearby were used significantly less than expected. Bridges on gravel and dirt roads were used significantly less than expected. Significantly more bridges oriented on a north-south axis were used than east-west bridges. Bridges with nests had a significantly shorter span (5.38 m compared with 11.79 m), higher end walls (1.76 m compared with 1.26 m), and were wider (12.18 m compared with 9.51 m) than bridges without nests. The minimum culvert opening it used was 0.9 by 0.9 m. The mean height above ground or water at the centre point of the bridge was lower for bridges with nests (2.12 m compared with 2.57 m), but the difference was not significant. Nests were very close to the floor (4.34 cm from the top of the nest to the floor of the bridge) and away from the edge of bridges (average 4.25 m). Cement construction was the main factor in determining bridge use for nest construction. Reasons for selecting these nesting parameters may be that utility lines provide necessary perches; wooden bridges are more accessible to predators and may contain creosote that may be toxic or noxious to birds; unpaved roads are more likely to have wooden bridges through which dust and small pebbles can sift through to the nest; and bridges with a north-south exposure of the opening may afford protection from prevailing winds and adverse conditions (Jackson and Burchfield 1975).

Nest-site selection is influenced by the presence of old nests. Some nests have been used for as long as 30 years. Birds that use old nests lay their clutches an average of 12 days earlier than those constructing a new nest and fledge 44% more young. Previous reproductive success at a given nest does not affect the likelihood of it being reused (Safran 2006). In Colorado, 60% of pairs switched nests between their first and second broods. This proportion did not change even if the number of vacant nests increased. Pairs were more likely to settle in old (86%) than new nests (14%). Pairs were more likely to switch to an old (81% of birds that switched) than a new nest (19%), especially if they had first occupied an old nest. Nest switching provided some pairs the opportunity to decrease nest mites in their second nest compared with the first. Birds that settled in an old nest then switched raised significantly more fledglings. The optimum reproductive strategy appears to be to use an old nest for the first nesting attempt and switch to another nest for the second attempt (Donahue et al. 2018).

The Barn Swallow is a territorial species that nests singly or in small, loose colonies. In Ontario, 161 colonies supported 2-59 nests (average 10). When nesting in caves, there are usually only 1-2 nests present. Occasionally colonies of 3-30 pairs have been found in natural areas. Colonies are more common at artificial sites. Colony size increases with barn size. At 15 barns in Wellington County, colony sizes ranged from 1 to 48 nests (average 14). Colony sizes reported elsewhere were: British Columbia, 3-83 nests, mostly 5-14; New York, 2-22 and 2-30; Kansas, 2-14; and an average of 2-3 in Mississippi. Colonies larger than 35 nests are infrequent, with 90 nests the largest reported colony. It appears to be ill-adapted to colonial nesting and may be forced to form colonies where nest sites are limited. Pairs within colonies maintain individual distance and act independently of other pairs. Nests tend to be spaced 2-4 m apart, but may be as close as 61 cm to each other if the birds cannot see each other. Nests without visible neighbours are occupied much more frequently than those with visible neighbours. Hiding the nest from neighbours can reduce the amount of time spent guarding the nest. Nesting in colonies may be disadvantageous because reproductive success may be lower in colonies, less food is available near large colonies, and there is more ectoparasitism, predation, infanticide, and brood parasitism in colonies. Males defend nest sites and their mates, as well as preferred perches nearby. Birds defend from neighbours and unmated birds searching for nest sites or mates. Individuals defend against others of the same sex. Two active Ontario nests were touching each other and 2 on the same beam were only 20 cm apart. Elsewhere, nests have been reported as close together as 10 cm, but nests are typically much further apart. Mean internest distances were 1.7 m in British Columbia, 2.3-3.7 m in Nebraska, and 3.7 m in Oklahoma and in Missouri. Close nests almost always have different approaches for the adults (Bent 1942; Brown and Brown 2020; Campbell et al. 1997; Mercadonte and Stanback 2011; Peck and James 1987; Salvadori et al. 2011; Shields and Crook 1987; Smith and Montgomerie 1992; Snapp 1976).

Home range size is variable, depending on weather and availability of mud for nest building. Birds in larger colonies may have to travel further for insects due to local depletion. In Kansas, 1 pair confined most of their foraging to 8 ha. Most activity of nesting birds occurred within 100 m of the nest barn, but birds occasionally foraged 400-800 m away. Most years, nesting material was gathered close to the nest site, but in a drought year a pair travelled 850 m to gather mud (Fitch 1958). In New

York, birds foraged at sheltered beaver ponds during cool, windy weather. These were 1-6 km from the colony (Shields 1984). In West Virginia, birds foraged within 1.2 km of the nest (Samuel 1971).

Natal philopatry is low: 0.44% in Kansas, 0.57% in Oklahoma, 0.0% in Nebraska, 1.0% in Pennsylvania, and 2.0% in New York and Massachusetts. The 2% that returned in New York represented 7 birds, of which only 5 nested. None bred in their natal colony and their median dispersal distance was 6,375 m with one recovered 15 km from the natal site. Three of the 4 known-sex returning birds were males. In Oklahoma, all nestlings that returned were males. All nested in a culvert other than their natal one. Of returning yearlings in Massachusetts, 95% were males (Brown and Brown 2020; Iverson 1988; Shield 1984).

Adult site fidelity is high. Once a site has been used, it is likely to be used long term. This includes unusual sites, such as an active steamer boat where birds nested in 55 consecutive years. Marked birds have returned to Ontario and British Columbia sites 5 consecutive years. In New York, approximately 40% of adults returned to breed the following year. Annual adult mortality may be 50-70%, so a high proportion of living birds returned. Of returning adults, only 7% changed colonies, 36% of those that returned to the same colony used the same nest, and an additional 29% returned to the same nest cluster. Forty-eight percent of males and 24% of females reused the same nest in subsequent seasons. Most of the colony switches between years were by females. One female moved to another colony and subsequently returned to the original one. Birds that changed colonies failed to raise young the previous year. Successful birds were much more likely to return to the same colony, nest cluster, and nest, and retain the same mate. Mean dispersal distances from the previous year's nest were 25 m for successful males, 820 m for unsuccessful males, 95 m for successful females, and 1,155 m for unsuccessful females. All colony switches and most cluster switches were associated with nest failure or loss of a mate. For replacement nests and second nests in a season, 53% reused the same nest, 88% nested in the same cluster, and 98% nested in the same colony. Within seasons, successful birds were more likely (78%) to switch nests than unsuccessful birds (32%), but the reverse was true between seasons: 53% for successful birds and 67% for unsuccessful birds. Other reported adult return rates are 87.5% and 19.6% in Oklahoma, 34.0% in Massachusetts, 21% in Kansas, 12.3% in Nebraska, and 13% in Pennsylvania. A 10-year study in southern Ontario documented a return rate of 25.9%. In Oklahoma, 16.6% of returning birds used the same nest; mean distance moved from the previous nest was 12.1 m (Bent 1942; Brown and Brown 2020; Campbell et al. 1997; García-Pérez et al. 2014; Iverson 1988; Peck and James 1987; Samuel 1971; Shields 1984; Weir 2008).

Limiting Factors

Eggs have been found in Ontario nests from the second week of May until the third week of August, mostly in the last 3 weeks of June (Peck and James 1987). In Algonquin Park, nests are under construction from early May to mid-July, eggs are present from mid-May to late July, nestlings are present from early June to early September, and dependent fledglings have been observed from mid-July to early September (Tozer 2012).

Nest building may start 5-14 days after spring arrival, but delays as long as 10 days are common during cold, wet weather. The average time to build a new nest was 6.4 days in West Virginia (range 3-10 days), 15 days in British Columbia, and 8-12 days in Illinois. New York nests took 11 days to build

whereas nest renovation time averaged 4-8 days; old nests took 2-5 days to repair in Kansas. Eggs may be laid 1 day after the lining is completed, or not until 2 weeks later. Eggs are laid at the rate of 1 a day, but occasional egg-laying intervals of 2-6 days occurred in Ontario. Initiation of incubation is variable and may start with laying of the third or penultimate eggs in 5-egg clutches. Incubation periods of 9-17 days have been reported in Ontario, mostly 13-14 days. These incubation periods indicate incubation well before clutches were complete as well as delays in incubation. In British Columbia, the incubation period was 12-17 days, mostly 15 and 16 days, and averaging 14.6 days in 1 study. Generally, the incubation period is reported as 13-16 days and most frequently as 15 days. The nestling period is 15-27 days, but mostly 20-23 days. The entire nesting cycle takes 41-51 days (Bent 1942; Brown and Brown 2020; Campbell et al. 1997; Graber et al. 1972; Peck and James 1987; Samuel 1941; Smith and Montgomerie 1992; Voss et al. 2008).

Many pairs raise 2 broods in a season. Second broods are common in Ontario and are often produced in the same nest. Occasionally a different nest is used for the second brood or a new nest may be built on top of the old one. Near Kingston, 30% of pairs raised 2 broods. Higher rates of second broods have been documented: 90% in Manitoba, 37% in British Columbia, 67% in Massachusetts, and 49% in New York. There are reports of the Barn Swallow raising 3 or 4 broods, but this has not been substantiated. These probably represent replacement nests; it may lay as many as 4 clutches in an attempt to raise 2 broods. Birds that initiate nesting early are more likely to raise a second brood; those that use an old nest are more likely to raise 2 broods than those that build a new nest. In New York, 18% of late nesters attempted a second brood compared with 82% of early nesters. In Manitoba, there was no difference in initiation dates at old and new nests. Clutches of 2-7 eggs have been reported in Ontario, with most containing 4 or 5 eggs. Throughout North America, the clutch size is 2-7 eggs, but mostly 4 or 5; clutches of 10 eggs have been reported in British Columbia. Five eggs are most frequent in first clutches and 4 eggs in second clutches. In West Virginia and Kansas, mean clutch size was 4.6 eggs for first clutches and 4.1 for second clutches. In New Brunswick, early nesting birds had larger clutches. Yearling females lay smaller clutches than adults. In small colonies, yearlings laid an average of 5.7-6.2 eggs for their 2 clutches compared with 6.8-7.5 for adults. In large colonies, yearlings laid 6.2-6.4 eggs compared with 7.9-8.3 for adults (Bańbura and Zieliński 1998; Barclay 1988; Bent 1942; Brown and Brown 2020; Campbell et al. 1997; Graber et al. 1972; Imlay et al. 2019; Peck and James 1987; Ramstack et al. 1998; Samuel 1971; Snapp 1976).

Both sexes are capable of breeding when they are 1 year old. In some populations, many yearlings are unable to find a mate and do not breed (Brown and Brown 2020; Shields 1984).

The Barn Swallow is typically monogamous. In Michigan, a male defended a territory with 2 active nests during the first clutch period in 1979. The 2 nests were 0.7 m from each other. The male guarded both females during and prior to egg laying, but only incubated eggs in the first nest. This was the first documented case of polygyny reported in North America (Wolinski 1985). Polygyny may be the reason that some nests have been reported unusually close to each other. The pair bond usually remains intact for both broods (Samuel 1971), but divorce may occur if the pair is unsuccessful in raising a brood in the first attempt. Successful pairs may reunite the following year. At some nests, there may be a third adult. These birds may contribute somewhat towards feeding

of young, but have no influence on reproductive success. Mostly they appear to be trying to replace one of the mated birds. Rarely, the presence of the third adult may result in formation of a polygynous trio (Brown and Brown 2020; Medvin et al. 1987). Extra-pair copulations are common with 22% of nestlings being extra-pair in an Ontario population (Smith et al. 1991). Females rarely parasitize other nests (Brown and Brown 2020).

The Barn Swallow typically forages aerially during the day. It tends to feed lower than Tree Swallows and especially Cliff Swallows, so there may not be significant competition for food among these species. The Barn Swallow seldom forages at heights greater than 10 m and often feeds less than 1 m from ground; occasionally it forages at heights of 20-30 m. Many of the other swallow species feed on small, swarming insects. The Barn Swallow prefers single large prey but takes small insects when they are abundant. It prefers to forage in open habitats over grassy pastures, plowed fields, and water, and around farmyards and domestic animals. In Illinois, favoured foraging habitats were shrubby edges, alfalfa and sweet clover fields, pastures, ungrazed grasslands, roadsides, and drainage ditches. In Saskatchewan, it tended to forage within 400 m of the nest. It preferred to forage in and near wetlands and avoided crop fields. Often it feeds on insects flushed by farm implements, grazing livestock, humans, and flocks of other bird species. Occasionally it lands on the ground to feed on dead or moribund insects, or picks insects off plant, artificial, or water surfaces while it is in flight. During bad weather, it may fly a few centimetres above water and pick insects out of the water, or pick flies off barn walls. It has foraged at night in artificially illuminated areas or even in darkness when attempting to raise a very late brood (Bent 1942; Brown and Brown 2020; Cohen and Dymerski 1986; Graber and Graber 1963; Greenberg 2001; Harris et al. 2024; Hobson and Sealy 1987a; Paton and Fellows 1994; Ramstack et al. 1998; Samuel 1971).

Nestlings are fed insects exclusively. Females feed the young of the first brood more frequently than the male. If a second brood is attempted, feeding frequency by the female starts to decrease 5 days before egg laying in the second nest and ends once laying begins. The male does not increase his efforts in feeding to compensate for less feeding by the female. Survival rates of first broods decline once the female stops feeding and survival decreases with decreasing time between the first and second nests (Naef-Daenzer et al. 2011). Adults do not compensate for poor aerial insect supply on cool days and decrease their energy expenditure by foraging less under these conditions. The energy expended foraging increases with temperature, resulting in a surplus intake under favourable conditions and allowing the brood to accumulate body reserves (Schifferli et al. 2014). Brown and Brown (2020) found 21 families of insects in nestlings' diet in Nebraska. The 15 most common families were, in decreasing order of abundance: dance flies, long-legged flies, blow flies, flower flies, snout moths, snipe flies, ants, scarab beetles, clear-winged moths, flesh flies, lanternflies, house flies, robber flies, soldier flies, and picture-winged flies. Near Cambridge, fecal sample analyses determined that the first brood consumed 11 taxa and the second brood consumed 13 taxa. Only 2 species (9.1%) were eaten by both broods: a stream mayfly and a blow fly. The first brood consumed tiger moths, tent caterpillars, 3 genera of net-spinning caddisflies, mosquitoes, black flies, and horse flies. The second brood consumed 2 species of plant bugs, gypsy moths, oblique-banded leafrollers (a moth), crane flies, 3 species of bristle flies, and weevils. Caddisflies appeared to be important in the diet of the first brood but were not consumed by the second brood. Flies appeared

to be more important in the diet of the second brood. Results suggested that prey availability changes seasonally resulting in the 2 broods having differing diets (Sandilands and Morningstar 2018). McClenaghan et al. (2019a, 2019b) conducted a similar but more comprehensive study in Peterborough County based on 271 nestling fecal samples. A total of 472 taxa were identified, including 130 arthropod families in 13 orders. Flies were the most frequently detected order in nestlings' diet. Bristle flies were the most abundant family, and a cluster fly that is parasitic upon earthworms was the most frequently detected species. Mosquitoes, horse flies, and house flies were frequently fed to nestlings. Small aerial insects less than 3 mm in length represented 76.3% of available insects but constituted only 6.8% of nestlings' diet. Larger aerial insects represented 23.7% of available insects and constituted 16.7% of the diet. Prey items averaged 4.9 mm in length (range 1.1-20.3 mm); available insects averaged 3.4 mm (range 0.1-38.9 mm). Diet varied by site, brood, and year, with site explaining most of the variance. Nestlings were fed different prey items over time and at different sites because prey availability changed temporally and among sites. Eight families of flies were consistently fed to nestlings across sites, broods, and years: bristle flies, limoniid crane flies, crane flies, blow flies, root-maggot flies, house flies, deer flies, and mosquitoes. Change in diet among sites and years was related to prey availability; most prey was fed to nestlings when it was more abundant. Their results indicated that the Barn Swallow has a flexible diet that is adjusted according to changing prey availability; reproductive performance was not affected by prey availability (McClenaghan et al. 2019a, 2019b). Bumelis et al. (2022) determined that nestlings were fed predominately terrestrial prey. Tree Swallow nestlings fed mostly on aquatic prey; Cliff Swallow nestlings had an intermediate diet. In Saskatchewan, Barn Swallow nestlings were fed mostly terrestrial prey, only increasing their aquatic food input when water sources were more available (Diaz Bohorquez et al. 2025).

Adults feed themselves while capturing food for their young, so it is likely that the adult diet is similar. Adults may occasionally eat eggshells or oyster shells provided by humans. Beal (1918) examined 476 stomachs. The diet consisted of 99.8% animal material, almost entirely insects except for a few spiders and snails. Small amounts of vegetation were taken incidentally, but occasionally a berry or seed was ingested intentionally. Real plant food was found in only 4 stomachs and consisted of elderberry, dogwood, and buckwheat seeds. Flies dominated the diet at 39.5% of items; flies were found in 75% of stomachs and constituted 82% of the March diet. House flies dominated the flies consumed, but Barn Swallows also ate crane, horse, and robber flies. Beetles were next in abundance at 15.6%. Eighty species of beetles were found in stomachs, with weevils and ground, lady, and scarab beetles dominating. Bugs comprised 15.1% of the diet, mainly leafhoppers, aphids, and seed, stink, and leaf bugs. Hymenopterans other than ants comprised 12.8% of the diet; ants constituted 9.9%. The lepidopterans consumed were mostly adults, and these comprised 2.4% of the diet. Other items in the diet included grasshoppers and crickets (0.51%), dragonflies (4.0%), mayflies, spiders, and snails. At Vancouver International Airport, it consumed insects from 8 orders, but predominantly hymenopterans (40%), flies (31%), bugs (15%), and beetles (12%). It also ate lepidopterans, odonates, and thrips. The hymenopterans were mostly ants. The flies were predominantly blow flies and the bugs were mostly leaf-footed, seed, and stink bugs. Compared with the abundance of insects captured in traps, it selected for hymenopterans, selected against beetles, flies, and lepidopterans, and consumed bugs at rates similar to their abundance. It selected for insects 4-8 mm in length and

against large (more than 8 mm) and small (0-4 mm) insects. Insects 4-8 mm long represented only 10% of available prey but comprised 70% of the diet. Small insects represented about 80% of insects captured in traps but slightly less than 30% of the diet. Although a wide range of insects was consumed, over half the diet consisted of only 4 taxa: 29% ants, 12% blow flies, and 11% seed and stink bugs. It appeared to select aerial insects of intermediate size, with weak flight, and that occurred at relatively high densities. Selection against beetles and flies may have been due to their small size; lepidopterans may have been selected against because of their large size. Prey profitability increases with the tendency of prey to aggregate in large swarms, such ants and blow flies (Law et al. 2017). Nancekivell and Nocera (2025) used DNA to analyze the adult diet in New Brunswick and compared the diet of the Barn Swallow with those of Alder and Least flycatchers and Bank, Tree, and Cliff swallows. All species differed in their dietary breadth and prey preferences. The Barn Swallow and the 2 flycatcher species consumed a greater diversity of terrestrial flies than the other species, which ate more aquatic taxa. Barn and Tree swallows and the 2 flycatcher species had broader generalist diets whereas Bank and Cliff swallows had more restricted diets. The approximate frequencies of occurrence of invertebrate groups in the diet of the Barn Swallow were 90% aquatic flies, 90% terrestrial flies 10% terrestrial beetles, 10% bugs, and 5% or less lepidopterans, aquatic beetles, hymenopterans, mayflies, odonates, and spiders. The approximate frequencies of occurrence of invertebrate families in the diet of the Barn Swallow were 30% bristle flies, 30% dung flies, 30% root-maggot flies, 30% deer flies, 30% house flies, 25% flower flies, 20% snipe flies, 10% ground beetles, and 5% or less leafroller moths and marsh beetles.

Four of 3,351 Ontario nests (0.12%) were parasitized by the Brown-headed Cowbird. In British Columbia, 0 of 2,426 nests were parasitized. In Oklahoma, 2 of 67 nesting attempts were parasitized, both in the same nest. There are single records of parasitism from Iowa, Manitoba, and Maryland, 3 from Oklahoma and Pennsylvania, and an undetermined number from Kansas. Parasitism does not have serious implications. Cowbird eggs rarely hatch and there is only 1 record of a cowbird fledging from a Barn Swallow nest (Brown and Brown 2020; Campbell et al. 1997; Lowther 1985; Peck and James 1997; Rothstein 1975; Wolfe 1994).

Extreme weather conditions may be one of the greatest limiting factors to the Barn Swallow, particularly cold, wet weather in spring. Adverse spring weather may result in death of nestlings and adults. Adults may huddle together and manage to survive 2-3 days when temperatures are –8 to –9°C, but colder temperatures or prolonged cold results in mortality. Spring weather temperatures probably regulate population sizes at the northern limits of its range. Extremely hot summer temperatures often result in nestling mortality. Mortality is more common in steel-roofed buildings than in wooden barns (Bent 1942; Brown and Brown 2020; Campbell et al. 1997; Samuel 1971). Higher survival rates occur in years with lower wind speeds (Imlay et al. 2022).

García-Pérez et al. (2014) studied the influences of climate on annual survival rates in Barn Swallows in Seattle and southern Ontario. They estimated survival rates in relation to the El Niño Southern Oscillation (ENSO), the North Atlantic Oscillation (NAO), and the total number of consecutive days with maximum daily temperatures less than 11°C during the breeding season. In the Seattle area, both the ENSO and NAO affected survival, but these had no effect on southern

Ontario swallows, with survival rates remaining constant. Temperature also had no effect on Ontario Barn Swallow survival.

In New Brunswick, Imlay et al. (2017) determined that insect abundance did not affect nestling survival or mass. Near Peterborough, McClenaghan (2018) concluded that food availability during the breeding season may not be a limiting factor. Prey availability was unrelated to timing of reproduction, the number of nests at a breeding site, or the reproductive output of individual nests. Put et al. (2021) concluded that Canadian populations were below carrying capacity and that food limitation was not regulating populations.

The House Sparrow may be a significant limiting factor to the Barn Swallow in some areas. In the late 1800s, significant declines of Barn Swallows occurred as a result of House Sparrows, and it was extirpated from large areas of New England at this time. House Sparrows affect Barn Swallow nests by removing nest material, pecking eggs, and removing or pecking nestlings. In Maryland, egg loss resulted in decreased clutch size, some nests were abandoned as a result of egg or nestling loss, and fewer birds had time to raise a second brood. It was estimated that House Sparrows caused a decline of 44.7% in reproductive output (Brown and Brown 2020; Graber et al. 1972; Weisheit and Creighton 1989). In Wellington County, Salvadori et al. (2011) concluded that House Sparrows were a significant problem at some sites, evicting Barn Swallows or forcing them to nest in suboptimal locations.

The Northern House Wren may occasionally puncture eggs, and other species have been known to usurp nests. These include Eastern Phoebe, Tree Swallow, Cliff Swallow, and bats. This happens infrequently and is usually not a significant limiting factor (Bent 1942; Brown and Brown 2020; Butler and Campbell 1987). In Wellington County, Salvadori et al. (2011) concluded that Cliff Swallows were affecting Barn Swallow populations at some sites by nesting in Barn Swallow nests and immediately inside barn doors, forcing Barn Swallows to nest deeper in the barn. The Barn Swallow prefers to nest in good light.

Mite infestations in nests and blowflies may cause nestling mortality, and mites may significantly reduce reproductive success. Adults avoid nests with high mite populations. Presence of mites may explain why some pairs move to another nest for their second brood (Barclay 1998; Bent 1942; Brown and Brown 2020).

Habitat availability for the Barn Swallow has fluctuated considerably. Initially nests sites were scarce, but increased with human settlement and construction of barns and outbuildings that provided ideal nesting habitat. Forest clearing greatly increased the amount of foraging habitat. Many wooden barns have since been replaced by steel structures that provide limited nesting sites and often no access to the interior of the building. The tendency to larger farms has reduced the number of outbuildings. In Wellington County, old wooden barns supported larger colonies than modern, 1-storey structures. Barn Swallows are more abundant in pastured areas than fields with cereal crops, and the number of dairy farms, dairy cows, and pastures in Ontario has declined significantly since 1978. Conversely, increased numbers of cottages and camps in the north, as well as more roads with bridges and culverts have increased potential nest sites (Bent 1942; Brown and

Brown 2020; Campbell et al. 1997; Graber and Graber 1963; Landry and Bombardier in Gauthier and Aubry 1996; Salvadori et al. 2011; Sheppard et al. 1936).

The Barn Swallow may be adversely affected by disturbance. Birds nesting in barns frequently leave when disturbed, even if it is dark outside. Nests in barns may be abandoned if livestock is placed below them. Checking nests after nestlings are 15 days old or disturbing poorly attached nests may result in nestlings jumping to their death or the nest becoming dislodged (Campbell et al. 1997; Samuel 1971). Humans may actively destroy nests due to the nuisance from excreta (Salvadori et al. 2011) and nests may also be removed to avoid the annoyance of the aggressiveness of the adults.

In Wellington County, Salvadori et al. (2011) suggested that predation by cats could be a significant problem for swallows nesting in barns. At a minimum of 2 of the 15 barns they surveyed, cats contributed to the loss of Barn Swallows.

At Vancouver International Airport, the Barn Swallow constituted approximately 35% of all birds struck by aircraft (Law et al. 2017). Collisions with aircraft may be common at airports throughout its range.

Status

The Barn Swallow was probably rare in Ontario and much of North America prior to European settlement. Population increases probably started in the early 1800s when it began nesting on buildings. Baillie and Harrington (1937) considered it a common breeder near habitation from Lake Erie north to at least Lake of the Woods and Chapleau, and they had a record of a dead bird from Moose Factory. Sheppard et al. (1936) reported that it was common throughout Niagara Region, especially around mixed farming areas. In the Clay Belt, it was common wherever there was a settlement (Smith 1957). Peck (1972) reported an old nest in a shed at Cape Henrietta Maria. During the first atlas, it was common in the south, except for a gap in the heavily forested Algonquin Highlands; uncommon to the transcontinental railway; and rare in the north where there are few buildings (Clark and Clark in Cadman et al. 1987). James (1991) considered it abundant in the south and locally uncommon in the north to Hudson Bay.

The second atlas demonstrated that the probability of observation of the Barn Swallow had declined significantly province-wide and in the Great Lakes–St. Lawrence and Boreal forest regions. It was found in every square in the Great Lakes–St. Lawrence Forest Region south of the Canadian Shield except for a few on Manitoulin Island. Breeding evidence was obtained in every square but one in the Carolinian Forest Region. The decline was most prevalent in the Shield. It was most abundant south of the Canadian Shield, particularly in the agricultural areas of the southwest. It was less common south of the Shield in areas that were extensively forested and in large urban areas (Lepage in Cadman et al. 2007).

Barn Swallow populations have fluctuated considerably throughout North America. Populations may have peaked in the mid-20th century. In Illinois, the state population was estimated at 300,000 in 1909 compared with 910,000 in 1957. Graber and Graber (1963) attributed this in part to alfalfa, which became the dominant hay crop. Alfalfa fields were one of the best foraging habitats. Repeat surveys in Illinois in the early 2000s indicated that it had continued to increase its range and numbers

since earlier surveys. This was despite the facts that there were fewer open barns for nesting and less grazed pastureland, a favoured foraging habitat. It began nesting under bridges and large culverts there (Walk et al. 2011).

Long-term (1970-2021) Breeding Bird Survey (BBS) trends indicate that the Barn Swallow decreased at an annual rate of 2.55% in Canada and 2.04% in Ontario. The short-term (2011-21) trends were annual decreases of 1.1% in Canada and 2.23% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

In Wellington County, Salvadori et al. (2011) monitored Barn Swallow populations at 15 farms from 2008 to 2010. The number of first broods decreased at a rate of less than 1%, indicating more stable populations than the decline reported by the BBS. Despite the small drop in numbers of breeding pairs, the number of young produced increased by 0.5% from 2008 to 2009 and increased a further 8.2% from 2009 to 2010. It has declined significantly in Algonquin Park. Until the end of the 1980s, it nested on almost every building and culvert with suitable nest sites along Highway 60. Surveys conducted from 2007 to 2011 indicated a maximum of about 25 pairs along this route. At 7 sites that formerly supported a cumulative total of 82-87 nests, 0 supported nesting swallows in 2011 (Tozer 2012). Savignac (2011a) concluded that, although the Barn Swallow has declined significantly in Canada and Ontario, it is still more abundant than it was prior to European settlement.

Michel et al. (2016) used BBS data to analyze population trends of the Barn Swallow over broad geographic areas and to compare its trends with those of other aerial insectivores. The Barn Swallow declined throughout New England, the Maritimes, and the Great Lakes region, with strongest declines to the north and east. It increased in Wisconsin, Indiana, Illinois, and Ohio. In the southeast, it was largely increasing or stable, with declines in the mid-Atlantic region, Kentucky, and Tennessee. There was little concordance among the trends of the aerial insectivores. The strongest relationship was observed in the Great Lakes area where declining trends of the Barn Swallow were positively correlated with those of the Purple Martin and Tree Swallow. Of the 5 species studied, the Barn Swallow exhibited the third-highest probability of decline behind the Chimney Swift and Purple Martin. Although the aerial insectivores are often considered a guild that is described as having a negative trend, only 1 of the 5 species examined, the Chimney Swift, exhibited significant declines in over half its population trajectories. Results indicated that declining population trends among aerial insectivores are not universal either within or across species. Put et al. (2021) determined that the Barn Swallow had declined significantly throughout Canada, but the severity of the decline varied geographically.

The Barn Swallow is currently listed special concern in Ontario and Canada.

POSTFLEDGING PERIOD

Broods may travel 0.5 km or further from the nest to roost on wires and remain close by for several days, although young may return to sleep at the nest a few nights after fledging. Young are fed by adults about a week after fledging then disperse widely. A Kansas nestling was found 115 km from the natal area 41 days after banding (Brown and Brown 2020). In British Columbia, fledglings in non-agricultural habitats travelled a maximum of 5 km from the natal site compared with 19 km for those raised in cropland and pasture (Boynton et al. 2020).

In British Columbia, habitat use by fledglings was not random. Cropland was selected, followed by marshes, grasslands, pastures, urban areas, water, barren sites, unknown habitats, and treed areas. Cropland was used significantly more than all other habitats; 36% of habitat used was cropland, which constituted 22% of available habitat. Marshes were used significantly more than all lower-ranked habitats; 20% of habitat used was marshes, which constituted 27% of available habitat. Natal habitat had no effect on postfledging survival, which was low (44%). Crop habitat appeared to be important for fledglings (Boynton et al. 2020).

The Barn Swallow often congregates in diurnal and nocturnal roosts from postfledging until autumn migration. During the day, it regularly perches on fence wires and hydro and telephone lines approximately 10 m up, but does not use high-tension lines that are 30 m up. A nocturnal roost of about 5,000 birds was reported in London in 1898 in a dense stand of willows. The traditional roost at Pembroke is in a stand of black willows at the confluence of the Muskrat and Ottawa rivers. This site was used for more than 15 years. Barn Swallows also roost in the marshes at Presqu'ile Provincial Park and in the Cataraqui Marsh and Little Cataraqui Marsh near Kingston. In addition to traditional late summer nocturnal roosts, it may temporarily roost in cornfields and grain fields (Bent 1942; Campbell et al. 1997; Graber et al. 1972; LaForest 1993; Ross et al. 1984; Samuel 1971; Weir 2008).

D.R. Evans et al. (2020) tracked Barn Swallows from fledging until autumn migration. Only 40-44% survived to migrate. Nestling body condition was significantly correlated with survival.

MIGRATION

The Barn Swallow migrates by day, typically at heights of 30 m or less, but occasionally as high as 75 m. It may also migrate nocturnally when crossing large water bodies such as the Gulf of Mexico. In spring, it tends to migrate singly, in pairs, or in small groups. Autumn flocks may be much larger and mixed with other swallow species (Bent 1942; Brown and Brown 2020; Graber et al. 1972). Birds banded in Ontario have been recovered in Massachusetts and Louisiana; a bird banded in New Jersey was recovered in Ontario (Brewer et al. 2018).

McIlwraith (1894) stated that the Barn Swallow arrived early in May. It typically arrives in the southern portion of the province in mid-April now, occasionally in late March. Arrival in the southern Shield is typically in the last week of April with early arrivals in early to mid-April (Black and Roy 2010; Lancaster et al. 2004; Mills 1981; Smith and Montgomerie 1992; Tozer 2012; Weir 2008).

Spring arrival usually coincides with the first few days when temperatures reach about 20°C. Arrival dates at a particular colony may be very consistent year to year, but vary considerably from colonies a short distance away. In Illinois over a 25-year period, swallows arrived at 1 barn 11-13 April and 13-17 April at another. In Virginia, arrival at 4 barns in a small study area was on 6, 16, 20, and 21 April (Graber et al. 1972; Samuel 1971).

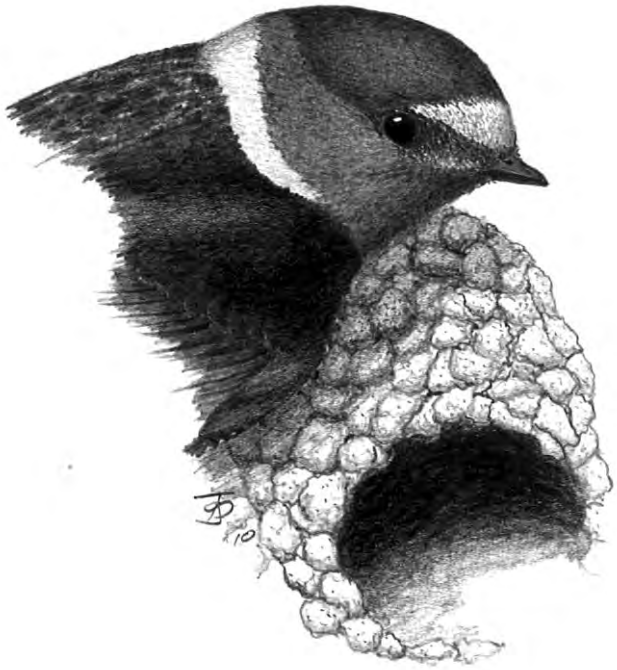
Autumn migration may begin in mid- to late July, with peak numbers in Ontario postbreeding roosts in the last week of July and first week of August. Most birds leave the province by the last week of August or first week of September, but in southern Ontario there are occasional stragglers into late October, rarely to mid-November or even early winter (James 1991; Smith and Montgomerie 1992; Tozer 2012; Weir 2008).

The Barn Swallow forages while it migrates and occurs in habitats similar to those used during the breeding season. Migration often occurs along coastlines, rivers, and lakeshores, and birds concentrate over lakes and ponds during cold weather. It occurs in suburban areas during migration where it forages over gardens, parks, fields, shopping malls, airports, and anywhere with open space. It is probably more abundant outside suburban areas in habitats such as fields, orchards, farmyards, feedlots, rural residences, and anywhere with an abundance of insects. During migration, it tends to avoid forested areas (Brown and Brown 2020; Campbell et al. 1997).

The Barn Swallow is common to abundant during migration. Spring flocks tend to be smaller, with flocks of about 100 common, but flocks larger than 1,000 occasionally occur. Large numbers may occur in roosts prior to autumn migration: 4,000-6,000 have been reported in the Cataraqui Marsh; 5,600 along Little Cataraqui Marsh; 3,000 in Dundas Marsh; and 4,000 in the Presqu'ile Marsh. During autumn, flocks of 500-1,000 or as many as 1,500 may occur (Curry 2006; James 1991; LaForest 1993; Weir 2008).

Cliff Swallow

Petrochelidon pyrrhonota

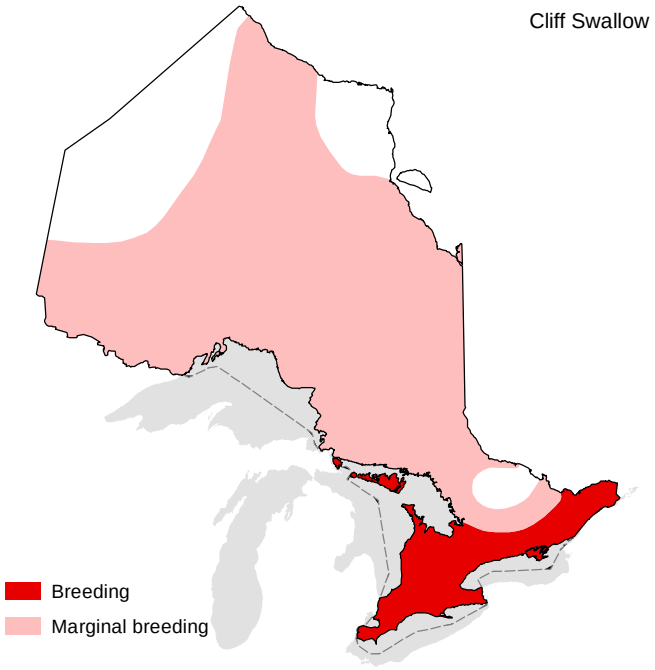


BREEDING SEASON

Habitat Requirements

In Ontario, Cliff Swallow breeding habitat includes rural residential, urban, and industrial areas (31.4% of records); farmland, including pastures (22.1%); shorelines of rivers, lakes, and marshes (20.4%); clearings in wooded areas (8.9%); cottage areas, parklands, mines, and hatcheries (6.0%); roadsides (4.6%); cliffs (0.9%); and sand dunes (0.3%; Peck and James 1987). One southern Ontario colony was on a rock face created by a quarry. Another nest was reported from a cliff in Dundas in 1932 and a single pair nested on the Niagara Escarpment face in 1989 and 1990 (Curry 2006).

Over 80% of British Columbia sites were in human-influenced areas: 40% in urban and suburban areas; 26% in rural areas; 15% in cultivated farmlands or pasture; and miscellaneous sites including reservoirs, industrial areas, and recreational areas. Water, in the form of rivers, streams, lakes, marshes, and estuaries, was present at 13% of sites (Campbell et al. 1997). The Cliff Swallow avoids extensively forested areas and is found in grasslands, towns, fragmented forests, and riparian areas (Brown et al. 2020). Its essential habitat requirements are open areas for foraging; a vertical surface for nesting, preferably with an overhang; a supply of mud for nest building; and fresh water for drinking



(Mayhew 1958). Throughout its range and particularly in the east, it is strongly associated with water. Aerial insects tend to be more abundant near water and bridges and culverts are potential nest sites.

Early in the season, the Cliff Swallow roosts in trees before a nesting colony is selected and until the nest site is big enough to sleep in. One female roosted in the same tree 4 consecutive nights (Brown et al. 2020).

Ontario nests were in or on buildings (73.7% of records), under bridges (25.0%), on rock cliffs (0.9%), in a road culvert (0.2%), and on the wall of a dam (0.2%). Buildings used, in order of preference, were barns, houses and cottages, commercial buildings, sheds, schools, boathouses, churches, airport hangars, lighthouses, grain elevators, train stations and firehalls, pavilions, post offices, and mobile homes. Most nests on outsides of buildings were under the eaves and placed against the overhang and the vertical wall. Some were on vertical walls only, under roof peaks, on light fixtures, under veranda roofs, and under balconies and window ledges. There were 15 reports of nests in buildings on beams, rafters, walls, and ceilings. Nests under bridges were on girders and abutment walls; cliff nests were on vertical surfaces beneath overhangs. More nests (46.7%) faced southerly than in any other direction. Nests on buildings, bridges, and dams were 0.9-30 m from the ground, mostly 3-6 m up. Nests on cliffs and quarry faces were 3-9 m up. Occasionally, old Barn Swallow nests were domed over and used (Peck and James 1987).

Erskine (1979) examined more than 20,000 nest records in Canada and determined that 23% of them were in natural sites on cliffs, almost all in the west. The rest were on buildings, bridges, culverts, and dams. Less than 0.5% of nests from Ontario and Quebec were on natural sites with most on human-made structures. In British Columbia, 85% of reported nests were on bridges, and 9% were on other structures: water towers, a dam, and old Barn Swallow nests. The 5% natural nests were on rock cliff faces and consolidated sand or clay banks. There was 1 report of it using a nest box. In the Yukon, 50% of colonies were on buildings, 30% on bridges, and 20% on rock cliffs. The Cliff Swallow has also nested on irrigation structures; in concrete culverts; among the outer sticks of a Great Blue Heron nest; in or over old Barn Swallow, Eastern Phoebe, and American Robin nests, and active Bank Swallow nests; inside open sheds or barns; at entrances to caves; under branches of large trees; in water towers and grain elevators; under pilings; in an old freight car; and in road tunnels. It occasionally nests on sandstone, sand, and clay banks. It prefers bridges that are over water; when colonizing a new bridge, the area over water is selected first. Concrete culverts higher than 1.5 m are preferred, taller than the Barn Swallow prefers. Multiple culverts are preferred, and it

may switch culverts year to year. Wooden (and sometimes metal) bridges are avoided because mud does not adhere to them as well as to concrete bridges. The Cliff Swallow prefers painted barns with a rougher texture to painted barns for nesting. Caves used for nesting are usually of the limestone sinkhole type and nests are placed on the ceiling immediately inside the entrance. In buildings, the nest is usually at the closest available site to the entrance. It appears to require a large entrance when it nests in a barn or shed. In West Virginia, only 2 of 9 nest sites had entrances smaller than 2.4 x 2.4 m. When these entrances were even partially closed, the nests were abandoned. Although most nests on cliffs are under overhangs, some appear fully exposed. When it rains, it becomes apparent that these nests are situated in the only locations that do not become wet. The need to shelter the nest from rain explains the patchy distribution of nests on some cliffs (Brown et al. 1991, 2020; Campbell et al. 1997; Emlen 1952, 1954; Graber et al. 1972; Gross in Bent 1942; Leighton et al. 2002; Manning 1952; Mayhew 1958; McIlwraith 1894; Samuel 1971; Silver 1993; Sinclair et al. 2003; Storer 1927; Taverner 1928; Weir 2008).

Old nests are frequently reused and are preferred provided they are not infested with parasites. In British Columbia, 96% and 91% of pairs nested in old nests over 2 years. Use of an old nest saves considerable time and energy and may enhance reproductive success because the female expends less energy building the nest. Nests that are protected from the elements may last as long as 13 years. When a new nest is constructed, the Cliff Swallow prefers to build adjacent to another nest or between 2 nests, thereby reducing the effort required to build the nest. In Quebec, 86.6% more nests were built attached to another than expected by random, and 39.9% fewer solitary nests were built than expected. In some colonies, nests are so dense that some do not touch the original nesting substrate. It readily uses artificial nests constructed of clay, ceramics, plaster, and plaster of Paris. Placing horizontal boards under eaves can give swallows a better substrate for attaching the nest (Emlen 1954; Gauthier and Thomas 1993a; Meek and Barclay 1996; Storer 1927).

The Cliff Swallow is highly colonial but occasionally nests solitarily. Peck and James (1997) reported 488 colonies and 109 single nests representing 7,639 nests in Ontario. The average size of 359 Ontario colonies was 15 nests. Colonies tend to be small in the east and much larger in the west. Weir (2008) reported a colony with 100 nests, but most colonies in the Kingston area are smaller than 15 nests. In British Columbia, colonies contained 3-1,375 nests. Over 60% of colonies had 25 or fewer nests and another 33% had 26-100 nests. There were only 6 known colonies of 500 or more nests (Campbell et al. 1997). The largest colony in the Saskatoon area was 1,100 nests (Leighton et al. 2002). Graber et al. (1972) reported 1 colony of 256 nests in an Illinois barn, but stated that most colonies contained 12-100 nests. Mean size of colonies in Nebraska was 38 nests (range 2-3,700). In that state, colonies most frequently contain 200-400 nests and colonies of 1,000 are common (Brown and Brown 1996; Brown et al. 1991, 2020). Sinclair et al. (2003) stated that some Yukon bridges had 5,000-10,000 birds, but mostly 200-500. Brown et al. (2020) stated that colonies may contain as many as 6,000 active nests. Within a colony, nests may be in scattered clusters or in very dense concentrations; Storer (1927) reported 400 nests in an area of 9 m^2 in California and Emlen (1952) reported 900 nests merged into a single mass. Solitary nests are frequently close to a colony (Brown et al. 2020; Graber et al. 1972). Once a nest site is selected, the area where the nest is going to be built is defended. Once a nest is built, other birds attempting to build a nest 8-12 cm below

the nest entrance are attacked. In addition to defending the nest interior, birds defend the area that they can reach with their bill from the nest entrance. Spout entrances of occupied nests are seldom closer together than 10 cm (Brown et al. 2020; Emlen 1952).

Home range sizes may be very large. Birds may range widely in spring to inspect nesting colonies. In Nebraska, birds covered 23 km along a river and visited several sites before selecting one. Once a colony is selected, foraging occurs within a large area that may be as far as 6.4 km from the nest site, but usually within 1.5 km. Birds do not travel as far during nest building and egg laying, but wander further before and after these periods. Birds have been documented travelling 1.6 km for mud (C.R. Brown 1988; Brown et al. 2020; Buss 1942; Emlen 1952, 1954; Storer 1927).

In California, 19% of yearlings returned to the natal colony compared with 48% of adults. In West Virginia, no yearlings returned the following year; 37% of Nebraska yearlings returned. Of returning juveniles, 59% returned to the natal colony in California, 48% in Texas, and 74% in Nebraska. Of 551 returning juveniles in Nebraska that returned to a different colony, most returned to a colony within 3.5 km. One yearling hatched in Nebraska first nested near Edmonton, 1,700 km northwest. Some California yearlings first nested 77 km from the natal site. Males are slightly more likely to return to the natal site than females. Yearlings appear to prefer colonies similar in size to the natal one, even if they return to a different colony. Thirty to 50% of adults return to the colony where they were captured. Of returning birds captured the following year, 82% were at the same colony in California compared with 59% in Nebraska and 45% in Texas. Most others returned within 3.5 km, but some nested as far as 64-66 km away. Adults are more likely to return if they bred successfully the previous year. As birds age, they occasionally switch to smaller colonies in subsequent years. As many as 5-9% of adults switch colonies within a season, usually selecting a nearby colony but occasionally one as far as 64 km away. Most returning birds came from nests and colonies that had low parasitism rates by swallow bugs. Returning birds usually do not use the same nest; only 1 of 5,609 birds that returned in California used the same nest (Brown and Brown 1996; Brown et al. 2020; Mayhew 1958; Samuel 1971; Sikes and Arnold 1984).

Colonies may be used in alternate years, or as infrequently as once in 5 years; other colonies are used perennially. A colony at Moosonee was reported by Schueler et al. (1974) to be present from at least 1965; Wilson and McRae (1993) found that it still supported a minimum of 6 nests. Often only about a third of available colonies are used in a given year. Sites that support large colonies are most likely to be used the following year. When a colony is reused, colonies that were large in size tend to decrease; previously small colonies increase. Presence of fleas and swallow bugs that overwintered may be a factor in colony use; areas of high infestation are avoided (Brown and Brown 1996; Brown et al. 2020; Mayhew 1958; Sikes and Arnold 1984). C.R. Brown et al. (2002) found that the only reliable predictors of colony size were the amount of standing and flowing water within 1 km of the site. The amount of flowing water was associated with how frequently a site was used. Larger colonies had higher land-use diversity, more cultivated cropland, less grassland, and more roads and buildings within the foraging range than smaller colonies. Perennially used sites had more consistent colony sizes year to year. Rarely used colonies had varying colony sizes.

Brown et al. (2014) examined the relationships between colony size and age of birds in Nebraska. Colony age composition was not affected by colony size, colony initiation date, or parasites. As

colony size increased, the proportion of juveniles present increased. Colonies initiated later in the season supported more juvenile birds. Yearlings arrive later than adult males and seldom initiate nests in already occupied colonies. This explains the high proportion of juveniles in colonies that are initiated later in the season.

Limiting Factors

Eggs have been found in Ontario nests from the last week of May until the first week of August, with most present in June (Peck and James 1987). Presence of young in a nest on 4 May in Simcoe County and young being fed in the nest on 24 August in Haldimand-Norfolk suggest earlier and later egg dates (Peck and James 1997). In Algonquin Park, nests are under construction from mid-May to mid-July, eggs are present from early to late June, and nestlings are present from late June to mid-August (Tozer 2012).

Timing of colony occupation may vary significantly annually and is affected by temperature. Once birds have selected a colony, another 3-5 days may elapse before a nest site is selected; occasionally this takes as long as 12 days. Large colonies become active sooner than small colonies. The time it takes to build the nest depends on the time of year, weather, and location of the nest. In West Virginia, nests took an average of 13.0 days to build in May and June, but only 8.4 days in July. Nest building took about 7 days in Wyoming, 3-27 days in Nebraska, and 8-18 days in Quebec. Nest building may be suspended by as long as a week during cold weather and even longer during periods of drought when mud may be unavailable for nest construction. Nests that share walls with other nests take less time to build. Egg laying may commence before the nest is complete, even before the dome is completed. Eggs are laid at the rate of 1 a day. All laying within a colony may take place over a 9-12 day period. Intermittent incubation may start after 2-3 eggs are laid, but is not continuous until the last egg is laid. Incubation periods of 12-17 days have been reported in Ontario, and 20 days for 1 nest. In other areas, incubation periods of 10-19 days have been documented, but the typical incubation period is 13.5-16 days. Eggs that hatch in less than 11 days may have been physically transported into a nest but incubated elsewhere. All eggs typically hatch within a 24-hour period. Fledging occurs at age 20-26 days, mostly at 21-24 days. In West Virginia, the total time from laying of the first egg until fledging was 38-48 days (Brown and Brown 1996; Brown et al. 2020; Buss 1942; Campbell et al. 1997; Emlen 1954; Gauthier and Thomas 1993a; Grant and Quay 1977; Mayhew 1958; Meek and Barclay 1996; Myers 1957; Peck and James 1987; Ramstack et al. 1998; Samuel 1971; Stoner 1945).

It is uncertain whether the Cliff Swallow raises 1 or 2 broods annually. The confusion results because renesting birds typically move to another nest or even another colony for their second nesting attempt, and often use a nest where another brood was raised. Gross (in Bent 1942) stated that it regularly raised 2 broods. This was subsequently disproved, but many authors still cite this work and make the same mistake in interpreting their own data. Many studies with banded birds found no evidence of second broods, so it was generally concluded that second broods were never raised (Buss 1942; Grant and Quay 1977; Mayhew 1958; Ramstack et al. 1998). Rare cases of second broods have been documented in Nebraska (Brown et al. 2020), West Virginia (Samuel 1971), and Quebec (Gauthier and Thomas 1993b). Double broods have been reported in Ontario (Peck and James 1987) but it is uncertain if this was confirmed through banding. Renesting is common if a

clutch is lost. Clutches of 2-7 eggs have been reported in Ontario. One 7-egg clutch was laid by more than 1 female. Most clutches contained 3 or 4 eggs, and 4-egg clutches were most frequent (Peck and James 1987). Clutches of 1-8 eggs have been reported in North America, with rare records of 9, 11, 12, 13, and 15 eggs in a nest, but most clutches contain 3 or 4 eggs. Clutches larger than 6 eggs are probably due to intraspecific parasitism. Small clutches may be due to egg destruction by neighbouring birds. First clutches are larger than replacement clutches. Mean size of first clutches was 4.0 in British Columbia, 4.01 in Quebec, 3.74 in Nebraska, 3.32 in Virginia, and 3.31 in West Virginia. Mean size of second clutches was 2.7 in Quebec, 3.00 in Virginia, and 2.88 in West Virginia. In Quebec, first clutches fledged an average of 1.84 young per nest compared with 0.4 for second clutches. Clutch size declines by about 1 egg over the season and later clutches have lower success rates. Yearling females lay smaller clutches (3.3 eggs) than 2-3-year olds (3.7 eggs; Brown and Brown 1989, 1996, 1999; Brown et al. 2020; Campbell et al. 1997; Gauthier and Thomas 1993b; Grant and Quay 1977; Gross in Bent 1942; Imlay et al. 2019; Mayhew 1958; Myers 1957; Ramstack et al. 1998; Samuel 1971).

The age at first breeding for both sexes is 1 year, and breeding occurs every year thereafter. The mating system is seasonally monogamous, with the pair bond dissolving once young fledge. Renesting females frequently select a different mate. Reunion of pairs in subsequent years appears to be coincidental when both birds return to the same portion of the colony (Brown et al. 2020; Samuel 1971).

Intraspecific nest parasitism is common. In Nebraska, as many as 43% of nests contained parasitic eggs; 33% of Pennsylvania nests contained parasitic eggs. These are either laid in neighbours' nests or physically transferred in the bill. In most cases, the parasite's and host's nests are adjacent to each other or separated by 2-5 nests. Maximum distance recorded was 1.98 m. Nest-guarding males may tolerate intruding females while they lay an egg. Frequently the parasite removes one of the host's eggs before laying a parasitic egg. Parasitic females laid fewer eggs in their own nests, but more eggs overall than nonparasitic birds. The mean number of parasitic eggs in 21 nests was 1.57 (range 1-4). While the parasites are in hosts' nests, they may be parasitized themselves. In Nebraska, 54.2% of parasites were parasitized, and a third of birds that destroyed eggs in other nests had an egg destroyed. Birds occasionally parasitize nests by transferring young in their bills. Parasitism rates are highest in colonies where reproductive success is variable. Spreading eggs out enhances chances that some of the birds' reproductive effort will produce fledglings in colonies where success is uncertain (Brown and Brown 1988, 1989; Brown et al. 2020). Extra-pair copulations also occur, but the extent of extra-pair young in populations is unknown (Brown et al. 2020).

The Cliff Swallow prefers to forage over grasslands, hayfields, watercourses and water bodies, and shorelines, which may be particularly favoured. It may be attracted by hay mowers, horses walking through tall grass, and other activities that may stir up insects. Hills and wooded areas tend to be avoided, but it may feed on the lee side of bluffs or road cuts where insects concentrate. Although some birds forage singly, most forage socially. As many as 75-1,000 birds have foraged in areas as small as 10 m^2. More often they occur in towers of birds 5-30 m above ground. Most food is captured aerially, and it feeds predominantly on insect species that swarm. Although it may occasionally forage with Barn Swallows, the Cliff Swallow commonly feeds at heights of 30-50 m.

This is much higher than the Barn Swallow forages, so the 2 species are vertically stratified and have different diets. When the weather is cool or rainy, there are no thermals to push insects high, and the Cliff Swallow usually feeds at altitudes of 5 m or less over water. It has taken moribund midges from the surface of a pond in Colorado, mayflies from pavement in Alabama, and walked on the ground to feed on ants. At Great Salt Lake in Utah, foraging on the ground for brine flies was the most common feeding technique. Early in the nesting season, all birds may desert the colony for several hours to forage communally. Later on, foraging bouts are much shorter and less social. Birds in large colonies must travel further due to local depletion of insects around the colony (C.R. Brown 1988; Brown and Brown 1996; Brown et al. 1991, 2020; Cohen and Dymerski 1986; Emlen 1952, 1954; Graber et al. 1972; Hobson and Sealy 1987a; Paton and Fellows 1994; Ramstack et al. 1998; Samuel 1971; Stoddard 1988). Colonies act as information centres. When a bird returns to the colony after an unsuccessful foraging trip, it watches its neighbours. When a neighbour returns with food, the unsuccessful bird follows it to its food source. In large colonies, birds often join the large groups that continually stream between the colony and food source. In small colonies, birds may spend time on their own searching for prey (Brown et al. (2020). During cool weather when prey is scarce, individuals that find prey may give a special call to alert others to the food source (Stoddard 1988).

The Cliff Swallow feeds almost exclusively on flying insects, but rarely consumes spiders and snails. Prior to age 6-7 days, nestlings are fed small soft-bodied insects, often flies and soft-winged bugs. After that, the diet of young is similar to that of the adults (Brown et al. 2020). Bumelis et al. (2022) determined that the diet of nestlings consisted of a mix of terrestrial and aquatic emergent insects. Barn Swallow nestlings consumed predominantly terrestrial insects; Tree Swallow nestlings ate mostly aquatic emergent insects. In New Brunswick, Imlay et al. (2017) examined the effects of insect abundance on Cliff Swallow nestling survival and growth rates. Areas of lower insect abundance were not related to lower nestling survival or mass.

Beal (1918) examined 375 stomachs which contained 99.3% animal material. The vegetation included juniper berries; 2 stomachs were completely filled with them. The diet consisted of 26.9% beetles (weevils and lady, ground, and dung beetles), 26.3% bugs (leafhoppers and leaf, seed, leaf-footed, and stink bugs), 20.5% hymenopterans other than ants (mostly bees and wasps), 14.0% flies, 8.2% ants (mostly winged forms), 0.7% grasshoppers, 0.5% lepidopterans, and 3.0% dragonflies, lacewings, spiders, and snails. Brown and Brown (1996) examined the diet in Nebraska and found 17 insect families prevalent. In order of importance, they were leafhoppers, long-legged flies, black flies, ants, dance flies, midges, horse flies, mosquitoes, argid sawflies, lanternflies, sweat bees, hump-backed flies, crane flies, flower flies, ground beetles, green lacewings, and seed bugs. Eighty-four insect families from 10 orders were represented in the diet. These included 17 families of beetles, 18 families of flies, 2 families of mayflies, 17 families of bugs, 7 families of hymenopterans, 4 families of lepidopterans, 2 families of odonates, and 3 families of orthopterans. It also feeds on shore flies and shore bugs (Brown et al. 2020; Graber et al. 1972; Stoddard 1988; Storer 1927). The insects that are consumed reflect local availability and may vary considerably among colonies situated only a few kilometres apart. In Nebraska, 10 of the 15 insect families consumed most frequently were ones known to swarm or otherwise congregate. Cliff Swallows drink exclusively on the wing by skimming surface water (Brown et al. 2016). Nancekivell and Nocera (2025) used DNA to analyze the adult diet

in New Brunswick and compared the diet of the Cliff Swallow to those of the Alder and Least flycatchers and the Bank, Tree, and Barn swallows. All species differed in their dietary breadth and prey preferences. The Cliff, Bank, and Tree Swallows ate more aquatic taxa than the other species, which consumed more terrestrial flies. The Cliff and Bank swallows had more restricted diets whereas the other species had broader generalist diets. The approximate frequencies of occurrence of invertebrate groups in the diet of the Cliff Swallow were 80% aquatic flies, 30% terrestrial flies, 20% lepidopterans, and 5% terrestrial beetles. The approximate frequencies of occurrence of invertebrate families in the diet of the Cliff Swallow were 45% limoniid crane flies, 15% mosquitoes, 10% root-maggot flies, 10% leafroller moths, and 5% snipe flies.

Cowbird parasitism has not been documented in Ontario, but rare cases have been confirmed in British Columbia, Illinois, and Pennsylvania. Opportunities for parasitism occur because swallows often initiate egg laying before the nest is complete, and some nests lack spouts or cones. Rare incidents of parasitism by House Finches and House Sparrows have been reported. Swallow nestlings typically starve to death in parasitized nests (Brown et al. 2020; Buss 1942; Campbell et al. 1997; Graber et al. 1972; Gross in Bent 1942; Mayhew 1958).

The Cliff Swallow may be adversely affected by weather that is too cold, too hot, too dry, or too wet. Cold weather is the most significant factor. When spring temperatures are less than 10°C for 3-4 days, extensive mortality of adults may occur. During cold spells, adults may not leave the nest and die of starvation if the cold persists. As a result of unseasonably cold weather in June 1 year in Illinois, about 95% of the population died. Events such as these have been reported throughout much of its range. Females may be more susceptible to cold due to the stresses of egg laying. Cool weather may also have indirect effects on survivorship. Nesting may be delayed in late springs resulting in smaller clutch sizes and lower likelihood of renesting. Insects are less abundant in cool weather, so nestling growth rates may be retarded. Mortality and adverse effects due to cold weather are more severe in small than in large colonies (Brown and Brown 1996; Brown et al. 2018, 2020; Buss 1942; Graber et al. 1972; Gross in Bent 1942; Henny et al. 1982; Jaramillo and Rising 1995; Krapu 1986). Hot weather in June may result in extensive mortality of nestlings because they frequently attempt to fledge prematurely to escape the heat in the nest. In Nebraska, best success occurred in cooler summers, with lower brood survival in warmer Junes (Brown and Brown 1996, 1999; Graber et al. 1972). Dry weather reduces the availability of mud for nest construction. If mud is scarce, birds may have to travel further and expend more energy in nest construction. Birds may also be forced to use nearby mud supplies that are not of suitable texture. This has resulted in large-scale failure of colonies due to nests falling. In some cases, colonies moved and nested in unsuitable habitat or on unsuitable substrate so they were close to a supply of mud. Reproductive success at these colonies is typically low (Buss 1942; Emlen 1954; Graber et al. 1972; Krapu 1986). Nests on buildings and cliffs may be weakened by significant rainfalls and fall. In Nebraska, a thunderstorm resulted in at least 1,400 nests falling from a cliff and there are other reports of colonies failing completely due to severe rain events. Nests along watercourses may be swept away by high water levels (Brown and Brown 1989; Buss 1942; Graber et al. 1972; Silver 1993).

Cliff Swallow populations began to decline shortly after introduction of the House Sparrow. The problem is greatest in agricultural landscapes, but also occurs in natural cliff colonies. House

Sparrows actively take over swallow nests with essentially no resistance. Early in the breeding season, when adults leave the colony en masse to forage for 1-2 hours, sparrows often remove swallow eggs and nestlings and take over the nests. Hundreds of young may be killed even if sparrows do not use the nests. Small colonies are most vulnerable to House Sparrows, who usually take over the entire colony. Even very large colonies may eventually be lost to sparrows, with colonies as large as 2,000 nests being lost. Sparrows also fill nests with feathers, and swallows avoid using old nests containing masses of feathers. In bridge-nesting colonies in Arkansas, Cliff Swallows nesting near House Sparrows had significantly lower nest success (30% of nests fledging at least 1 young) than those nesting where there were no House Sparrows (61% of nests successful). Only 8% of nests were occupied by swallows nesting near sparrows compared with 48% in colonies with no nearby sparrows. Swallow colonies often increase in size if sparrow populations are controlled (Brown et al. 2020; Buss 1942; Campbell et al. 1997; Emlen 1954; Graber et al. 1972; Gross in Bent 1942; Krapu 1986; Leasure et al. 2010; Robinson 1989; Silver 1993, 1995).

Ectoparasites have a significant influence on the behaviour and reproductive success of the Cliff Swallow, with the primary parasites being the swallow bug and bird fleas. The swallow bug is found almost exclusively on the Cliff Swallow and can survive in unused nests for 3 years without feeding. Swallows avoid nests heavily infested with this species, and this explains why usage of many colonies is intermittent. Nestling weight is decreased by 18-22% in nests infected with swallow bugs and survivorship of nestlings declines by as much as 50%. Fleas appear to have no impact on nestling body weight or survivorship, but may reduce annual survival of adults by 33%. Feather mites are positively associated with the Cliff Swallow's daily survival rate and provide direct benefits by consuming old oil, pollen, fungi, and harmful bacteria on the feathers (Brown and Brown 1986, 1996, 1999; Brown et al. 2006, 2020).

Human activities and disturbance may affect Cliff Swallows. Once barn painting became fashionable, many colonies were deserted. The oil in the paint often makes the sides of the barn too slippery for nest attachment. Birds that nest in barns are frequently disturbed by human activities, and leave the barn even if it is dark outside. Nests within barns are usually abandoned if the entranceway is partially closed, if livestock is placed under nests, or if any building or structural alterations occur near the nest. Researchers often remove some or all the nest spout. In these nests, there is a significantly lower hatch rate, a longer incubation period, and a shorter fledging period. Time that adults expend repairing nests results in decreased time spent in care of young. Even minor changes to nests result in reduced reproductive success. Many colonies on buildings are destroyed by humans because of the mess that the birds make (Buss 1942; Campbell et al. 1997; Graber et al. 1972; Gross in Bent 1942; Hamilton and Martin 1985; Samuel 1971; Silver 1995).

The Cliff Swallow often rests on roads and is vulnerable to being killed by vehicles. A 30-year study in Nebraska found that the frequency of road-killed swallows declined sharply following occupancy of roadside nesting sites, and that birds found killed on roads had longer wings than the population at large. Swallows may have adapted to traffic by decreasing their wing length, thereby becoming more agile and improving chances of escape (Brown and Brown 2013).

The Cliff Swallow bioaccumulates contaminants such as toxaphene, mercury, lead, zinc, DDE, PCBs, chromium, and selenium in body tissues somewhat, and may be a reliable bioindicator (Brown et al. 2020).

Price (2004) concluded that the Cliff Swallow may no longer nest in southern Ontario if the average summer temperature increases by 2°C.

Status

Prior to European settlement, the Cliff Swallow was rare in eastern North America. Eastern populations initially increased due to construction of culverts, bridges, and buildings (Brown et al. 2020). In Toronto, Fleming (1907) considered it a regular but local breeder and noted that it was not as common as it had been. This was probably due to the presence of House Sparrows, which caused a population decline throughout its range. In the Kingston area, only one was reported in the mid-19th century, but by 1909 it was common. It declined in this area in the 1930s due to House Sparrows. It was formerly abundant in Leeds County, uncommon in the 1930s, and virtually absent during the first atlas (Weir 2008). In Elgin County, it was common in 1891, uncommon in 1954, and uncommon and local in 2000 (Lancaster et al. 2004). In Niagara Region, Sheppard et al. (1936) had only 2 records from 1918. Baillie and Harrington (1937) stated that it was irregularly distributed north to southern Sudbury District, Algonquin Park, and Ottawa, but with a breeding record at Severn River on the Hudson Bay coast. They concluded that it was not a common species and that it was declining. During the first atlas, most squares contained less than 100 pairs, but it was more abundant in the north within the few squares that it occurred than it was in southern Ontario squares. It was absent from much of the Algonquin Highlands and northern Ontario, with scattered records from Pickle Lake, Moosonee, Fort Albany, and Big Trout Lake. A small cliff-nesting colony was found along the Attawapiskat River about 100 km from James Bay (Taylor in Cadman et al. 1987). James (1991) considered the Cliff Swallow a locally common resident north to Pickle Lake and Moosonee and occasional to rare to Hudson Bay.

The second atlas indicated that the probability of observation of the Cliff Swallow had declined significantly since the first atlas province-wide and in the Great Lakes–St. Lawrence and Boreal forest regions. In the northern portion of the Boreal Forest Region, there was no apparent change, but there was a significant decline in the road-accessible portion of this forest region. There was a significant increase in the Carolinian Forest Region. It was most abundant south of the Canadian Shield, particularly in southwestern Ontario west of Toronto. An exception was Niagara Region where it was not detected in most of the inland squares (Cadman in Cadman et al. 2007).

In eastern North America, the Cliff Swallow initially increased significantly and then declined. It appeared to peak in numbers in the eastern United States from 1840 to 1860; population declines started about 1880 as the House Sparrow spread. In the early 20th century, its population increased in some areas, probably due to its adaptation of nesting under bridges and in large culverts (Graber et al. 1972; Landry and Bombardier in Gauthier and Aubry 1996; Mayfield 1988; Silver 1995; Walk et al. 2011).

Long-term (1970-2021) population trends determined by Breeding Bird Survey data indicated annual decreases of 1.53% in Canada and 4.44% in Ontario. The short-term (2011-21) trends were

annual decreases of 1.24% in Canada and 0.798% in Ontario. The long-term trends were highly reliable; the short-term trends were of medium reliability for Canada and low reliability for Ontario (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Both adults feed the fledglings for 3-5 days after they leave the nest. Young are often led back to the nest for the night when they are still dependent, and also during the day during adverse weather conditions. Soon after fledging, young gather together and form crèches that may contain as many as 1,000 birds. Crèches may assemble on wires, in trees, or on cliffs (Brown et al. 2020).

Once the young fledge, some adults roost in nests, but others use trees and marshes. Young and adults congregate together beginning in late July. Most frequently, they gather on wires, occasionally in trees and marshes and on cliffs. The roost may be 2-3 km or more from the colony, and birds from several colonies may join together. The Cliff Swallow tends to avoid roosting with other swallows. It rarely perches on low barbed-wire fences as the Barn Swallow does, and the Barn Swallow avoids high-power lines 30 m up that are regularly used by Cliff Swallows. Late-summer roosts in West Virginia and Maryland always had meadows nearby and there was usually a stream in the vicinity. Premigratory roost sites are traditional. Some in West Virginia have been used for 30 years. Birds congregate on the same location on power lines every year, although there are hundreds of kilometres of identical wires in the area. At one of these sites, all birds roosted 1 night in an adjacent cornfield, using corn leaf axes and tassels of cobs as resting sites (Brooks 1949; Brown et al. 2020; Emlen 1952; Gross in Bent 1942; Samuel 1971).

Once they are independent, juveniles travel among colonies and inspect nests, as do adults. Juveniles enter nests and actively defend them, and occasionally sleep at night in nests, often in a different nest or colony for 1-2 weeks before leaving the general area. It is likely that they are prospecting for suitable nest sites for the following year. After young fledge, birds of all ages travel widely and visit colonies 60 km or further away. In Nebraska, postbreeding males confined their activities to 15-19.5 km along a river valley for 6-8 days (Brown et al. 2020).

MIGRATION

The Cliff Swallow is a strictly diurnal migrant. It migrates in flocks, often in the company of other swallow species, especially Tree Swallows and Barn Swallows, but also Bank Swallows. Migration in both directions is very leisurely and spans several months (Brown et al. 2020; Gross in Bent 1942; Samuel 1971).

Adults that have previously nested at a colony are first to arrive, followed by other adults, and finally juveniles. Arrival is typically shortly after a few days of warm weather when temperatures are about 20°C. In Ontario, the Cliff Swallow arrives in late April or early May with most arriving in mid-May. Autumn migration begins shortly after the young fledge. Most have left the province by the end of August or mid-September, with stragglers persisting into October. In Algonquin Park, autumn migrants are evident as early as July (Curry 2006; Mills 1981; Tozer 2012; Weir 2008).

During migration, the Cliff Swallow is strongly associated with water, particularly in spring when insects may be scarce. In the Yukon, migrating flocks congregate at lakes and wetlands, and in British Columbia, flocks occur over lakes, ponds, sloughs, and marshes. These are important sources of

flying insects, but it also forages over cliff faces, fields, sewage lagoons, rivers, farmsteads, aspen groves, beaches, and sand dunes. During spring migration in Illinois, largest aggregations and peak numbers coincided with conspicuous swarms of midges (Campbell et al. 1997; Graber et al. 1972; Sinclair et al. 2003).

The Cliff Swallow is a common migrant in Ontario (James 1991), with most flocks containing 50 or fewer birds. An estimated 10,000 were seen at Callander in Parry Sound District and Nosbonsing in Nipissing District on 12 August 1949. Tremendous numbers were observed again at Nosbonsing on 26 August 1952 (Mills 1981).

Ruby-crowned Kinglet

Corthylis calendula

BREEDING SEASON

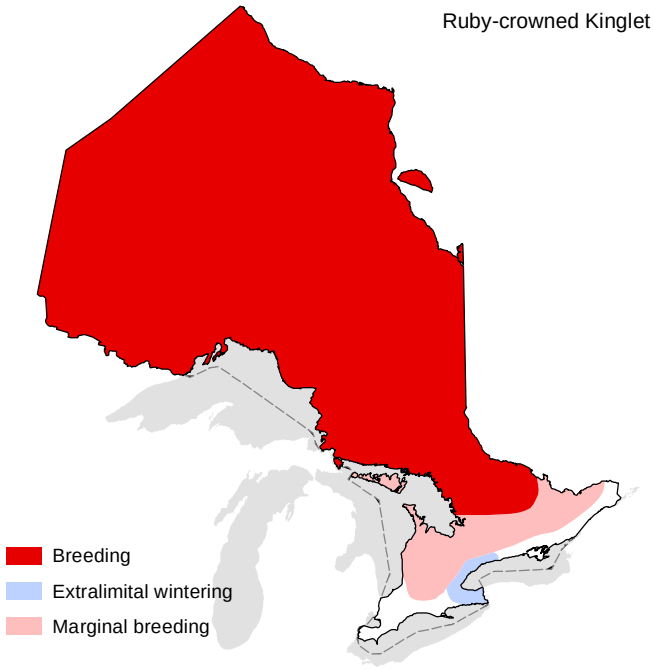
Habitat Requirements

In Ontario, the Ruby-crowned Kinglet has nested in open black spruce and black spruce–tamarack muskegs, and once each in mixed woods, the edge of a burn, an open jack pine stand, and in an isolated tree near a beaver meadow. Habitats used for breeding were typically open and were either wet or near water (Peck and James 1987).

In the Boreal Forest Region of Ontario, the abundance of the Ruby-crowned Kinglet was affected by the amount of merchantable hardwoods and decreased with increasing hardwoods. It was associated with stands dominated by conifers, especially those that were slightly older than average (Rempel 2007).

Near Pickle Lake, the Ruby-crowned Kinglet was the most frequently encountered species in coniferous and mixed forests (James 1980). In northwestern Ontario, it nested predominantly in coniferous forests and mixed forests and deciduous shrub communities, and seldom in deciduous forest and coniferous and mixed shrub communities (McLaren and McLaren 1981). On the eastern coast of James Bay and inland Quebec, it was one of the most common and evenly distributed breeding birds of spruce forests (Manning and MacPherson 1952). It occurred all along the northeast

shore of Lake Superior, but was most frequent in black spruce stands. One nest was in a wet swale at the edge of a burn that was overgrown with black spruce, white spruce, white birch, and alders (Baillie and Hope 1943). Near Hearst, it nested in lowland coniferous clear-cuts 13-19 years old and in uncut upland mixed and lowland coniferous stands (Welsh and Fillman 1980). In the Clay Belt it was significantly associated with nutrient-rich, dry forests (Welsh and Lougheed 1996).



In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Ruby-crowned Kinglet breeds in mature and old-growth white pine stands (Kirk et al. 2012). In jack pine stands near Gogama, it was rarely observed, usually wandering in from adjacent spruce swamps to forage. James and Peck (1995a) considered it conceivable that these birds could have nested, although there was no indication that they did. It appeared to be dependent on spruce for nesting. In Algonquin Park, MacLulich (1938) found it mainly in coniferous and black ash swamps. Also in Algonquin Park, Martin (1960) considered it characteristic of boreal forest. It was most frequent in balsam fir–spruce forests and also occurred in black spruce–white cedar swamps and rarely in hemlock stands.

Bent (1949) stated that the Ruby-crowned Kinglet was typical of black spruce bogs in the Toronto area and that it was rarely seen outside this habitat during the breeding season. In southern Ontario, there are records of it nesting in scattered conifers in highly disturbed areas. These included a nest in a large white spruce on the University of Guelph campus (Curry 2006), a pair in a grove of spruce in a camping area in Prince Edward County (Richards 1983), and a nest in 2 rows of spruce along a gravel road in a residential area of Fort Erie (Andrle 1978). The general habitat in this area was groves and rows of spruce and pine scattered among dwellings.

The Ruby-crowned Kinglet is one of the species characteristic of the Boreal Forest Region, where it occurs predominantly in spruce and balsam fir stands, but also occasionally in jack pine and rarely in hemlock stands (Erskine 1977). In the Saskatchewan boreal forest, it was in a guild associated with conifers and was typical of spruce stands. It occurred mostly in dry stands with moderate nutrient amounts (Kirk et al. 1996). It was associated mostly with drier stands in the Boreal Forest Region of Quebec and Labrador (DesGranges and LeBlanc 2012). In Alaska, it was the only species that showed differences in breeding density among forest stands suffering different levels of mortality due to an outbreak of spruce beetles. Breeding densities in stands of high spruce mortality were 45% of those in moderate mortality stands and 29% of those in low mortality stands. Matsuoka et al. (2001) concluded that the lower density was probably related to lower density of spruce in general rather

than to loss of large-sized white spruce. In subalpine areas of New Hampshire, it was most abundant in virgin spruce stands and was most likely to be found in swamps near a wet depression or small water body (Sabo 1980). In Minnesota, its abundance was associated with black spruce and lowland conifers. Thirty-two percent of the variation in its abundance was explained by the amount of conifers within 200 m, 30% by presence of nutrient-poor stands of black spruce and cedar, and 22% by the amount of upland forest within 500 m; 16% of variability was negatively associated with the amount of non-forest within 200 m. It preferred black spruce or white cedar forests with upland forests in the broader landscape, similar to the Golden-crowned Kinglet. The Ruby-crowned Kinglet preferred more nutrient-poor stands and the Golden-crowned Kinglet preferred more productive stands. Both species were found in some stands suggesting that they might also segregate on smaller microhabitat scales or by foraging techniques. The Ruby-crowned Kinglet was uncommon in tamarack stands (Zlonis et al. 2017). In Saskatchewan, its abundance was significantly correlated with the amount of forest in the landscape, with relative abundances of 78 in white spruce stands, 50 in mixed-wood stands, and 13 in trembling aspen stands (Hobson and Bayne 2000). In the northeast, it was in a guild associated with mature coniferous lowland forests (Niemi and Pfannmuller 1979). In the Great Lakes–St. Lawrence Forest Region, it breeds in forests with mixed conifers and northern hardwoods, particularly those with white spruce, black spruce, and white birch. Highest density occurs in black spruce bogs and it prefers areas close to water (Swanson et al. 2021). In balsam fir–white cedar stands in eastern Quebec, it occurred in equal densities in riparian and nonriparian stands (LaRue et al. 1995). In British Columbia coniferous forests, it was equally abundant in riparian and nonriparian forest during the breeding season and spring migration. During autumn migration and winter, it was significantly more abundant in riparian forest, which had an understory of alders and willows (Wiebe and Martin 1998). In the Yukon, it nests most often in mature, spruce-dominated forests and also in mixed forests dominated by conifers. It is scarce in deciduous trees, in mature black spruce forests, and in black spruce–tamarack forests (Sinclair et al. 2003). In British Columbia, 8 of 25 nest records (32%) were in suburban cultivated areas, but the high proportion of nests in this habitat was probably biased by observer distribution. In other habitats, 8 were in coniferous forest, 4 in mixed forest, and 1 in deciduous forest (Campbell et al. 1997). Barrette and Darveau (in Gauthier and Aubry 1996) considered the Ruby-crowned Kinglet a habitat generalist in Quebec. It nested in mixed woods, dense coniferous forests, stands of scattered spruce on the edge of tundra, jack pine plantations, stands of white spruce more than 50 years old, and sometimes in hardwood forests. Ralston et al. (2019) concluded that it had broad habitat preferences and an ability to use multiple boreal forest habitats.

In some areas, the Ruby-crowned Kinglet is associated with older-growth forest; in other areas it may nest in younger forests. In Saskatchewan, it occurred more frequently in forests that were older than 100 years old, typically those that were 100-110 years old. Abundance was considerably less in forests older than 140 years. Cumming and Diamond (2002) concluded that the association with age might be because the percentage of coniferous cover increased with forest age. Also in Saskatchewan, Kirk et al. (1996) considered it an old-forest species, but did not sample forests stands older than 80 years. Thompson et al. (1999) reported similar results in balsam fir forests in Newfoundland. In Quetico Park, it was most abundant in intermediate-aged forests (67-73 years), with slightly fewer numbers in mature and old-growth forests, and very few in early successional

forests (Apfelbaum and Haney 1985). In Quebec, it nested in clear-cuts with saplings less than 5 m tall, and in young and mature forests. Imbeau et al. (1999) did not observe it in recent burns. It was significantly less abundant in young clear-cuts where saplings were less than 2 m tall than in other habitats.

In the boreal forest of Newfoundland, the Ruby-crowned Kinglet tended to be more frequent in natural than harvested landscapes. In natural landscapes, the proportion of forested sites it inhabited varied by the percentage of the landscape that was forested. Occupancy rates were 10% in landscapes with 10% forest cover, 40% at 50% forest cover, and 70% at 60% and more forest cover. In harvested areas, occupancy rates were uniform at 30-40% regardless of the amount of forest cover (Taylor and Krawchuk 2006).

The Ruby-crowned Kinglet is not an area-sensitive species and has been found nesting in isolated groves and rows of conifers in southern Ontario. In Saskatchewan, its abundance was not correlated with forest size. It was significantly more common in fragmented mixed-wood forest than in contiguous forest and its presence was negatively correlated with the amount of forest cover within 5 km (Hobson and Bayne 2000). Lindell et al. (2007) reviewed studies that determined its abundance in relation to forest edge and found that it exploited edge habitat. In Newfoundland balsam fir stands, it was equally abundant in riparian edges, nonriparian edges, and forest interior. Its abundance was similar in 20-50-m riparian strips left adjacent to clear-cuts (Whitaker and Montevecchi 1997, 1999).

Limited data on nocturnal roosts indicate that the Ruby-crowned Kinglet rests solitarily on tree branches close to the trunk.

All nests reported to the Ontario Nest Records Scheme were in coniferous trees: 19 in spruce and 2 in pine. They were suspended from horizontal or drooping lateral branches or forks and supported by smaller twigs. Seven nests were positioned against the trunk of a tree and 10 were 0.9-3 m from the trunk, often at ends of branches. Nests were well concealed. Three were 0.9-1.2 m from the top of the tree and one was at the top of a small black spruce 1.3 m tall; another was only 0.4 m above ground in a pine sapling. Nests were 0.4-15 m from the ground, with most 2.7-7 m up (Peck and James 1987, 1997). Richards (1983) reported a nest in Prince Edward County 11.5 m from the ground and 2.5 m from the trunk near the end of a horizontal limb of a spruce. Andrle (1978) found a nest in a Norway spruce in Fort Erie that was 8 m from the ground, 1.5 m from the trunk, and 0.3 m from the tip of the branch. Swanson et al. (2021) described 11 nests found in Algonquin Park. Six were in black spruce and the other 5 were in white spruce. Their average height was 12.0 m (range 6-17 m). Nests in black spruce were usually 1-2 m from the top among dense foliage near the trunk. In white spruce, nests were 1.7-2.5 m from the trunk in dense clumps of hanging branchlets. In all cases, nests were protected from above by overhanging foliage.

Elsewhere, Ruby-crowned Kinglet nests are almost always in conifers, particularly spruce, but also in fir and some of the western conifers. In British Columbia, 3 of 25 nests (12%) were in deciduous trees. Nests are well concealed and usually near the top of a tree. Nest height varies depending on the height of available trees. Nest heights of 0-30 m have been reported (Bent 1949; Campbell et al. 1997; Swanson et al. 2021).

Territories in Algonquin Park averaged 2.9 ha (range 1.1-6 ha). One male regularly sang from a site 0.5 km from the nest. Territories were larger in mixed woodlands than in more homogeneous black spruce bogs. During a spruce budworm outbreak in Algonquin in 1945, territory size was 2.5 ha (Swanson et al. 2021). Also in Algonquin Park, territory depth was 3.6-18 m; the bottom of the canopy layer and the top of the shrubs was 3.0 m and treetop level was 23 m (Martin 1960). Kendeigh (1947) reported that 2 territories north of Lake Nipigon were both about 1.0 ha. Barrette and Darveau (in Gauthier and Aubrey 1996) reported that territory size was 1.01 ha in the Boreal Forest Region of Ontario. In subalpine forests of New Hampshire, territory size was 0.6 ha (Sabo 1980).

No information on natal philopatry is available and the only data on adult site fidelity are from Algonquin Park. Of 27 territorial males, only 1 (3.7%) was found the following year, more than 200 m from his previous territory (Swanson et al. 2021).

Limiting Factors

Eggs have been found 2-23 June in Ontario, with most reported 10-14 June (Peck and James 1997). In Algonquin Park, females were observed carrying nesting material almost immediately after arrival in mid-April. The nest takes about 5 days to complete. A new nest is built for replacement clutches following failure or predation. Both hatching and fledging occur over many days, so incubation may be initiated before the clutch is complete. The first nests were found in Algonquin Park on 12 May and the earliest incubating female was seen on 30 May. The first chicks fledged 1-2 July but renesting attempts continued into July; 1 female initiated incubation in her third nest on 3 July (Swanson et al. 2021). A captive pair incubated for 16 days (Swanson et al. 2021); the incubation periods at 2 natural Ontario nests were 13 and 14 days (Peck and James 1987). Hatching took place over a 3-day period for a captive pair. The young left the nest at age 16 days at 1 Algonquin nest (Swanson et al. 2021), but young left at age 12 days at 1 British Columbia nest (Campbell et al. 1997).

A single brood is raised annually, but renesting occurs if a clutch is lost. Ontario clutches contained 5-10 eggs (average 8 or 9 eggs; Peck and James 1997). The overall range of clutch size is 4-12 eggs, with average clutch size variously reported as 7.25, 7.64, and 9.8 eggs. In British Columbia, clutches of 1-9 eggs were reported, with 4-7 eggs most frequent (Campbell et al. 1997). Bent (1949) reported that the Ruby-crowned Kinglet laid 5-11 eggs. He concluded that sets of 4 eggs were probably incomplete, 7-9-egg clutches were most common, and larger clutches were rare.

The Ruby-crowned Kinglet first breeds when it is 1 year old. It is monogamous and the pair bond lasts about 2 months. In Algonquin Park, pairing occurred in early May with the female leaving once the chicks fledged in early July (Swanson et al. 2021).

The Ruby-crowned Kinglet typically forages in trees during the breeding season, but also in shrubs, particularly in nonbreeding seasons. In Ontario and the Northwest Territories, 91.0-92.0% of foraging occurred in conifers. During the breeding season in Algonquin Park, it fed mostly in white and black spruce in dense foliage near the tops of trees. It also hover-gleaned for flying insects on flowering white birches. In Saskatchewan, it used spruce more for foraging than its availability; trembling aspen was used less than expected. In New Hampshire, 99.3% of foraging was in conifer foliage. Most prey is found by gleaning from the surface of leaves and branches with some hovering to capture prey under leaves. It occasionally hawks insects. In subalpine areas of New Hampshire, it

foraged aerially more than the Golden-crowned Kinglet, hovering 25-35% of the time and hawking 5-10% of the time. The Ruby-crowned Kinglet is a much more generalized forager than the Golden-crowned Kinglet. In New Hampshire, 61.4% of foraging occurred distal to the trunk and 38.6% near the trunk but it showed no significant differences in its usage of inner and outer branches in Saskatchewan. Mean foraging heights there were 7.3 m in conifers and 9.5 m in deciduous trees, significantly different from other species. In New Hampshire, 4.4% of foraging occurred 2-5 m from the ground, 52.2% 5-8 m up, and 43.4% more than 8 m up (Carlisle et al. 2012; Cumming 2004; Greenberg et al. 1999; Keast and Saunders 1991; Sabo 1980; Swanson et al. 2021). It may visit sapsucker wells to obtain sap and insects and there is 1 record of it visiting a hummingbird feeder (Swanson et al. 2021). Bain (1984) observed a Ruby-crowned Kinglet 2.5 km offshore over Lake Ontario actively feeding on clouds of tiny flying insects. During a sleet storm in North Carolina, kinglets either hovered close to a stone wall and jabbed their bills into the recesses in the wall or perched woodpecker-like on the rough surface to feed on remnants of dead insects trapped in spider webs (Hespenheide 1962).

In an aviary-raised brood, adults brought the young very small caterpillars, cicada larvae, small crickets, moths and butterflies, ant pupae, and snails. The Ruby-crowned Kinglet is predominantly an insectivore, preferring flying insects, but it eats other arthropods and some vegetable matter. Contents of 294 stomachs of birds in California consisted of 94% animal matter and 6% vegetable matter. Wasps and ants were favoured and comprised 32% of food items. Other animal food included 26% bugs (assassin and lace bugs, leafhoppers, jumping plant lice, and scale insects), 17% flies, 13% beetles, 3% lepidopteran caterpillars and adults, and 2% spiders and pseudoscorpions. Vegetable matter eaten consisted of 4% miscellaneous materials including seeds of poison oak and leaf galls; less than 1% fruit, mostly elderberries; and 0.01% weed seeds. Dogwood fruit and sumac berries are occasionally eaten. Other plant material reported in the diet includes red cedar and wax myrtle berries. Most of the arthropods eaten are small and less than 4.5 mm in length. Other insects eaten during the breeding season include aphids, mealy and leaf bugs, lady and bark beetles, and larch sawflies. During an outbreak of black-headed budworms in New Brunswick, the mean daily consumption was only 10 budworms indicating no significant response to the abundance of budworms. Over 2 years in Maine, spruce budworm larvae and pupae constituted 16% and 0% of the invertebrates consumed (Bent 1949; Gage et al. 1970; Keast and Saunders 1991; Mitchell 1952; Swanson et al. 2021). In New Brunswick, Morris et al. (1958) found no relationship between the abundance of the Ruby-crowned Kinglet and numbers of spruce budworms.

Cowbird parasitism has not been reported in any Ontario Ruby-crowned Kinglet nests (Peck and James 1997). Andrle (1978) reported a male feeding a young cowbird at Fort Erie. Boxall (1981) reported a young cowbird being fed by a pair of kinglets in British Columbia. This was only the 15th record of cowbird parasitism and only the third record of cowbirds being successfully fledged. Swanson et al. (2021) reported no additional cases of cowbird parasitism, but parasitism appears to be more prevalent in British Columbia where 3 of 21 nests (14.3%) were parasitized. In addition, there were 8 records of kinglets feeding fledged cowbirds (Campbell et al. 1997). In Quebec, 2 of 23 nests (8.7%) were parasitized (Barrette and Darveau in Gauthier and Aubry 1996). McIlwraith (1894) reported a nest from Lennoxville, Quebec that contained 8 kinglet eggs and 1 cowbird egg.

Habitat change or loss may be affecting abundance of the Ruby-crowned Kinglet. Initial forest clearing after European settlement reduced the amount of suitable breeding habitat. During the second atlas, it disappeared from a few areas where it was present during the first atlas. These included the Sault Ste. Marie area where there is much more young forest than previously, and east of Georgian Bay and south of Lake Nipissing, where there is currently much more deciduous forest (Crins in Cadman et al. 2007). These changes are probably due to forestry practices and natural succession. In boreal forest in Saskatchewan, Cumming and Diamond (2002) found it significantly more in post-rotation-aged forest. Barrette and Darveau (in Gauthier and Aubry 1996) concluded that logging was the biggest threat in the boreal forest but that it appeared to tolerate logging practices such as stand thinning and selective thinning. They noted that replanting of abandoned farmland with conifers had created suitable breeding habitat, including areas where the original forest cover was deciduous. Vanderwel et al. (2009) summarized studies examining the effects of partial timber harvesting in the Boreal Forest Region. Abundance of the Ruby-crowned Kinglet did not change when 30% or 50% of trees were removed, but it decreased when 70% of trees were removed. In the Ontario Canadian Shield, there was no difference in its abundance in mid-successional clear-cuts and similarly aged stands following fire. It was significantly more abundant in early successional clear-cuts than young burns. It was equally abundant in mid-successional and mature stands but significantly less abundant in early successional than mature stands (Zimmerling et al. 2017). In Newfoundland, its survival was significantly affected by landscape type. The breeding season survival rate of kinglets was significantly higher in natural landscapes than in clear-cut landscapes. Many birds in clear-cut landscapes appeared to be transients and there were 3-4 times more transients in cut than uncut landscapes (Whitaker et al. 2008).

On Anticosti Island, the Ruby-crowned Kinglet was not adversely affected by browsing by high populations of white-tailed deer. Browsing reduced abundance of deciduous species in recent clear-cuts but coniferous regeneration was unaffected. It made moderate use of the shrub layer for foraging, but preferred conifers (Cardinal et al. 2012).

In Alberta, there was no difference in the abundance of the Ruby-crowned Kinglet at noisy compressor stations and quiet well pads. It appeared to be unaffected by chronic noise (Bayne et al. 2008). It was significantly more abundant at seismic lines than in adjacent forest interior but was significantly less abundant at pipelines and well pads than in forest interior adjacent to these features (Bayne et al. 2016).

DesGranges and Morneau (2010) concluded that the Ruby-crowned Kinglet was sensitive to climate change in Quebec. Its abundance is correlated with the Boreal Forest Region and cooler and wetter summers, so it may be adversely affected by warmer summer temperatures. Its abundance in the Boreal Forest Region of Quebec and Labrador was associated with cooler temperatures and moderate amounts of breeding season precipitation (DesGranges and LeBlanc 2012). In Ontario, its distribution was negatively correlated with the end of the growing season and positively correlated with total precipitation during the growing season (Venier et al. 1999).

Status

McIlwraith (1894) was not aware of any breeding records for the Ruby-crowned Kinglet from southern Ontario and did not report on its occurrence elsewhere in the province. Baillie and

Harrington (1937) concluded that it was an uncommon summer resident throughout Ontario, but that it was much more regular and common north of Muskoka District. They considered it a common breeder at Moose Factory. Near Pickle Lake, it was uncommon to common throughout the area and exhibited the highest breeding density of any bird species (James 1980). During the first atlas, Klinkenberg (in Cadman et al. 1987) concluded that it was common throughout central and northern Ontario but was rare in southwestern and southeastern Ontario. James (1991) considered it a common summer resident across the north and in the southern Canadian Shield and occasional and rare south of the Shield.

The second atlas demonstrated that the Ruby-crowned Kinglet continued to be rare south of the Shield and common further north, although it was sparsely distributed in the extreme southern portion of the Shield. South of the Shield, there were few squares where it was observed in during both atlases except on Manitoulin Island and the Bruce Peninsula indicating that it is an irregular breeder south of the Shield. Its abundance increased with latitude, perhaps reflecting the abundance of spruce. Its probability of observation increased significantly for the entire province between atlases. Significant increases occurred in the Boreal Forest Region and the Hudson Bay Lowland, but there was a significant decrease in the Great Lakes–St. Lawrence Forest Region both in and south of the Canadian Shield (Crins in Cadman et al. 2007). The area south of the Shield is marginal habitat due to scarcity of natural spruce. The decline in the extreme southern portion of the Shield may be due to maturation of forests and gradual replacement of conifers by tolerant hardwoods.

Long-term (1970-2021) Breeding Bird Survey data indicate an annual increase of 0.532% in Canada and an annual decrease of 0.794% in Ontario. The short-term (2011-21) trends were an annual decrease of 1.4% in Canada and an annual increase of 1.86% in Ontario. All trends were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

At an Algonquin Park nest, the female left after the young fledged and the male fed them for 10 days with the fledglings following him over the full extent of the territory (Swanson et al. 2021).

Major and Desrochers (2012) captured 7 Ruby-crowned Kinglets in Quebec regenerating clear-cuts during the postfledging period. None were captured in plots where the fruit had been removed.

MIGRATION

The Ruby-crowned Kinglet is thought to be a nocturnal migrant (Graber et al. 1979), although there is evidence of daytime movement as well. Bain (1984) reported occasionally observing kinglets reaching the northern shore of Lake Ontario in an exhausted state, having flown directly across the lake during spring migration.

The sexes exhibit differential timing of migration, with males migrating earlier than females in spring, and females migrating earlier than males in autumn (Swanson et al. 2021). At Long Point, males arrive 12.0 days earlier in spring than females. Females leave 3.4 days earlier than adult males and 5.0 days earlier than hatch-year birds in autumn (Mills 2005a). Swanson et al. (1999) examined differences in timing of migration of the sexes for South Dakota and eastern North America. Males

migrated significantly earlier in spring at all latitudes by 10-15 days and migrated significantly later than females in autumn.

McIlwraith (1894) stated that the Ruby-crowned Kinglet was present for only 2-3 days in southern Ontario during spring, but that it was exceedingly abundant in the latter part of August and early September. It is now present for a more extended period in spring and the peak of autumn migration is in late September, with it rarely appearing in very late August during autumn migration. At Long Point, the spring passage midpoint in spring was 29 April over 21 years (Mills 2005a). In southern Ontario, a few may arrive in late March, but most arrive in mid-April through mid-May. Autumn migration begins in early September in Muskoka and Parry Sound districts and peaks around 1 October. In the south, birds arrive in mid- to late September and are common throughout October. Most leave the province by early November, but stragglers persist into December (Curry 2006; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). At Long Point, the autumn passage midpoint over 19 years was 12 October (Mills 2005a).

During migration, the Ruby-crowned Kinglet is often associated with flocks of chickadees, warblers, nuthatches, the Brown Creeper, and the Golden-crowned Kinglet. It uses a variety of habitats during migration. It may occur in swampy thickets along streams or around bodies of water, in trees and shrubs in residential areas, in coniferous and deciduous forests, in thickets, and in brushy hedgerows. In British Columbia, it prefers mixed coniferous forests during migration and often inhabits edges of muskegs, lakes, ponds, and alpine meadows. In the Yukon, it usually forages in shrubby areas, with highest concentrations occurring in wetlands, but it is also common in backyards and shrubby areas in towns. In Kansas, it preferred edge situations and thickets of willows, dogwoods, vines, and tall elm saplings (Bent 1949; Campbell et al. 1977; Fitch 1958; Leighton et al. 2002; Sinclair et al. 2003; Swanson et al. 2021). It prefers gaps in forest to forest interior for foraging (Swanson et al. 2021). Rodewald and Brittingham (2002) compared its abundance in different habitats during autumn migration in Pennsylvania. It was most abundant in forest interior followed by pole-stage forest, suburban forest, forest edge, shrub-sapling-stage forest, and forest-agricultural edge. Results were significantly different only between forest interior and forest-agricultural edge. Rodewald and Brittingham (2004) found that it was significantly more abundant in shrub-sapling-stage forest than other habitats studied. Of the remaining habitats, it was more abundant, in decreasing order, in forest-agricultural edge, pole-stage forest, forest interior, and suburban forest, with no birds detected in the latter habitat. In Pennsylvania, the Ruby-crowned Kinglet was found significantly more in shrub-dominated habitats than in forest (Smith and Hatch 2008). In Pennsylvania forests during spring migration, it selected upland forest significantly more than riparian forest, which had an understorey of shrubby species (Rodewald and Matthews 2005). Kirsch et al. (2013) found no difference in its abundance in upland and floodplain forests in Wisconsin and Minnesota during spring migration. On 2 islands in the Gulf of Maine, it was significantly more abundant on the island dominated by shrubs than the one dominated by trees (Suomala et al. 2010). These studies suggest that the Ruby-crowned Kinglet may be present in a variety of habitats and that usage of given habitats may vary geographically.

The Ruby-crowned Kinglet may defend territories during migration, at least in spring. In Illinois, males defended territories against other males in a ritualistic display. The length of time that

territories were defended was uncertain, but some birds appeared to remain in the same area for about a week (Graber et al. 1979). In Kansas, it was solitary during migration and individuals tended to settle for days in 1 location. No birds were marked, but birds were often seen on successive days in the same tree or thicket. Those kept under observation for extended periods usually remained within a radius of a few metres (Fitch 1958).

Limited data suggest that the Ruby-crowned Kinglet may exhibit site fidelity during migration. Somershoe et al. (2009) reported a kinglet that was caught at a Florida banding station during 3 different migration periods.

Outside the breeding season, the Ruby-crowned Kinglet may use a wider range of woody species for foraging. At Prince Edward Point during migration, 55% of feeding groups were in deciduous trees and the remainder were in conifers; 39% of foraging was by foliage gleaning (Keast and Saunders 1991). During autumn migration in Idaho, it foraged more in deciduous trees and shrubs than in conifers. Feeding in Illinois may occur in hawthorns and other small trees during spring migration. During migration and winter, it usually forages among leaves on the outer tips of high, smaller (less than 1.3 cm diameter) branches, but also on buds and at the base of pine needles, on the bark of small branches, and rarely on the ground or dead herbaceous plants (Graber et al. 1979).

Beal and McAtee (1912) analyzed the contents of 294 stomachs collected in the United States during migration and winter. The diet consisted of 94% animal matter (insects, spiders, and pseudoscorpions) and 6% vegetable matter (fruit and weed seeds). Ants and wasps were the dominant food items, comprising 32.4% of the diet. Bugs were next in importance, constituting 25.7% of the diet. They included leafhoppers, jumping plant lice, aphids, scale insects, and assassin, mealy, and lace bugs. Thirteen percent of the diet consisted of beetles, including bark and lady beetles and weevils. Flies constituted 16.9% of the diet, with the greatest numbers consumed in January and February. Lepidopterans comprised only 3% of the diet. Although it ate a few caterpillars, minute cocoons of clothes moths were the most important lepidopterans. Two stomachs contained grasshoppers, and spiders and pseudoscorpions constituted 2% of the diet. Fruit represented less than 1% of the diet and most of it was elderberries. Most vegetable food consisted of seeds of poison oak and leaf galls. Some diet information is available for Illinois migrants, but data for the 2 kinglet species were combined. Spring data were mostly for Ruby-crowned Kinglets; autumn results were mostly for Golden-crowned Kinglets. In spring, gnats were most frequent in the diet (33% of food items), followed by beetles (black-margined loosestrife and water scavenger beetles) at 25%. The autumn diet consisted of 33% lepidopterans, especially winged moths, and 29% bugs. Both species of kinglets were opportunistic, feeding on the most abundant insects and sometimes exclusively on 1 species (Graber et al. 1979). During autumn migration in Idaho, the Ruby-crowned Kinglet foraged on spiders, stilt and spittle bugs, leafhoppers, jumping plant lice, and beetles at a rate greater than their abundance. Species consumed less than their abundance included stink bugs, ants, wasps, yellowjackets, lepidopterans, and moths (Carlisle et al. 2012).

Mills (2005b) examined spring and autumn migration dates for the Ruby-crowned Kinglet at Long Point from 1975 to 2000 to determine if there were any responses to global warming. Based

on first arrival dates, it arrived significant earlier with time, advancing spring migration by 5.3 days per decade. When quartile means were used to analyze spring migration, the trend was toward later arrival, but not significantly. In autumn, hatch-year birds departed significantly later over time, 2.2 days per decade during 1981-2000.

The Ruby-crowned Kinglet is vulnerable to being killed at television towers and other tall structures. In Illinois, it represented 1% (46 of 4,700) of all birds killed at television towers (Graber et al. 1979). Seventy-three were killed at the Lennox generating station near Kingston (Weir 2008). During migration in Toronto, the Ruby-crowned Kinglet was among the species least vulnerable to striking urban windows (Colling et al. 2022).

In Pennsylvania, an outbreak of the viburnum leaf beetle resulted in almost complete mortality of the southern arrowwood, formerly the third most abundant shrub species. Prior to the infestation, spring migrating Ruby-crowned Kinglets gained significant mass after daylight but no weight gains occurred after the infestation (Smith and Hatch 2017).

McClure et al. (2013b) created a phantom road by playing traffic noise in an otherwise undisturbed forest during autumn migration. Abundance of the Ruby-crowned Kinglet declined somewhat with increasing noise intensity. At 37 dB(A), an average of 3.0 kinglets was detected compared with 2.0 at 55 dB(A). It may have a tendency to avoid noisy environments during migration.

The Ruby-crowned Kinglet is an abundant migrant in Ontario (James 1991). At Presqu'ile, sightings of 300 a day are common in spring. At Prince Edward Point, 2,000 have been recorded on a single spring day. Autumn numbers are often higher, with record daily numbers at Prince Edward Point of 4,000 (LaForest 1993; Weir 2008).

WINTER

In winter, the Ruby-crowned Kinglet occurs in habitats similar to those used during migration. In the lower Colorado River valley, it was most abundant in areas of tall, dense vegetation and scarce or absent from areas with low volumes of foliage (Laurenzi et al. 1982). In California, its abundance increased with the availability of shrubs or trees and decreased with presence of roads or structures (Kalinowski and Johnson 2010).

During severe cold, significant mortality of the Ruby-crowned Kinglet may occur which may depress breeding populations the next spring (Swanson et al. 2021).

The Ruby-crowned Kinglet is rare and irregular in winter in Ontario north to Durham Region (James 1991). In the Hamilton area, some birds have persisted into February or even March, suggesting successful overwintering (Curry 2006).

Ontario winter population trends determined from Christmas Bird Count data indicate an annual decrease of 0.85% 1970-2021 and an annual increase of 5.21% 2009-21 (National Audubon Society 2022).

Golden-crowned Kinglet

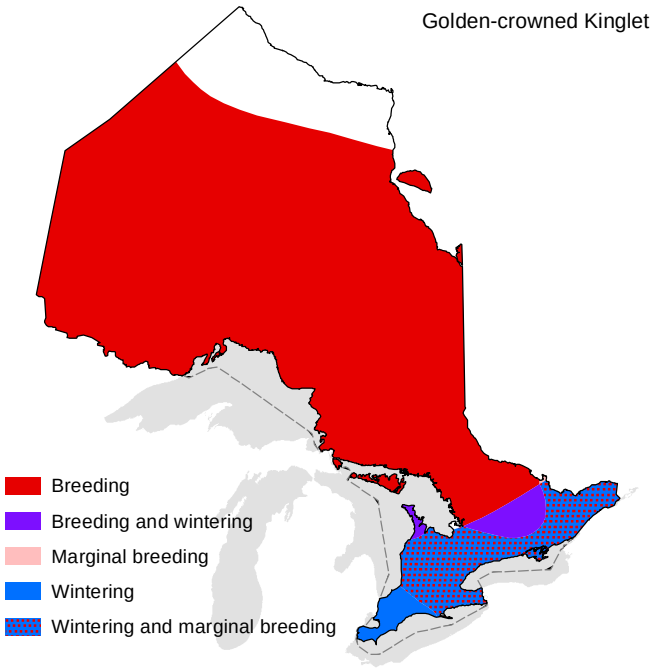
Regulus satrapa

BREEDING SEASON

Habitat Requirements

In Ontario, the Golden-crowned Kinglet nests in dense stands of large coniferous trees. Nest sites may be either within forests, at edges or clearings, or near water (Peck and James 1987).

In the Boreal Forest Region of Ontario, the Golden-crowned Kinglet was associated with older, closed, coniferous forests that were in a mature forest matrix. It was also associated with intact forests with low amounts of edge (Rempel 2007). Near Pickle Lake and in northwestern Ontario, it was most abundant in mixed forests, followed by coniferous forests without and with understorey. It was absent from deciduous forests (McLaren and McLaren 1981). Near Pickle Lake, it seldom occurred in small numbers in coniferous forests (James 1980). Along the northeastern shore of Lake Superior, it preferred mixed woods containing a high percentage of spruce and balsam fir (Baillie and Hope 1943). Near White River, it was significantly more abundant in mature forests than in clear-cuts 3-25 years old. It was the most specialized species for residing in mature forests (Venier and Pearce 2005). In the Clay Belt, it was associated with dry stands with moderate nutrient levels (Welsh and Lougheed 1996) and was a late-succession species (Welsh 1993).



In white pine stands in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, abundance of the Golden-crowned Kinglet was significantly correlated with the basal area of non-pine conifers (Kirk et al. 2012). In jack pine stands near Gogama, it readily foraged on pines but was only present where a small proportion of the forest was spruce, where there was suitable nesting habitat. Some territories included deciduous trees but these were essentially unused. It first appeared when trees approached 20 years of age, but was never numerous in any age of forest, probably because spruce was never abundant (James and Peck 1995a). In Algonquin Park, it was most abundant in fir-spruce forests followed by black spruce forests, black spruce–white cedar forests, mixed white birch–poplar–balsam fir–black spruce forests, and hemlock stands. It was absent in stands without a significant coniferous component (Martin 1960). In southern Ontario, the Golden-crowned Kinglet has recently started breeding in mature spruce and pine plantations, particularly those with spruce (Curry 2006; Lancaster et al. 2004).

In Ontario, the Golden-crowned Kinglet is associated primarily with spruce and fir in the Shield and Hudson Bay Lowland. These stands may occur in upland and lowland habitats as well as bogs and fens. In the southern portion of the Canadian Shield, it may occur in mixed stands of spruce, fir, and occasionally hemlock associated with deciduous species. Bogs and fens dominated by black spruce, occasionally mixed with tamarack or white cedar, may also be inhabited. South of the Shield, it occurs in older plantations dominated by spruce, bogs and fens, and occasionally in hemlock stands or mature mixed-wood forests containing hemlock or spruce.

The Golden-crowned Kinglet is an obligate conifer specialist. Throughout its range, spruce is the most important species, with black spruce important in the Boreal Forest Region, white spruce in the Great Lakes–St. Lawrence Forest Region and western Canada, and red spruce in the east. Balsam fir is another important species in Ontario and eastward. It may nest in pine–balsam fir stands but at lower densities than in spruce. Nesting may also occur in pure hemlock and tamarack stands in the east, but at much lower densities than in spruce or fir. It occasionally inhabits stands of white cedar, but only if they are mixed with spruce or another preferred coniferous species. There appear to be few records of it nesting in white cedar, but it has been reported nesting in cedar bogs (more likely fens) in Michigan. Nesting is frequent in black spruce–balsam fir stands and may be common in mixed deciduous-coniferous stands, especially those with a high proportion of spruce and/or fir present. In New Hampshire and Maine, it was most abundant in spruce–balsam fir stands, followed by pure balsam fir stands and those dominated by white pine. Nesting seldom occurred in

deciduous stands with scattered conifers. In the south outside its traditional breeding range, it may nest in coniferous plantations dominated by white spruce or Norway spruce or spruce mixed with pine. Pure pine plantations do not appear to be acceptable, but kinglets have nested in 10-20-m wide strips of spruce and pine plantings in New York. Plantations become suitable for breeding when the trees are about 15 cm diameter at breast height (DBH) and 35-40 years old. Kinglets select the densest areas in plantations for nesting. Plantations that have been row-thinned are usually unoccupied. In the Yukon, it is a habitat specialist that nests only in old-growth white spruce forest that borders rivers, lakes, and wetlands. Forests that are inhabited are characterized by dominant large white spruce, a high density of snags, and an extensive ground cover of mosses, forbs, and dwarf shrubs. In British Columbia, it inhabits forests that are primarily dense and old-growth or advanced second growth. Mixed forests of fairly open structure are preferred, but even isolated trees in city parks or similar settings have been used for nesting. In Saskatchewan, the Golden-crowned Kinglet nested most frequently in mixed forests dominated by white spruce and trembling aspen. It was absent in stands younger than 100 years old and occurred most frequently in stands older than 140 years. These stands tended to have a higher proportion of conifers than younger stands. In northern Minnesota, it preferred to nest in black spruce–tamarack bogs, although it also nested in mixed stands dominated by balsam fir, white spruce, and red pine with scattered tamarack, white birch, trembling aspen, and jack pine. In subalpine areas of New Hampshire, it was associated primarily with virgin spruce stands and was usually associated with water, but only damp depressions rather than larger bodies of water as in the Yukon. In natural stands, it may prefer more open canopies with 70% or less canopy closure, but only the densest plantations are used. In spruce-fir stands in Maine, it was associated with a dense coniferous overstorey and an open forest floor, and was positively correlated with softwoods with DBH of 10-15 cm. On the Apostle Islands in Wisconsin, it was most abundant in jack pine–white pine stands followed by hemlock–yellow birch and aspen stands. In central Quebec, its abundance was higher in jack pine stands than in spruce stands and other habitats surveyed. In Newfoundland, it was 1 of the 10 most abundant species in balsam fir stands. In Idaho, it nested in pure pine plantations. The Golden-crowned Kinglet may persist in burned forests if the burn is light and in selectively thinned woodlands, but is absent in severe burns and clear-cuts (Andrle 1971; Beals 1960; Bent 1949; Bock and Lynch 1970; Campbell et al. 1997; Capen 1979; Crawford and Titterington 1979; Cumming and Diamond 2002; Dawson 1979; DeGraaf et al. 1998; Erskine 1977; Galati 1991; Galati and Galati 1985; Larivée and Darveau in Gauthier and Aubry 1996; Niemi and Pfannmuller 1979; Sabo 1980; Sinclair et al. 2003; Swanson et al. 2020; Temple et al. 1979; Thompson et al. 1999; Titterington et al. 1979). The Golden-crowned Kinglet nests in forests with no to dense understorey, but its abundance is inversely correlated with the intensity of understorey browsing by deer (Swanson et al. 2020).

In most natural forests, the Golden-crowned Kinglet appears to prefer mature stands. In the Yukon, it is an obligate old-growth spruce forest species (Sinclair et al. 2003) and it prefers older growth in British Columbia (Campbell et al. 1977) and Saskatchewan (Cumming and Diamond 2002). In the northern boreal forest of Saskatchewan, it was associated with older stands more than any other species analyzed and occurred only in old-forest sites. It also occurred in the driest stands available with slightly below average nutrient enrichment (Kirk et al. 1996). It was most abundant in Quetico Park communities that were 112 years old; it was not present in younger or older stands

(Apfelbaum and Haney 1985). It was associated with mature stands in the Ontario portion of the Clay Belt (Welsh 1993) and most abundant in mature stands near White River (Venier and Pearce 2005). In Quebec, it bred in black spruce clear-cuts with saplings 2-5 m tall and in young and mature forests. It was absent in recent cuts and burns (Imbeau et al. 1999). In Pennsylvania, it had a positive affinity for old-growth forest and exploited coniferous cover and complex vegetation structure typically associated with older forests. It occurred in 18.2% of old-growth hemlock–white pine–hardwoods forests compared with 3.7% of similar forests state-wide in Pennsylvania and 5.7% of forests on the Appalachian Plateau (Haney 1999). In New England, it was most prevalent in forests of sawtimber size, averaging 23 cm DBH or greater for coniferous species. These stands were dominated either by spruce-fir or hemlock (DeGraaf and Chadwick 1987). In West Virginia, spruce forests were colonized once trees reached a height of 10-15 m (Swanson et al. 2020).

DeGraaf et al. (1998) characterized the microhabitat preferences of the Golden-crowned Kinglet in New Hampshire and Maine. It was positively correlated with coniferous trees larger than 10 cm DBH and negatively correlated with deciduous trees 2-10 cm DBH and the total foliage volume of deciduous trees larger than 10 cm DBH and smaller than 2 cm DBH. In boreal forest habitat in New York, Vermont, Maine, Nova Scotia, and Newfoundland, it occurred in a variety of spruce-fir forest types. It was negatively correlated with the number of dead snags and preferred low canopy cover with low coverage by deciduous tree species (Ralston et al. 2019). In Minnesota, it was positively associated with the amount of coniferous cover within 200 m, the amount of upland deciduous forest within 1 km, the amount of upland coniferous forest within 500 m, basal area, black spruce and white cedar stands, and stand age. It was negatively correlated with non-forested habitat, the amount of tamarack within 200 m, and the number of habitat patches within 200 m. Both species of kinglets preferred black spruce or cedar forests with upland forests in the broader landscape. They appeared to be separated based on the productivity of stands, with the Golden-crowned Kinglet preferring more productive stands than the Ruby-crowned Kinglet (Zlonis et al. 2017).

Freemark and Collins (1992) and McCracken et al. (1998) considered the Golden-crowned Kinglet to be a forest-interior or area-sensitive species. Neither of these designations appears to be correct. In New York, Andrle (1971) found it nesting in plantations ranging in size from 0.8 ha to approximately 24 ha, and almost half of those in which kinglets were found were smaller than 4 ha. Peck and James (1987) reported that it frequently nested on woodland edges. In Newfoundland balsam fir stands, Whitaker and Montevecchi (1997, 1999) considered it a habitat generalist with respect to forest edge. There was no significant difference in its abundance in riparian edges, nonriparian edges, and forest interior.

All Ontario nests were in living conifers: 9 in spruce and 1 in a hemlock. Two nests were within 1 m of the top of the tree. Nests were suspended from horizontal branches or forks and secured to smaller, drooping branches. They were well concealed and placed near the tree trunk to as far as 4 m from it. Nest heights were 2.4-13 m, with most 2.4-10.7 m up (Peck and James 1987, 1997).

Throughout its range, the Golden-crowned Kinglet nests almost exclusively in coniferous trees, but 2 British Columbia nests were in deciduous trees. In the east, the most common nest trees are black and white spruce and balsam fir, with substantially fewer nests in hemlock. In plantations, Norway spruce may be used for nesting and there is 1 record of a nest in a red cedar. Nests are

extremely well hidden and essentially invisible from the top or sides. The sun never shines in nests and they are so protected by overhanging foliage that they remain dry even in torrential rain and heavy wind. A high proportion of nests are in the crowns of trees and most are near the end of limbs. Some nests may be near the trunk, but do not touch it so that they are unaffected by rainwater running down the trunk. Nests have been reported 1.3-19.6 m from the ground. These heights are biased towards lower nests because they are easier to find. Nests are more typically near the top of trees. In a Minnesota area, all nests were found and the average height of 19 nests was 15.3 m (range 8.2-19.6 m). Eleven faced east, 6 southwest, and 1 northwest; prevailing winds were from the west (Bent 1949; Campbell et al. 1997; Galati 1991; Galati and Galati 1985; Swanson et al. 2020).

Territorial defence is by the male, predominantly by singing but skirmishes occasionally occur between males. Both sexes remain within the territory during the breeding season and the male tends to perch in the same trees each day vocalizing from dead branches of coniferous trees 3.6-10.7 m from the ground. Territorial defence ceases after young of the second brood fledge. North of Lake Nipigon, territory size ranged from 0.4 to 2.0 ha (average 1.2 ha). In Algonquin Park, territory size averaged 0.34 ha (range 0.09-1.3 ha). In balsam fir–spruce stands, territory depth ranged from 3 m (the bottom of the canopy and the top of the shrub layer) to 12 m, which was the top of the conifers. In hemlock stands, territories ranged from 3 to 8 m from the ground, which was below the bottom of the canopy. In subalpine forests in New Hampshire, territories averaged 0.6 ha. In northern Minnesota, territories averaged 1.6 ha (range 0.9-2.5 ha). The pair with the largest territory had no competing kinglets on its border. Territory size appeared to be determined by the number of pairs present and the type of vegetation bordering the territory. Six territories in Maine spruce forests averaged 0.72 ha (Galati 1991; Galati and Galati 1985; Kendeigh 1947; Martin 1960; Morse 1977; Sabo 1980; Swanson et al. 2020).

Limited information is available on natal philopatry. In northern Minnesota, Galati (1991) banded 57 nestlings and none returned. There is no information on adult site fidelity.

Limiting Factors

Eggs have been found in Ontario nests in late May and are presumably present throughout May (Peck and James 1987). In Algonquin Park, nest construction occurs from late April to early May and a second-brood nest was built in mid-July, nests with young have been documented in mid-June, and dependent fledglings occur from late June to mid-August (Tozer 2012).

In northern Minnesota, nests were constructed in an average of 5 days (range 4-6 days). One nest in Maine was initiated in early April and took about a month to complete. If a nest is abandoned or destroyed, construction of a new nest begins the next day and is usually completed in about 5 days as are nests for the second brood. The first egg is usually laid the day after the nest is completed, and 1 egg is laid per day. Usually effective incubation does not occur until the laying of the last or penultimate egg, but 1 female started incubating when the second of 9 eggs was laid. The incubation period is typically 14-15 days, with some eggs taking as long as 19 days to hatch. Hatching may take place over 2-4 days. Young start to crawl out on twigs and branches 30-60 cm from the nest about 2 days before they fledge. The entire brood fledges within a period of 15-105 minutes. Although young have left the nest at age 14-19 days, 18-19 days is typical. Young that leave the nest at age 14-16 days do so prematurely and few of these survive. In second broods, the last

fledglings were independent 58 days after the second nest was started and the time spanning both broods was 94 days (Bent 1949; Galati 1991; Galati and Galati 1985).

The Golden-crowned Kinglet regularly builds 2 nests and raises 2 broods per season. Pairs begin building the second nest about 8 days after eggs begin hatching in the first nest and initiate egg laying in the second nest 6 days after the construction of it is started. Pairs regularly renest after a clutch is lost or abandoned. In northern Minnesota, all first clutches contained 9 eggs. Of the second clutches, 4 had 9 eggs and 2 had 8. The average clutch size was 8.85 eggs including both first and second clutches. Eastern birds tend to lay larger clutches than western birds. Average clutch size for eastern birds is 8.6 eggs (range 5-11); western birds lay an average of 7.6 eggs. Overall clutch size has been reported as 4-11 eggs, with 8 or 9 eggs most frequent. In an experiment, eggs of 2 pairs were destroyed each time they completed a clutch. Both females laid 9 eggs in the first 2 nests and 8 eggs in the third (Bent 1949; Campbell et al. 1997; Galati 1991; Galati and Galati 1985; Swanson et al. 2020).

No information is available on the age at first breeding. The mating system is monogamous and pairs remain together for a single breeding season. The pair typically raises both broods in the territory established in the spring by the male. One pair abandoned its territory after 2 unsuccessful nesting attempts and established another approximately 60 m away (Galati 1991; Swanson et al. 2020).

The Golden-crowned Kinglet prefers to forage in the mid-canopy of coniferous trees, typically by gleaning insects from outer twigs. In the Boreal Forest Region of Ontario, 96.0% of foraging occurred in conifers (Greenberg et al. 1999). In the Kingston area, 80% and 88% of feeding groups at 2 sites were in conifers and the remainder were in low shrubs. The Golden-crowned Kinglet was a conifer specialist whereas the Ruby-crowned Kinglet was a generalist. Foliage gleaning predominated by both species (42% of attacks on prey by the Golden-crowned Kinglet) and the Golden-crowned Kinglet fed much more by clinging to or hanging from the foliage (Keast and Saunders 1991). In Maine, it foraged at heights of 0-16.8 m (mean 8.0 m). Foraging occurred mostly in spruce, 38.2% of the time at the tip of foliage, 9.2% on small live twigs as large as 5 mm, 13.9% on dead twigs, 30.3% on dead branches, 5.2% distally on branches, 1.6% proximally on branches, 0.8% in deciduous growth, and 0.8% on the ground (Morse 1967). In Arizona, the diet of the 2 kinglets was similar but they differed significantly in their method of prey attack and in their choice of tree species for foraging. The habitat selection of the 2 species differed mostly in tree species selection. The Golden-crowned Kinglet hovered less (11.2% compared with 18.2% of attacks by Ruby-crowned Kinglets) and gleaned more (86.9% compared with 80.3%). For the Golden-crowned Kinglet, 44.3% of foraging was 0-33% of the distance from the tip, 31.8% was 33-66% of the distance, and 23.9% further than 66% from the tip. Foraging occurred more frequently in tall trees than expected, but Golden-crowned Kinglets selected the middle portions of trees more frequently. Ruby-crowned Kinglets preferred the upper third (Franzreb 1984). In Parry Sound District, there was no significant change in the Golden-crowned Kinglet's foraging habitat during the breeding, midsummer, and autumn periods. It was associated with conifers at all times. Foraging was mostly by hovering and occurred at heights of 6.5-13.4 m (Mills 2007). In Saskatchewan, it used white spruce more for foraging than its availability and trembling aspen less than its availability. It occurred slightly more

frequently in canopy than subcanopy trees. Although there was no significant difference in foraging rates from the inner portions of branches to their tips, usage increased from the inner portion of the tree to the outside (Cumming 2004). In subalpine forests in New Hampshire, foraging locations were 51.6% distant from the trunk and 48.0% proximal to the trunk; 94.1% in conifer tree foliage, 5.5% in deciduous foliage, 0.4% on the forest floor, and 0% in herbaceous foliage. Foraging frequencies were 38.2% at 5-8 m, 34.9% at 2-5 m, 23.3% above 8 m in the upper canopy, and 3.3% in the understorey 0.1-2 m above ground (Sabo 1980). In northern Minnesota, it foraged almost exclusively among spruce, fir, and pine branches (Galati 1991; Galati and Galati 1985).

Both parents are required to raise a healthy brood. Nestlings are initially brought tiny insects; the size of prey increases as they age. Spiders are initially rejected as food by nestlings but are eaten when they are older. Of 98 food items brought to nestlings at Minnesota nests, 90 were insects and 8 were spiders. The dominant food items were aphids (21.4%), flower flies (15.3%), geometer moths (11.2%), and harvestmen (10.2%) as well as bugs, flies, caddisflies, butterflies, sawflies, and bark lice. Other prey items fed to young include lacewings, crane flies, mosquitoes, treehoppers, midges, and small snails. A single Golden-crowned Kinglet north of Lake Nipigon had eaten 35 spiders and 65 flies. Adults feed largely on bark beetles, scale insects, moth adults and larvae, and aphids and their eggs. Other insects eaten include springtails, grasshoppers and crickets, book and bark lice, adult damsel and harlequin bugs, treehoppers, aphids, leafhoppers, lacewings, weevils, click beetles, lady beetles, soldier beetles, caddisflies, adult and larval butterflies and moths, march flies, gall midges, leaf-miner flies, flower flies, crane flies, midges, mosquitoes, deer flies, bees and wasps, larch sawflies, and braconid wasps. This kinglet is fond of spruce budworm caterpillars and moths, but it seldom consumed black-headed budworms in New Brunswick even when they were abundant. It has been observed apparently drinking from Yellow-bellied Sapsucker wells, but it may be attracted to the insects rather than the sap. It has taken insects attracted to sugar maple sap in the spring. It drinks at seeps, springs, and streams and obtains water from snow or frost when water is frozen (Bent 1949; Gage et al. 1970; Galati 1991; Galati and Galati 1985; Kendeigh 1947; Swanson et al. 2020). Near Manitouwadge, abundance of the Golden-crowned Kinglet increased significantly overall and in young and intermediate-aged stands (1-36 years old) with increasing numbers of spruce budworms. There was no significant response to budworm numbers in stands 60-223 years old (Venier et al. 2009). In New Brunswick, Morris et al. (1958) found no relationship between its abundance and spruce budworms. In Maine spruce-fir forests, it showed a significant feeding response to increasing numbers of spruce budworm larvae and pupae; its abundance was significantly associated with budworm larvae numbers. Because it feeds on the tips of branches where budworms first appear in early stages of an infestation, it has the opportunity to respond reproductively to this early increase in food (Crawford and Jennings 1989). Mitchell (1952) examined 23 stomachs during a spruce budworm outbreak in Maine. They contained 13% and 0% budworm larvae and pupae by volume in 2 years.

Brown-headed Cowbird parasitism rates of Golden-crowned Kinglet nests appear to be low, although few nests have been reported. In British Columbia, 3 of 22 nests (13.6%) were parasitized and there were an additional 6 incidents of Golden-crowned Kinglets feeding cowbird fledglings

(Campbell et al. 1997). In Port Colborne, Black and Roy (2010) reported adult kinglets feeding a cowbird on a branch with a young kinglet still in the nest.

Golden-crowned Kinglet populations may be affected by logging activities or die-off of spruce or fir. Vanderwel et al. (2007, 2009) summarized studies that examined the effects of partial timber harvest in the Boreal Forest Region with particular reference to Ontario. There was no change in its abundance when 30% of trees were removed. It decreased when 50% of trees were removed and became locally extirpated when 70% of trees were removed. It experienced a 25% decrease when about 35% of trees were removed, a 50% decrease when 50% of trees were removed, and a 75% decrease when about 67% of trees were removed. In the Canadian Shield of Ontario, it was significantly more abundant in early successional clear-cuts than in early successional burns, but equally abundant in mid-successional clear-cuts and burns. It was significantly less abundant in early successional than mature stands and equally abundant in mid-successional and mature stands (Zimmerling et al. 2017). In Alberta, it declined significantly when 80% of trees in deciduous forests were removed and when 50-100% of trees were removed in coniferous forests. In Saskatchewan, it was significantly more abundant in stands older than typical rotation age. In Idaho, light selective thinning in stands had no significant effect on its density. In British Columbia high-elevation forests, it was more affected by forest harvesting (clear-cuts of 10, 1, and 0.1 ha, and selection thinning) than most species. Maturation of spruce plantations in the south is increasing available habitat in this area. Once these stands become mature enough to be row-thinned, they may become less suitable (Andrle 1971; Cumming and Diamond 2002; Dickinson et al. 1988; Harrison et al. 2005; Medin and Booth 1989; Swanson et al. 2020).

In Alberta, Bayne et al. (2016) studied the effects of energy sector disturbances on the Golden-crowned Kinglet. It exhibited no response; its abundance at seismic lines, pipelines, and adjacent forest interior was similar.

Cold spring weather may delay nesting. In Minnesota, clutch initiation varied by as much as a month (Galati 1991).

Status

McIlwraith (1894) concluded that the Golden-crowned Kinglet was generally distributed as a breeder throughout the province, but was aware of only a single breeding-season record from the south. Baillie and Harrington (1937) considered it an uncommon summer resident from the southern border north to at least the transcontinental railway and west to Thunder Bay District and probably to Lake of the Woods. They concluded that it was probably much more common than the scattered breeding records indicated and that its breeding range likely included the entire province. In Muskoka District, it was regular only in the northeast during the breeding season. Although more widely distributed in Parry Sound District, it was still not very common (Mills 1981). During the first atlas, it was sparsely distributed in the Hudson Bay Lowland due to the scarcity of tall, mature conifers; widely distributed through the Boreal Forest Region where it probably occurred in every square; scattered in distribution in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield; and confined to a few mature plantations south of the Shield (Klinkenberg in Cadman et al. 1987). James (1991) considered the Golden-crowned Kinglet common across the central forested portion of the province and rare and local in the northern Hudson Bay Lowland and south of the

Shield. In many areas south of the Shield, it was unknown as a breeder historically and has colonized plantations within the last 2-4 decades (Curry 2006; LaForest 1993; Lancaster et al. 2004; McCracken et al. 1998; Weir 2008).

The breeding distribution of the Golden-crowned Kinglet remained essentially the same between the atlases. Its probability of observation increased significantly province-wide and in the Great Lakes St. Lawrence and Boreal forest regions. Increases south of the Canadian Shield were probably due to maturation of coniferous plantations, but the reasons for increases in other regions are uncertain. Highest densities occurred in northwestern Ontario, including Woodland Caribou Provincial Park and a substantial area north and east of Red Lake. Densities were almost 4 times as high in the Boreal Forest Region than in the Shield portion of the Great Lakes St. Lawrence Forest Region. Highest densities in the southern Shield area occurred in the Algonquin Highlands (McLaren in Cadman et al. 2007).

Long-term (1970-2021) population trends determined from Breeding Bird Survey data indicate an annual decrease of 0.356% in Canada and an annual increase of 0.842% in Ontario. Short-term (2011-21) trends were annual decreases of 4.22% in Canada and 4.85% in Ontario. The long-term results were highly reliable; the short-term trends were of medium reliability for Canada and low reliability for Ontario (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings group together on a branch on an adjacent tree and remain close to each other for the first 3-4 days. One family remained within 120 m of the nest for the first 11 days out of the nest. For the first 8 days after fledging, young were never seen outside their parents' territory, but they began to wander further after that. About 5 days out of the nest, fledglings make their first attempts to catch food and by days 12-16 they collect a good deal of food on their own, although they still actively pursue the adults for food. Young are not fed by the adults after they are 16-17 days out of the nest (Swanson et al. 2020).

Major and Desrochers (2012) captured small numbers of Golden-crowned Kinglets in regenerating clear-cuts in Quebec during the postfledging period.

MIGRATION

Long-distance migration is nocturnal as evidenced by kills at television towers and large overnight changes in populations at staging areas (Graber et al. 1979; Swanson et al. 2020). Birds have been recovered in Ontario that were banded in New Jersey, Ohio, Pennsylvania, and Michigan, and 1 bird that was banded in Tilbury was recovered in Louisiana (Brewer et al. 2018). Miles and Prior (1999) demonstrated that diurnal movement occurs at least during spring migration. A male banded at Long Point was recaptured at Selkirk Provincial Park exactly 3 hours later. The straight-line distance between the 2 banding station is 45 km, almost all over the open water of Lake Erie. It is more likely that it travelled overland, meaning that it would have travelled a minimum of 58-70 km depending upon the route followed.

Spring migrants typically return to the southern portion of the province in late March and early April, although some may occur in early March. The peak of spring migration is in mid-April with most migrants gone by early to mid-May; stragglers rarely persist until 1 June. Autumn arrival in southern Ontario is in mid- to late September with the heaviest flight in the first half of October. Most of those that leave the province are gone by mid-November. The peak of female migration in autumn is 10-15 days earlier than for males (Curry 2006; Keast 1980; Lancaster et al. 2004; Tozer 2012; Weir 2008). In Illinois, waves of autumn migrants were associated with the passage of cold fronts (Graber et al. 1979).

During migration, the Golden-crowned Kinglet still shows a propensity for habitats dominated by or containing coniferous tree species. It may occur in a much wider variety of habitats than during the breeding season. Migration habitats may include pine, fir, and spruce forests; mixed forests; deciduous forests; old fields; urban parks; urban and suburban yards; homesteads; rangelands; fencerows; shelterbelts; brushy thickets; orchards; and gardens. During autumn migration in Pennsylvania, its relative abundance by habitat was forest interior, 0.67; forest edge, 0.52; shrub-sapling-stage forest, 0.21; suburban forest, 0.20; pole-stage forest, 0.19; and forest-agricultural edge, 0.03. There was no significant difference in its abundance among these habitats (Bent 1949; Campbell et al. 1997; Graber et al. 1979; Rodewald and Brittingham 2002; Swanson et al. 2020).

During autumn migration in Idaho, the Golden-crowned Kinglet was associated with conifers and foraged mostly by gleaning from a perch, although hovering was also common. Hovering was done much less frequently than by the Ruby-crowned Kinglet (Carlisle et al. 2012).

During migration, the Golden-crowned Kinglet is an opportunistic forager, taking insects that are most abundant and sometimes feeding exclusively on a single species. Information on diet of migrants was collected from Illinois but results from the 2 kinglet species were pooled. In spring, gnats were most common in the diet (33%), followed by beetles (leaf and scavenger beetles). In autumn, lepidopterans were most important (33%), especially winged moths; bugs comprised 29% of the diet (Graber et al. 1979). During autumn migration in Idaho, it foraged on spittle bugs, jumping plant lice, beetles, wasps, and lepidopterans in greater proportion than their availability. Potential prey items that were consumed less than their availability included spiders, stilt and stink bugs, leafhoppers, hymenopterans, ants, yellowjackets, moths, and flies (Carlisle et al. 2012).

On rare occasions, the Golden-crowned Kinglet collides with television towers and windows during migration (Graber et al. 1979; Swanson et al. 2020).

The Golden-crowned Kinglet is a common to locally abundant migrant in Ontario (James 1991).

WINTER

Lepthien and Bock (1976) analyzed Christmas Bird Count (CBC) data and concluded that the Golden-crowned Kinglet preferred areas with significant levels of winter precipitation. Root (1988) observed that it avoided the northern boreal woodlands and coniferous forests of Canada. It avoided areas where January temperatures were colder than −18°C; all the highest abundance peaks occurred where the temperature rarely dropped below freezing. Lawrence (1949a) reported 2 overwintering Golden-crowned Kinglets near the Mattawa River where night-time temperatures dropped as low as −23°C.

In winter, the Golden-crowned Kinglet continues to be associated mainly with coniferous habitats, which may be either upland or lowland forests. Its affinity for older-growth conifers disappears in winter and it may be found in conifers of all age classes. Other habitats may be used, including deciduous and mixed forests, riparian areas, urban and suburban habitats, orchards, and shrubbery around houses. South of the Shield, coniferous plantations provide important winter habitat. In Ohio, the minimum size of woodland it was observed in during winter was 24 ha, but the Golden-crowned Kinglet demonstrates no evidence of area sensitivity in winter in Ontario (Bent 1949; Graber et al. 1979; LaForest 1993; Lancaster et al. 2004; Mills 1981; Swanson et al. 2020).

Smith (2003) analyzed results of Winter Bird-Population Studies in southern Ontario. The Golden-crowned Kinglet was one of the species that showed the clearest affinity for forest habitat. Numbers of birds detected per km^2 were: farmland, 0; mixed-rural, 2.5; forest, 4.4; urban natural, 0.7; urban natural areas smaller than 10 ha, 0.2; urban natural areas with open water, 0; and city, 0. In Missouri, it was almost twice as abundant in fully stocked forests than in open forests (Kendrick and Thompson 2013).

The Golden-crowned Kinglet is the smallest North American passerine and is therefore susceptible to freezing during cold weather. In Missouri, its detectability increased with decreasing temperatures. It appeared to be more active during cold weather (Kendrick and Thompson 2013). Blem and Pagels (1984) determined that the lipids stored during the day by foraging kinglets were insufficient to prevent hypothermia if the birds were exposed to 0°C overnight. They observed kinglets moving into squirrel dreys at dusk, presumably to roost. They concluded that roosting within squirrel dreys and even huddling would be insufficient to prevent hypothermia. Heinrich (2003) confirmed that Golden-crowned Kinglets huddle together during winter nights. Roosts of 2-4 huddled together in a snow-covered brush pile, a branch of a spruce 12 m up, and 4 m up under thick branches in a white pine. They did not go into torpor to conserve energy. The birds apparently did not return to the same roost every night but instead foraged until nightfall and huddled together tightly near where they ended up at dusk. Despite its habit of huddling at night, the Golden-crowned Kinglet is highly vulnerable to mortality during cold winter weather. During severe weather during the winter of 1976-77, Graber and Graber (1979) found 2 dead kinglets in their Illinois study area. Density of birds in all habitats dropped to zero and they believed that the population had suffered 100% mortality. Late-winter declines have been noted in Saskatchewan and Ohio and these may be related to mortality. Spring and summer numbers fluctuate considerably, probably due to differing winter mortality rates. Severe declines have been documented after harsh winters. In New Hampshire, breeding season populations decreased 56% after the severe winter of 1976-77 and sharp declines in populations were observed across the continent after the unusually harsh winters of 1976-77 and 1977-78 (Graber et al. 1979; Larivée and Darveau in Gauthier and Aubry 1996; Sabo 1980; Swanson et al. 2020).

In winter, the Golden-crowned Kinglet continues to forage mainly in mid-portions of tall trees (predominantly conifers). It also forages on branches and dead leaves in shrubs. Occasionally it feeds on the ground and in winter may find considerable food on the snow under trees. It may also forage subnivally by going under branches partially covered by snow and feeding in melted areas close to

the base of the trunk, or by going down holes in the snow (Bent 1949; James 2001; Swanson et al. 2020).

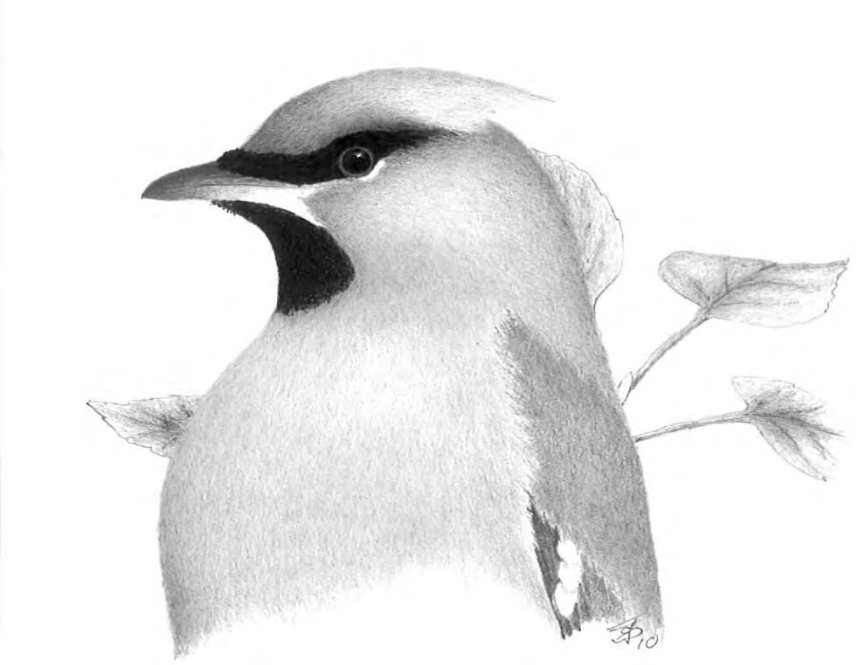
The winter diet of the Golden-crowned Kinglet consists of soft-bodied arthropods such as insects, mites, and spiders and their eggs, and very small amounts of vegetable matter (Swanson et al. 2020). Heinrich and Bell (1995) examined 15 gizzards of Maine kinglets foraging in spruce-fir stands in winter. Of 483 prey items, 59% were lepidopteran caterpillars, and 95% of these were geometer moths. Small caterpillars were the only food items found consistently in all birds. The volume of caterpillars consumed was greater than any other prey. Other prey items included spiders, aphids, flies, beetles, springtails, and insect eggs. Four individuals had eaten small seeds and 3 had a red flocculant in their gizzards that was presumably fruit. Noticeably scarce in the diet were springtails. Only 4 had been eaten in total by all the birds. These were of at least 2 species, neither being the snow springtail which was present in the millions on the snow. They concluded that it foraged opportunistically and that their diet reflected prey abundance in conifers, except for the very abundant springtails. The winter diet of a few kinglets was reported from Illinois (Graber et al. 1979), but results from the 2 species were combined. The diet consisted of 39% bugs, 25% mistletoe fruit, 17% spiders, and 16% cutworms. In winter, it has been documented eating stoneflies (Swanson et al. 2020) and taking bites out of a persimmon fruit (Bent 1949).

The Golden-crowned Kinglet is uncommon during winter in the south (James 1991). Its presence may be somewhat sporadic; it is more common during mild winters (Weir 2008).

CBC data for Ontario from 1970 to 2021 indicate that the Golden-crowned Kinglet population increased annually by 1.18%. During 2009-21, the population decreased 8.67% annually (National Audubon Society 2022).

Bohemian Waxwing

Bombycilla garrulus



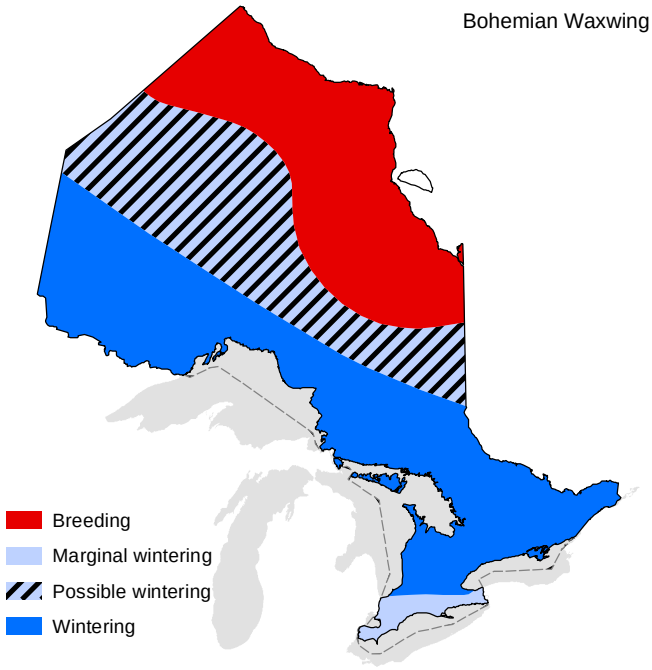
BREEDING SEASON

Habitat Requirements

During the first atlas, most records of the Bohemian Waxwing were along major northern rivers. All were observed along river banks with none seen on open muskeg (Cadman in Cadman et al. 1987). During the second atlas, it was also found inland in open spruce-tamarack woods with an understorey of willow and alder. This habitat is where the first nest was discovered in the province. The pair was observed at the ecotone of this habitat and a sedge meadow (Peck and Coady in Cadman et al. 2007; Peck et al. 2004a).

Throughout its range, the Bohemian Waxwing breeds predominantly in open coniferous forests, ecotones of boreal forest with tundra and alpine habitats, and early stages of succession after burns or clear-cuts. It nests most often in open coniferous stands, especially those dominated by spruce and pine, and, to a lesser extent, tamarack and balsam fir. It also nests in stands with a mixture of conifers and birch or poplar. Trees tend to be widely spaced in breeding habitat, but there may be a dense understorey of willows or alders; some stands have few shrubs. Virtually all nest sites are near plentiful supplies of fruit and open areas where waxwings can capture insects by flycatching. Beaver ponds, swamps, muskegs, taiga, and older burns and cuts provide good breeding habitat. In British Columbia, habitats also include mature, open coniferous forest edges (dominated mostly by

spruce), with interspersed aspens, alders, and willows and numerous drowned or dead trees. Edges of ponds, swamps, or bogs provide open foraging areas and dead trees are used for perching when hawking insects (Anderson 1909, 1915; Bent 1950; Campbell et al. 1997; Erskine 1977; Sinclair et al. 2003; Witmer 2020).



The first and only nest found in the province was 3.2 m from the ground in a 7-m tall white spruce with a diameter at breast height of 24 cm. It was on a horizontal branch with some additional branches supporting it along the sides. The nest was 15 cm from the tree trunk. The nest was poorly concealed, but blended in well with the moss and other twigs at the site (Peck et al. 2004a).

Most nests are in conifers, particularly older ones with hanging moss, although the Bohemian Waxwing may also nest in small, dead black spruce in shrubby bogs. It has nested in black and white spruce, jack pine and other pine species that do not occur in Ontario, tamarack, and balsam fir. There is 1 record of it nesting in alder, a deciduous species. Nests have been reported 1.2-15.2 m from the ground, but most are 3.0-7.6 m up. It tends to nest lower in bogs and very wet areas because the trees are stunted, but in drier areas it may nest near treetops at greater heights. Nests may either be on a horizontal limb near the tree trunk or at the tip of a branch. One nest was in the fork of the main trunk of a small fir (Anderson 1909, 1915; Bent 1950; Campbell et al. 1997; Sinclair et al. 2003; Witmer 2020).

The Bohemian Waxwing is nonterritorial. Conspecifics may be tolerated within 1 m of the nest provided they are not courting the female. Male aggression toward others near incubating females is probably mate guarding rather than territoriality. It is gregarious even during the breeding season. Although many pairs nest individually, there is a tendency for small groups (2-5) of pairs to be clumped together, with large expanses of potentially suitable habitat unused. Nests are situated near areas of high concentrations of fruit; proximity to water may also be important. Observations over a 3-day period confirmed that Ontario's first nest was solitary and not part of a nesting aggregation. No information is available on the size of the breeding season home range (Bent 1950; Campbell et al. 1997; Jehl 2004; Peck et al. 2004a; Witmer 2020).

No information on natal philopatry is available, but it is highly unlikely that any juveniles return to their natal area to nest. The Bohemian Waxwing is highly nomadic. It is unlikely that breeding birds return to the same general area in subsequent years. Breeding locations usually vary annually, probably in response to fruit supplies. It may be a common to abundant breeder at a site in 1 year and rare or completely absent the next (Bent 1950; Jehl 2004; Witmer 2020).

Limiting Factors

The Bohemian Waxwing is often a late breeder, timing nesting so that there are ample supplies of ripe fruit when the young fledge. Nest building most commonly occurs from mid-June into July, but some nests are built in late May. Fledging may occur from mid-June until mid-August, but mostly in July. The Ontario nest had a full clutch on 13 June. Nest building takes 3-5 days. It is likely that 1 egg is laid per day. The female begins incubating once the last egg is laid. The incubation period is 13-15 days, but mostly 13-14 days (Campbell et al. 1997; Letourneau in Gauthier and Aubry 1996; Peck et al. 2004a; Sinclair et al. 2003; Witmer 2020).

There are no records of second broods for the Bohemian Waxwing and it is unknown if renesting occurs if the first nest fails. The Ontario nest contained a clutch of 4 eggs. The typical clutch size is 4-6 eggs, although at least 1 2-egg clutch appeared to be complete and clutches of 7 eggs have been reported. The most common clutch sizes are 4 and 5 eggs (Anderson 1915; Bent 1950; Campbell et al. 1997; Letourneau in Gauthier and Aubry 1996; Peck et al. 2004a; Witmer 2020).

There is little information on the age of first breeding, but it is known that at least some yearling birds do not breed. The mating system is apparently monogamous, with pairing occurring as early as in winter. There is no information on whether mates remain together for more than 1 year (Witmer 2020).

Early in spring, the Bohemian Waxwing may feed on sap oozing from trees, particularly maples and birches. It may consume flowers of various tree species. During the early part of the breeding season, it is largely insectivorous. It gleans insects from vegetation and is a proficient flycatcher, sallying from exposed perches that are usually near water to capture aerial insects. Fruit becomes very important in the diet as the breeding season progresses and continues to predominate in the diet until spring. Fruit is so important in the diet that it regulates its distribution and possibly its population. It plucks and swallows whole fruits from a perch, often clambering or occasionally briefly hovering to obtain fruit. It sometimes feeds on the ground for fallen fruit or fruits of herbaceous species such as strawberries (Anderson 1909; Bent 1950; Sinclair et al. 2003; Witmer 2020).

Both parents feed the young regurgitated food that includes buds, fruits, and insects. Insects fed to young include mosquitoes, beetles, flying ants, dragonflies, and caddisflies. Adults eat a variety of insects such as scale insects, flies (especially mosquitoes and midges), mayflies, stoneflies, beetles, dragonflies, sawfly larvae, bugs, grasshoppers, and aphids. It may also consume spiders and snails. Although arthropods may be seasonally important in the diet, sugary fruits are characteristic of the Bohemian Waxwing's diet. Its diet is much like that of the Cedar Waxwing but differs from other frugivores that feed both on sugary and fatty fruits. Early summer fruits that are consumed include strawberries, mulberries, and juneberries. Later in the summer, fruits of raspberries, blackberries, honeysuckles, and cherries are important. It may feed extensively on buffalo-berry, but the most important fruits in late summer through winter are those of mountain-ash and red cedar. Other fruits commonly eaten are those of hawthorn, rose, chokecherry, cotoneaster, highbush cranberry and guelder-rose, bearberry, snowberry, hackberry, barberry, alder, holly, buckthorn, asparagus, greenbrier, bittersweet, mistletoe, dogwood, sumac, spicebush, columbine, matrimony vine, black alder, Russian olive, wild grape, apple, and viburnum (Anderson 1909; Bent 1950; Witmer 2020).

No cases of parasitism by the Brown-headed Cowbird have been reported. It is unlikely that the Bohemian Waxwing could successfully fledge cowbirds because of its predominantly fruit diet and late nesting. In addition, the cowbird is scarce or absent in large portions of this waxwing's range. A deserted nest containing 3 waxwing and 2 cowbird eggs was reported in British Columbia, but the record was not accepted because of potential confusion with the Cedar Waxwing (Campbell et al. 1997; Witmer 2020).

Status

Schueler et al. (1974) reported that the Bohemian Waxwing was fairly common near the confluence of the Sutton and Warchesker rivers in 1962, 1964, and 1965. They obtained the first evidence of breeding for the province when they collected a female with a brood patch there on 19 July 1964. Birds were reported near Kapuskasing in the summer of 1976 (Speirs 1985). During the first atlas, family groups were found in 3 locations and young being fed by adults were photographed along the Winisk River in 1984 for the first confirmation of breeding. It was found in 13 squares along several rivers in the Hudson Bay Lowland in northwestern Ontario. Birds appeared to be very thinly scattered and possibly confined to river valleys, although that is where more atlassing effort was directed (Austen et al. 1994; Cadman in Cadman et al. 1987). James (1991) considered the Bohemian Waxwing a locally rare summer resident in the northern portion of the Hudson Bay Lowland. Wilson and McRae (1993) reported it erratically through June and July at Ekwan with a high count of 10 on 14 June. They concluded that breeding probably took place somewhere nearby. They observed 4 on 4 June in a tamarack fen near Moosonee but were uncertain if these were migrants or breeding birds.

During the second atlas, the Bohemian Waxwing was found in the eastern portion of the Hudson Bay Lowland and at 4 locations in the Boreal Forest Region. It was detected in 16 squares during the second atlas compared with 13 in the first, confirming that it remained a rare and local, but widespread breeder. The most southern record was approximately 80 km northeast of Cochrane, at about the same latitude of the Kapuskasing record. Breeding was confirmed in 2 locations during the second atlas. In addition to the nest found near the James Bay coast north of the Swan River, fledged young were found 50 km southeast of Peawanuk in an extensive burn with bog vegetation on 13 July 2003 (Peck and Coady in Cadman et al. 2007; Peck et al. 2004a).

Peck et al. (2004a) found the first nest for the province on 12 June 2003 north of the Swan River near the James Bay coast. This was the most eastern nest record for the Bohemian Waxwing for North America and it now appears to be established as a summer resident in northern Ontario and Quebec. In Quebec, there have been several sightings of individuals and flocks during the breeding season, including several flocks seen in June 1991 on the east side of James Bay (Letourneau in Gauthier and Aubry 1996). Results of the second atlas and other records demonstrate that the Bohemian Waxwing is not confined to river valleys as appeared to be the case during the first atlas.

The overall North American population appears to be stable or increasing. A population increase in the 1970s was attributed to widespread planting of ornamental fruiting plants in the wintering range, particularly mountain-ash (Witmer 2020). Breeding Bird Survey data for 1970-2021 indicated that the Bohemian Waxwing decreased at the rate of 2.66% annually in Canada. Results were of low reliability and there are no data for Ontario (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Nestlings fledge when they are 14-18 days old and depend upon their parents for at least 2 weeks. In British Columbia, fledged young still dependent upon the adults can be observed until the end of August. In North America, families may stay together for long periods, even until the end of January (Campbell et al. 1997; Witmer 2020).

During late summer in the postbreeding period, Bohemian Waxwings in British Columbia occur in wet coniferous forests with white or black spruce and tamarack, in subalpine firs, and pine stands growing close to lakeshores, muskegs, swampy areas, river banks, and old burns. These habitats are often interspersed with birches, alders, willows, and shrubs such as red-osier dogwood and highbush cranberry (Campbell et al. 1997).

MIGRATION

The Bohemian Waxwing withdraws from the most northerly areas of its breeding range and undertakes regular migration. In British Columbia, few remain north of latitude 56°N, but it winters in the southern portion of the Yukon. Most winters some appear as far south as Atikokan and presumably along most of the northern shoreline of Lake Superior. It migrates from the breeding areas in northwestern North America to the western United States, eastern Canada, and the northeastern United States. It is highly gregarious during migration, forming flocks that range in size from a few individuals to hundreds or even thousands of birds. It is also irruptive, occasionally occurring in large numbers far south of its normal wintering area, and there is no regular periodicity to these flights. During strong flight years, thousands may occur along a broad axis that extends from Atikokan east to Sudbury and Ottawa. Some wander south into the Kingston area where the largest flocks usually occur around Perth and Westport. In some years, large flocks reach the shores of Lake Ontario, especially at Prince Edward Point. At Kingston, irruptions occurred in 20 of 59 years, but a few birds appeared during 42 of these years. During migration, flocks may be comprised solely of Bohemian Waxwings, but they are often mixed with Cedar Waxwings and occasionally with American Robins and Pine Grosbeaks. At the southern edge of its range, small flocks or individual birds are most frequent, often associated with Cedar Waxwings (Bent 1950; Campbell et al. 1997; Elder 2002; McIlwraith 1894; Sinclair et al. 2003; Weir 2008; Witmer 2020).

Single birds and small flocks are more common in early autumn and late spring. It is often difficult to distinguish autumn migration from winter wanderings. Within the normal winter range, birds arrive in early November and northward migration begins in mid-March (Bent 1950; Elder 1997; Tozer 2012; Weir 2008; Witmer 2020).

During migration, the Bohemian Waxwing abandons the coniferous forests that are favoured for breeding and seeks habitats that support fruit-bearing trees and shrubs. These include roadsides, riparian corridors, gardens, towns, cities, open forests, orchards, vineyards, parks, lakeshores, and aspen stands. In Algonquin Park, it regularly feeds on the berries of winterberry holly (Campbell et al. 1997; Tozer 2012; Witmer 2020).

In Atikokan, robins migrated through the area in late October. They often seriously deplete fruit resources before the waxwings arrive (Elder 2002).

WINTER

Although there is no regular frequency to winter invasions, they appear to be related to crop failures in the normal wintering range. Large invasions to southern Ontario often coincide with failure of showy mountain-ash berries, a favoured winter food of the Bohemian Waxwing (Bent 1950; Campbell et al. 1997; Earley 2008; Poon 2008).

In non-irruption years, a high proportion of the Bohemian Waxwing population winters in the Boreal Forest Region. In this region, small flocks may occur in uninhabited by humans where fruits from native trees and shrubs provide an adequate food source. It is likely that the bulk of the population winters near human habitation where it feeds on fruit on ornamental plantings. In the Saskatoon area, where it is an abundant winter resident, it occurs mostly within the city where there is abundant fruit, as well as in surrounding towns, villages, and farmyards. Much smaller numbers occur in natural habitats. In southern Ontario, it is mostly associated with residential areas, but may occur anywhere that there is suitable fruit, such as along roadsides and at the University of Guelph arboretum. The presence of fruit is the key habitat component for wintering Bohemian Waxwings. They wander widely in search of fruit and have an incredible ability to find isolated fruit crops. Once a suitable supply of fruit is found, the waxwings remain until it is completely exhausted and then move on. In the Atikokan area, birds arrive each autumn, eat all the available fruit and then disappear until the next year. The composition of flocks is fluid, being small in autumn and building up through winter with largest flocks in December and January. Winter aggregations of birds are very mobile locally, but flocks tend to be sedentary over winter on a regional basis. Despite the mobility of wintering flocks, at least some wintering birds return to the same location between years (Earley 2008; Elder 2002; Erskine 1977; Leighton et al. 2002; Sinclair et al. 2003; Witmer 2020).

In extreme cold, Bohemian Waxwings may clump together or roost together in the cover of vegetation (Witmer 2020).

In winter, the Bohemian Waxwing eats predominantly sugary fruit and may eat 2-3 times its own weight in fruit a day. Mountain-ash is highly preferred over other fruits. In the north it eats mostly showy and American mountain-ash berries; in the south it mostly eats European mountain-ash berries. Red cedar berries are also a favourite. Highbush cranberry and guelder-rose berries may be important in the diet in late winter and early spring because these berries persist through the winter. Other fruits it eats in winter are those of hawthorn, grape, rose, apple, cotoneaster, pear, privet, barberry, Russian olive, buckthorn, bittersweet, common lilac, holly, flowering crab, gooseberry, dogwood, and buffalo-berry. It requires some protein in its diet, so it may eat scale insects; silver maple stamens; buds of white elm, ash, red and silver maple, cottonwood, cherry, and poplar; seeds of Siberian elm, Manitoba maple, birch, and hollyhock; tree bark (which may be roughage rather than food); and mineral sources such as dirt, chalk, and bits of white-washed walls. It rarely comes to feeders because few people put out the fruit that it requires, but it has taken raisins, dried currants, and minced prunes. When food resources become scarce, the Bohemian Waxwing may resort to eating canned peas, rotten apples, and cranberries gleaned from garbage, and food put out for dogs. Because most of the winter diet is sugary fruit, it needs to drink copious amounts of water. When water is unavailable, it eats snow. There is an observation of a flock of waxwings flying out from perches in dead trees to catch snowflakes in the same manner that they capture flying insects

(Bent 1950; Bergtold 1931; Black and Roy 2010; Campbell et al. 1997; Dunn and Tessaglia-Hymes 1999; Earley 2008; Elder 1997, 2002; Jensen 1959; Leighton et al. 2002; McIlwraith 1894; Mills 1981; Pittaway 1990; Poon 2008; Sinclair et al. 2003; Witmer 2020).

The American Robin competes with both waxwing species and defends food resources against them. A single robin can defend a fruit tree against as many as 15 waxwings at once, but once flock sizes become larger, the waxwings prevail (Bent 1950; Pietz and Pietz 1987; Witmer 2020).

The Bohemian Waxwing is especially vulnerable to collisions with windows because ornamental fruit trees are often near them. It is also vulnerable to collisions with cars while feeding on fruit along roadsides (Witmer 2020).

This waxwing may be particularly vulnerable to pesticide poisoning when feeding on fruit crops and insects that have been treated. It increased significantly in the mid-1970s after the banning of DDT, suggesting that it was adversely affected by this pesticide (Witmer 2020).

In winter, the Bohemian Waxwing is a rare winter resident in the north south to Lake Superior, but it may be irregularly rare to locally abundant south to Lake Erie in irruption years (James 1991).

The Bohemian Waxwing appears to be occurring more frequently in southern Ontario than formerly and also in larger numbers. It was first recorded on the Guelph Christmas Bird Count (CBC) in 1993, although there were a few previous count-week records. Numbers on subsequent CBCs there were 237 in 1995, 7 in 1997, and 308 in 2007 (Earley 2008). In the Hamilton area, its frequency of occurrence and numbers increased dramatically starting in 1955. From 1960 to 1986, the annual winter totals were in the single digits, but larger numbers have been present since the winter of 1989-90. At least some are seen almost every winter now in the Hamilton area (Curry 2006). During the invasion winter of 2007-08, there were 48 April records for the Greater Toronto Area, especially in the City of Toronto. Most sightings were of flocks. Prior to that winter, there were records from April for only 8 years, and most of these were of 1-3 birds (Poon 2008). CBC results for Ontario indicate an annual increase of 7.42% 1970-21 and an annual decrease of 10.24% 2009-21 (National Audubon Society 2022).

Cedar Waxwing

Bombycilla cedrorum

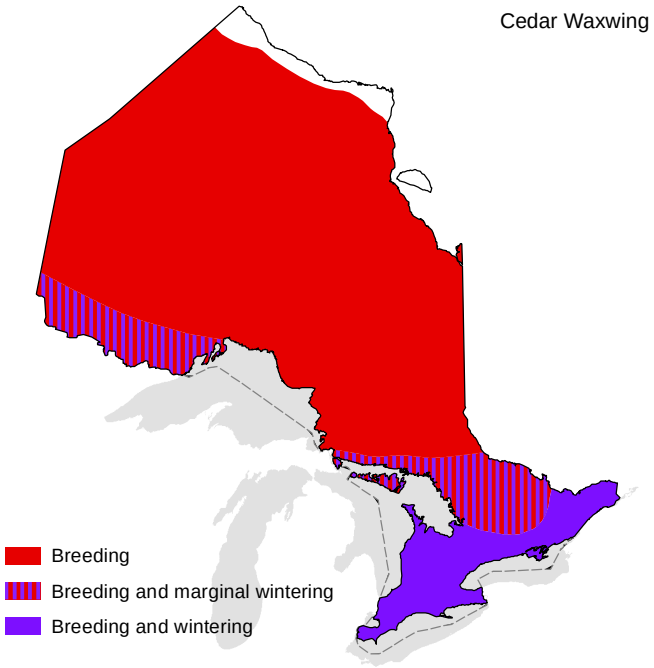
BREEDING SEASON

Habitat Requirements

Ontario Cedar Waxwing nests were found in both upland and wetland forests (36.6% of nests). Forests that were used for nesting were usually open and included deciduous, mixed, and coniferous stands. Overgrown fields and pastures supported 25.9% of nests, which included hawthorn meadows, the most commonly used habitat of this type in the south. Urban gardens and parks supported 14.7% of nests; 7.2% were along roads and shorelines of lakes and rivers; 6.3% were in campgrounds and cottage areas; 4.9% were in orchards; 1.7% were in treed bogs, beaver ponds, and marsh edges; 1.4% were in rocky outcroppings; and 1.2% were in treed sand dunes (Peck and James 1987).

In the Clay Belt portion of the Boreal Forest Region, the Cedar Waxwing exhibited a preference for bogs and shorelines of lakes and rivers (Smith 1957).

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Cedar Waxwing nests in mature and old-growth white pine stands (Kirk et al. 2012). Near Gogama, it did not nest in pure



jack pine stands, but probably nested in young mixed woods where pin cherry provided fruit (James and Peck 1995a). It was also absent in pure jack pine stands near Parry Sound (James 1979a). It was common along rivers and on lakeshores in Algonquin Park (MacLulich 1938). Also in Algonquin Park, it nested in wet and dry bogs, black spruce stands, black spruce–white cedar stands, and in white birch–poplar forests. In bogs, it spent most of its time on snags, and occurred from the top of the shrub layer (1.5 m from the ground) to heights of 9 m atop dead stubs. In spruce-cedar stands, it occurred from the bottom of the canopy and top of the shrub layer (2 m) to near the top of the canopy (5.8 m). In poplar-birch stands, it occurred from the top of the shrub layer (1.5 m) to the canopy top (11 m). Martin (1960) considered it a boreal forest species.

In Durham Region in the Great Lakes–St. Lawrence Forest Region south of the Shield, it nested in a very young pine plantation still dominated by willow shrubs, in open deciduous woods, and in a mature pine plantation with a small patch of sugar maple–red oak forest (Speirs and Orenstein 1975).

In southern Ontario, the Cedar Waxwing was more abundant on organic than conventional farms, but not significantly. Its presence was significantly correlated with the presence of hedgerows and road, railway, and hydro rights-of-way. It was also associated with the amount of riparian and upland woods but these relationships were not significant. It was negatively associated with farmsteads, number of large isolated trees, and grassy strips between fields that often supported fences, and pastures, but not significantly (Kirk et al. 2011).

Throughout its range, the Cedar Waxwing nests in open woodlands, old-field habitats with numerous trees and shrubs, orchards, and urban and suburban areas with fruit-bearing trees and shrubs. It frequently nests in riparian areas that provide trees and shrubs for nesting, fruit, water for drinking, and emerging aquatic insects. Other habitats it may use include semi-open upland woods on river bluffs, hills, and escarpments; shrub thickets; pine and oak barrens and savannahs; pine plantations; and utility rights-of-way. In British Columbia, most nests were in human-created habitat such as suburban gardens (42.7%) and rural areas (18.7%) where low trees and shrubs were abundant, water was available, and there were good supplies of insects, berries, and other soft fruit. Natural breeding habitats included riparian thickets and forests along rivers, edges of lakes, and beaver ponds; tamarack muskegs; edges of second-growth coniferous forests; and regenerating burns. In North Carolina, its occurrence was significantly negatively correlated with forest canopy

(Bielefeldt and Rosenfield 1994; Campbell et al. 1997; Crouch 1936; Faanes and Andrew 1983; Gentry et al. 2006; Inman et al. 2002; Lea 1942; Leighton et al. 2002; Lumpkin and Pearson 2013; Mossman and Hoffman 1989; Mossman et al. 1991; Rothstein 1971; Shaffer and Tardif in Gauthier and Aubry 1996; Witmer et al. 2020; Yahner et al. 2002).

Some studies examined the habitat of the Cedar Waxwing at the landscape scale. In North Dakota, it did not exhibit a clear response to amount of tree cover in either open or wooded landscapes. It preferred areas with 52-75% tree cover (Cunningham and Johnson 2016, 2019). In North Carolina, it was negatively correlated with the amount of tree canopy at the 200-m scale. As canopy cover increases, shrub coverage decreases. It was positively correlated with landscape diversity at the 200-m scale, but not significantly. Heterogeneous landscapes consisted of a mosaic of forest patches, lawns, and pastures with interspersed infrastructure. Homogeneous landscapes consisted of unbroken tracts of forest. It was negatively correlated with the amount of exurban development at the 1,000-m scale (Gilbert and Ferguson 2019). In Saskatchewan, it showed no preference for forest type, but was more common than expected in fragmented landscapes (Hobson and Bayne 2000).

Forest type does not appear to be particularly important but Erskine (1977) noted that the Cedar Waxwing was one of the most frequently detected species in tamarack bog forests in the Boreal Forest Region. Other forest types it has nested in include hardwood swamps, ash-basswood lowland forests, aspen-birch, pine and mixed pine-hardwood stands, coniferous lowland forests, bur oak–green ash lowland forests, white birch–yellow birch–white cedar, hemlock–yellow birch, and red maple swamps (Back 1979; Beals 1960; Capen 1979; Dawson 1979; Faanes and Andrew 1983; Golet et al. 2001; Niemi and Pfannmuller 1979; Noon et al. 1979; Samson 1979).

Temple et al. (1979) considered the Cedar Waxwing associated with late seral stages of mixed-wood forests. Most authors consider it to be an early successional species. In Pennsylvania, Haney (1999) reported it in 18.2% of old-growth forests, 82.4% of woodlands statewide, and 91.9% of forests in the Appalachian Plateau. He considered it to have a negative affinity for old-growth forest. In Alberta aspen stands, it was significantly more abundant in young than mature or old-growth stands (Schieck et al. 1995). In Quebec, Imbeau et al. (1999) detected it in recent burns and clear-cuts where saplings were shorter than 2 m to 5 m tall. It was absent in young and mature forests. Erskine (1977) reported that it occurred in burns and clear-cuts in the Boreal Forest Region that were in the early shrubby stages of succession. Kirk et al. (1996) stated that it was associated mainly with young stands in the western Boreal Forest Region and virtually absent in mature stands. In northeastern hardwood stands, it occurred in 27% of plots in disturbed and successional habitats, but in only 3% of mature undisturbed areas (Noon et al. 1979). In northeastern aspen-birch stands, it occurred only in the seedling-sapling stage and was absent in more mature stands (Back 1979). In northeastern pine stands, it was absent in mature stands, but occurred in the seedling-sapling and pole stages (Capen 1979). In New York over a 35-year period, a successional plot transformed from an open agricultural field to a second-growth forest. The Cedar Waxwing increased significantly with time on this plot (Brooks and Bonter 2010).

Some studies identified habitat associations of the Cedar Waxwing. In North Dakota aspen forests, its abundance was positively correlated with the percentage of ground cover. This is a

function of its preference for open-canopy areas because ground cover tends to be sparser under closed canopies (Grant and Berkey 1999). In northeastern mixed-wood forests, it was associated with increasing abundance of spruce or fir (Temple et al. 1979). In the northeast, it was in a guild that was most abundant in young plantations and disturbed shrubby areas; very common in alder, mature coniferous lowland forests, aspen regeneration, and recent clear-cuts; and common in grassland, and mature coniferous upland and deciduous forests (Niemi and Pfannmuller 1979). In Wisconsin, it was associated with the Black-throated Green Warbler, which had an affinity for yellow birch and its associates: spruce, fir, white cedar, and hemlock (Beals 1960). In the western Boreal Forest Region, it was in a guild associated with coniferous tree species. It occurred in mesic stands with moderate nutrient levels (Kirk et al. 1996). In the mid-Atlantic states, it was negatively correlated with the basal area of trees and positively correlated with coniferous trees, moisture, percent ground cover, slope, and the amount of forest cover within 2 km (Robbins et al. 1989).

The Cedar Waxwing is an edge species. It occasionally nests in the interior of forests, but only if the trees are well spaced with openings between them. It nests in small and large gaps in forests as well as at edges. In southern Ontario, its probability of observation was negatively correlated with the amount of forest 100 m from edge, woodlot size, the amount of forest within 2 km, and the amount of regional forest cover; the last 3 relationships were statistically significant. It had some of the strongest relationships for edge of all species tested (Austen et al. 2001). In Pennsylvania, it nested on hydro rights-of-way cut through forests, but not in the forests. In Michigan, 20 nests were found in a small white pine plantation, and there was a definite tendency to place nests at either end of it. The most central nests were about equidistant from the 2 ends of the plantation, 47 m and 48 m from edge. The most plausible explanation for nesting near the edge of the plantation was to be near suitable foraging habitat. In Rhode Island red maple swamps, the Cedar Waxwing occurred in swamps smaller than 1 ha, but was absent in swamps 1-5, 6-10, and 11-20 ha (Erskine 1977; Golet et al. 2001; Rothstein 1971; Taylor and Taylor 1979; Witmer et al. 2020; Yahner et al. 2002).

Ontario nests were usually well hidden in living trees, shrubs, and vines. The Cedar Waxwing nested both in deciduous (32 species, 65.5% of nests) and coniferous (8 species, 34.5%) species. The most frequently used species were hawthorn (57 nests), spruce (46), pine (42), maple (38), apple (34), and white cedar (21). Nests were placed in crotches as well as on horizontal limbs and were more often away from the trunk than against it. Distances from the trunk ranged from 0.2 to 4.6 m, but mostly 0.9-2.4 m. One nest was wedged between a rock face and the roots of a cedar tree. It usually builds its own nest, but 1 pair added to an old Common Grackle nest and used it. One female laid eggs an empty Willow Flycatcher nest and shared incubation duties with the flycatcher. Another nest was built on top of a deserted Yellow Warbler nest. Nests were 0.8-18 m from the ground, with most 1.8-3.7 m up (Peck and James 1987). Nests in Muskoka and Parry Sound districts were often at the edge of a forest 0.8-13.7 m from the ground (Mills 1981). Burton (1958) found 41 nests in York, Peel, and Simcoe. Thirty-three were in hawthorns, 7 in maples, and 1 in an apple tree. Nests were 1.1-4.6 m from the ground, but most were within 3 m of the ground. Other nest-tree species previously reported for the province were red cedar, black spruce, Norway spruce, willow, pine, and hemlock and one nest was in a grape vine. In eastern Ontario, common nest-tree species were red cedar, hawthorn, bur oak, white cedar, and apple (Witmer et al. 2020).

Throughout its range, the Cedar Waxwing nests predominantly in living trees and shrubs, and occasionally in vines. Unusual nests were in woodpecker holes, on lampposts, on a building, and on a cliff. Nests were in sugar and red maple, red and bur oak, white birch, white and red pine, red cedar, apple, pear, hackberry, domestic plum, sycamore, white elm, Kentucky coffee-tree, dwarf chinquapin oak, cottonwood, hawthorn, European larch, staghorn sumac, and willow. In British Columbia, deciduous trees (29 species) were used 3 times as often as conifers, except in the interior where twice as many deciduous trees were used. Willows, alders, and domestic fruit trees were used for nesting most often. Nine species of conifers and 15 species of shrubs were used. In New York, the Cedar Waxwing used hawthorns for nesting more than expected based on their availability. Sixty percent of nests were in hawthorns. White pine was also used more than expected; areas selected for nesting had more hawthorns and apples than random sites. Nest orientation relative to the trunk did not deviate from random. In order of frequency, nests may be saddled on a horizontal branch, in a fork in a branch, on a branch next to the trunk, in a fork in the trunk, or in a vine supported by a tree or shrub. Nests have been reported as far as 4.1 m from a tree trunk. Nest heights range from 0 (on a cliff) to 15.2 m with most 2.0-4.0 m up. Height of nests in southeastern Ontario was 1.1-9.2 m, with an average of 2.59 m (Campbell et al. 1997; Crouch 1936; Lea 1942; Lovell and Stamm 1948; Murphy et al. 1997; Nickell 1955; Post 1916; Putnam 1949; Rothstein 1971; Saunders 1911; Tyler in Bent 1950; Witmer et al. 2020).

Although some authors stated that the Cedar Waxwing is nonterritorial, it defends a small area around the nest. The defended area includes a perch from which the male can see and guard the nest. In Ohio, 3 territories measured 226, 188, and 918 m^2. In 1 case, a territory was almost 0.4 ha in area and the guarding post was on a tall elm 91 m from the nest. The territories reported in Ohio may be larger than average because some authors described the territory as extending only a few feet from the nest. Because only a small area is defended, nests may be quite close to each other and semi-colonial nesting may occur. Active nests are commonly only 6-7 m from each other and occasionally there is more than 1 nest in a single tree. Near Toronto, 11 nests were within a radius of 7.6 m in a clump of white pine. Densities of 4.9, 14.1, and 44.4 nests per ha have been reported in loose colonies. The only activities confined solely to the territory are incubation and feeding of the nestlings. Territoriality diminishes as the season progresses. Even at the height of the breeding season, the Cedar Waxwing is highly gregarious, forming flocks that forage together. At a colonial nesting area in North Carolina, 1 pine tree was used as a congregating point for the flock and adults hawked insects from it to feed their young. Adults flew to the activity tree and congregated prior to departing as a group to the food supply to feed the nestlings. When adults returned with food for their young, they again congregated in the activity tree before dispersing to their respective nests. Banding has demonstrated that flocks during the breeding season are cohesive units. Flocks from different areas may gather together in prime foraging areas, but individual flocks arrive and depart at different times. Home ranges may be quite large; adults may forage 2 km from where they gather food for their young (Allen 1939; Crouch 1936; Lea 1992; Mountjoy and John in Cadman et al. 1987; Putnam 1949; Rothstein 1971; Snavely and Witherington 1986; Tyler in Bent 1950; Witmer et al. 2020).

There is no evidence that any birds return to their natal area to breed. In Ontario, 0 of 42 nestlings returned the following year to breed and 0 of 174 nestlings returned in Ohio. Adult site fidelity is

very low and consistently lower than for most passerines. In Ontario, 0 of 27 adults returned; 2 of 54 (3.7%) returned in Ohio (Putnam 1949; Witmer et al. 2020). Low site fidelity may be related to the Cedar Waxwing's habit of nesting wherever fruit is abundant, and this may vary from year to year. It may be abundant at a given location in 1 year and absent in the next (Saunders 1911).

Limiting Factors

The Cedar Waxwing is one of the later-nesting species. Eggs have been found in Ontario nests from the last week of May until mid-September, with most reported in the last week of June and first half of July (Peck and James 1987). In York, Peel, and Simcoe, the peak of nesting occurred in July and August, although there were numerous records from June and September. The earliest record was a nest with 3 eggs on 8 June and the latest was one with 3 young on 20 September (Burton 1958). In the Kingston area, nest building began in early June and peaked in the fourth week of June (Witmer et al. 2020). In Algonquin Park, nest construction extends from late May to early July, eggs are present from late May to mid-July (mostly late June to mid-July), nestlings occur from mid-July to late August, and recently fledged young have been documented from late July to early September (Tozer 2012). Throughout its range, the Cedar Waxwing nests late so that there is ample fruit available to feed the nestlings. In the northeastern United States and eastern Canada, some birds may nest as early as the first week of June, but the peak of nest initiation occurs in the last half of June with a suggestion of a second peak of activity at the end of July. Second broods or replacement clutches may be initiated in late August. Eggs may be present in nests as late as the end of September and there is 1 record of a bird incubating eggs in mid-October in Michigan. The Cornell Nest Records Scheme indicated a shift in timing of nesting in the east. Prior to 1970, 17% of nests had their first egg after 24 July and 36% of nests were initiated after 15 July. After 1970, 44% of nests were initiated after 24 July making the number of nests started early and late in the season almost equal. It is possible it is evolving toward later nesting to reduce cowbird parasitism (Allen 1939; Crouch 1936; Leck and Cantor 1979; Putnam 1949; Tyler in Bent 1950; Witmer et al. 2020).

First nests may take 3-9 days to build, but usually 5-7 days. The time taken to complete a nest decreases with the season; replacement nests may be built in 2 days. In Ohio, it took 6-8 days to build nests between 30 May and 10 June compared with 4.5 days between 12 and 21 June. Egg laying usually starts as soon as the nest is complete but as many as 3 days may elapse before the first egg is laid. Eggs are laid at the rate of 1 per day. Incubation may be initiated from the laying of the first egg to laying of the last egg. The incubation period of 31 Ontario nests was 10-13 days, but mostly 11-13 days. Other studies reported incubation periods of 10-16 days, but 12-13 days appears to be the most frequent incubation period. Hatching takes place over a 2-day period, confirming that incubation usually begins before the clutch is complete. It has been estimated that 2 broods could be raised in approximately 75 days from the beginning of the construction of the first nest to fledging the second brood. Laying of the first egg in the second nest occurs from the day before the young in the first nest fledge until 3 days after fledging. Second nests are usually in the same territory and within 10 m of the first nest (Allen 1939; Campbell et al. 1997; Crouch 1936; Lea 1942; Lovell and Stamm 1948; Nice 1941; Peck and James 1998a; Post 1916; Putnam 1949; Saunders 1911; Snavely and Witherington 1986; Tyler in Bent 1950; Witmer et al. 2020).

The Cedar Waxwing frequently raises 2 broods. In eastern Ontario, less than a third of pairs raised 2 broods; 7 of 8 Ohio pairs (87.5%) raised a second brood. One author suggested that 3 broods were probably raised in a season, but there is no evidence of this and it appears unlikely. The author of a Michigan study concluded that only a single brood was raised. Renesting is common if a clutch is lost. Ontario birds used the same nest or built a new one nearby for replacement clutches. Second nests are often in the same tree as the first. One Ontario study found no evidence of second clutches or renesting. Clutches of 2-6 eggs have been reported in Ontario, with most containing 4 or 5 eggs. A single 8-egg clutch was laid by 2 females. Throughout its range, clutches of 2-7 have been reported, but the normal clutch size is 3-5 eggs. Six-egg clutches are rare and larger clutches may be laid by more than 1 female. Most nests contain 4 or 5 eggs. Clutch size diminishes as the season progresses. In Ohio, first clutches averaged 4.57 eggs compared with 3.86 eggs for second clutches (Allen 1939; Burton 1958; Crouch 1936; LaForest 1993; Lea 1942; Leck and Cantor 1979; Peck and James 1998a; Putnam 1949; Tyler in Bent 1950; Witmer et al. 2020).

The age at first breeding is 1 year and it appears as though all birds breed every year. The mating system is monogamous and no cases of polygyny have been reported. Pairs tend to remain mated for all nests within a breeding season, but it is unknown if the same birds pair again in subsequent years. Birds do not attain the full complement of waxy appendages on their wings until their third year. Most birds mate with birds of the same age, having the same tip-index category. Third-year birds tended to initiate nesting earlier and have larger clutches and raise more young than younger birds (Mountjoy and Robertson 1988; Putnam 1949; Witmer et al. 2020).

The Cedar Waxwing is an accomplished flycatcher and often perches near watercourses or water bodies to capture emerging aquatic insects. It inspects and gleans the bark of trees for insects and may occasionally forage on insects on tree trunks by hovering or perching on the bark or small twigs beside the trunk. It also forages in the peripheral branches of fruiting trees and shrubs to obtain fruit or insects and takes arthropods from spider webs. In spring, it feeds on sap of maples. It has taken insects from floating waterlily pads. While feeding on grapes in Niagara Region, it perched on wires or trees near the edge of the vineyard, descended to the top of the nearest vine, plucked a single grape, and returned to the perch to eat it. Birds may occasionally hover and pluck fruit from a tree or shrub. In a laboratory experiment, blueberries in the 7.5- and 11.0-mm classes were eaten 97% and 80% of the time, respectively; 71% of the berries in the 12.8-, 14.0-, and 20.5-mm size classes were picked up and dropped within 2 seconds. Berries in the 17.6-mm size class were never eaten. Berries in the 2 smallest size classes (7.5 and 11.0 mm) were swallowed with little or no manipulation but waxwings were able to eat larger fruits only by smashing them repeatedly with their bills. Although larger berries provided a greater absolute amount of sugar, the 7.5-mm size provided the highest rate of sugar ingestion because they were handled faster. The Cedar Waxwing has been known to gorge itself to death on fruit and it is also vulnerable to alcohol intoxication and death after eating fermented fruit. It drinks copious amounts of water and occasionally pecks at mud of sodium-rich roadside pools. Occasionally it eats snow to obtain water and may flycatch snowflakes from a perch (Allen 1939; Avery et al. 1993; Burtt et al. 1976; Campbell et al. 1997; Crins 2002; Gorchov 1988; McIlwraith 1894; Nice 1941; Pinkowski 1976c; Putnam 1949; Royall 1989; Somers 2010; Tyler in Bent 1950; Witmer et al. 2020).

The male feeds the female fruit, frequently chokecherries and black cherries, while she is incubating. Both adults feed the young by regurgitation. Only the male feeds the fledglings of the first brood if a second brood is attempted. Initially nestlings are provided small insects, spiders, and juice of cherries and other small fruits. By age 4 days, young are fed whole fruits and rarely insects. In Michigan, 87% of food brought to nestlings consisted of fruit, predominantly juneberries, pin cherries, and blueberries. Young may also be fed beetles, snails, and the fruit of black cherry, chokecherry, and pokeweed. In the Kingston area, red-osier dogwood fruits were the most frequent food item fed to nestlings; they were also fed raspberries and chokecherries. As early as the first day out of the nest, young often peck at matter on leaves and one was seen walking up and down a limb hunting and eating insects on its second day out of the nest. A captive bird first fed itself at age 21 days, or 3-7 days after fledging (Allen 1939; Crouch 1936; Lea 1942; Nice 1941; Post 1916; Putnam 1949; Saunders 1911; Snavely and Witherington 1986; Tyler in Bent 1950; Witmer et al. 2020).

The Cedar Waxwing eats more fruit than most other birds throughout the year (84% of the diet), selects sugary fruits, and captures aerial and vegetation-borne insects. Beal (1897a) analyzed the contents of 152 stomachs collected in the United States. The diet consisted of 87% vegetable matter and 13% animal matter. The vegetable matter included 74% wild fruit or seeds and 13% cultivated fruit. Except for a few snails, the animal food consisted of insects, including the elm leaf beetle, aphids, grasshoppers, and bugs. Witmer (1996a) examined 212 stomachs from the northeastern United States and compared the diets of the Cedar Waxwing and the American Robin. The waxwing's annual diet was comprised of 84% fruit, 4% flowers, and 12% insects. It ate fruit almost exclusively (99%) from October through April. Frugivory declined dramatically in May when there was low availability of fruit, accompanied by a significant increase in consumption of petals and stamens of flowers (44% of the May diet). Frugivory increased sharply in June with the ripening of early summer fruits such as juneberry, mulberry, and strawberry. Insects were consumed May through September but fruit dominated the diet in these months. It was consistently more frugivorous than the robin in every month. Red cedar berries were prominent in the waxwing's diet in winter and spring (40-50% October through April, 27% of the annual diet) and apples and crabapples were next in prominence in the diet in winter (21% February through April). Cherries comprised 37% of the diet June through September. Naturalized cherries were consumed in June and July, pin cherries July through September, and chokecherries and black cherries were eaten mostly in August and September. There was a broad overlap in fruit selection by the Cedar Waxwing and the robin, but the overall patterns of fruit use were different. In winter and spring, the waxwing ate more red cedar berries (45%) than the robin (5%); sumac was eaten by the robin most of the year, but not by the waxwing; in autumn, berries of 4 species of dogwoods were prominent in the robin's diet (7% of its annual fruit diet), but the waxwing ate the fruits of only the flowering dogwood (3% of its annual fruit diet). In Ontario, however, the Cedar Waxwing has eaten the berries of other dogwood species. The waxwing avoided the fruits of gray dogwood, southern arrowwood, spicebush, Virginia creeper, staghorn sumac, and bayberry, but these were all eaten by the robin. The waxwing ate fruits of many nonnative species such as Morrow's honeysuckle, guelder-rose, and common buckthorn. The waxwing and robin ate similar amounts of cherries during summer and autumn, 50% and 69%, respectively. The fruits eaten by this waxwing had lower lipid and higher hexose content, larger fruit mass, higher water content, and more dry pulp per fruit than those that

were avoided. It cued in on fruits with high sugar content and avoided lipid-rich fruits. Five insect orders comprised 81.7% of the animal food consumed: beetles (mostly scarab and leaf beetles), hymenopterans, flies, lepidopterans, and bugs. Scale insects were eaten in May and June. Mollusc shell fragments were found in the stomachs of 3 females. Of 33 birds collected in a Maine spruce forest, 28 had eaten spruce budworm larvae and pupae. These birds had eaten an average of 82.5% insects in July. Fruits reported in the diet of the Cedar Waxwing by other authors include those of silverberry; downy, roundleaf, and alder-leaved juneberry; red cedar; hackberry; white and red mulberry; chokecherry; black cherry; wild strawberries; golden currant; cultivated blueberries; Morrow's honeysuckle; bittersweet; cultivated grapes; mountain-ash; English hawthorn; asparagus; apple; privet; red-osier dogwood; crabapple; huckleberry; and Canada moonseed. Beetles are the most important animal food, especially leaf beetles and weevils. It also eats carpenter ants, willow and other sawfly larvae, caterpillars, crane flies, spiders, mayflies, emerging winter stoneflies, cankerworms, tent caterpillars, and rarely dragonflies (Allen 1939; Avery et al. 1993; Breiding 1946; Campbell et al. 1997; Dexter 1951; Dowler and Swanson 1982; Fitch 1958; Gorchov 1988; Pinkowski 1976c; Putnam 1949; Saunders 1941; Shane and Shane 2000; Somers 2010; Tyler in Bent 1950; Witmer 1996b).

In the past 50 years, Cedar Waxwings have appeared in the east with orange instead of yellow tail bands. This colour variation is caused by pigments derived exclusively from dietary sources, particularly Morrow's honeysuckle. The introduction of Morrow's honeysuckle has had a positive effect on the Cedar Waxwing. It performs well on this fruit and includes much of it in its diet from July until mid-October. The abandonment of farmland created large areas of suitable habitat for nonnative honeysuckles, and they also thrive in disturbed areas such as roadsides, old fields, and stream banks (Hudon and Brush 1989; Witmer 1996b). Birds with orange-tipped feathers have been observed in Ontario, indicating that it has consumed Morrow's honeysuckle berries (Curry 2006).

The Cedar Waxwing does not defend food resources, but it may be affected by other species that do. Pietz and Pietz (1987) observed a single robin that defended an ornamental crabapple tree against flocks of Cedar Waxwings over a period of 2 weeks. The robin was successful in preventing waxwing flocks as large as 15 from foraging in the tree but was overwhelmed once waxwing flock size reached 30. The Northern Mockingbird also defends fruit resources and is most aggressive toward the Cedar Waxwing. Mockingbirds have been known to force waxwings to the ground and kill them with their bills (Hedrick and Woody 1983).

Peck and James (1998a) reported that 70 of 952 Ontario Cedar Waxwing nests (7.4%) were parasitized by the Brown-headed Cowbird. In York, Peel, and Simcoe, 4 of 41 nests (9.8%) were parasitized. More than half the nests were found in mid-July and none of these were parasitized (Burton 1958). Parasitism rates vary considerably geographically. In Michigan, the overall parasitism rate in 4 studies was of 27 of 345 nests (7.8%). In Ohio, no parasitism was observed in 200 nests; 0 of 23 Minnesota nests were parasitized; 4 of 445 British Columbia nests (0.9%) were parasitized; and 4 of 329 southern Quebec nests (1.2%) were parasitized (Campbell et al. 1997; Hanski et al. 1996; Lea 1942; Putnam 1949; Rothstein 1976a). The Cedar Waxwing is a poor host for the Brown-headed Cowbird. Most nests are initiated after the cowbird's peak egg-laying period, the waxwing is a rejecter of cowbird eggs, and the fruit diet that adult waxwings feed nestlings may be inadequate

for cowbird young because they are adapted to developing on insects. There are a few reports of waxwings feeding cowbird fledglings and waxwings have successfully fledged cowbirds in Illinois. Almost 90% of cowbird eggs are rejected and some of the accepted ones may fail due to the frugivorous diet (Campbell et al. 1997; Lowther 1991, 1997; Rothstein 1976a). Parasitism typically occurs during the host's laying period and about 85.5% of these eggs are rejected by nest desertion and egg damage or ejection. Three days after the last egg is laid, the waxwing switches from rejection to acceptance. In many parasitized nests, all waxwings fledge; in other cases, all young starve. Even though fruit does not provide adequate nourishment for the cowbird nestling, it continues to beg and receive the bulk of the food (Campbell et al. 1997; Rothstein 1975, 1976a, 1976b).

Rothstein (1973a) found a high rate (24.7%) of hatching failure in nests near Michigan farms and 12.0% of nests completely failed. The percentage of eggs not hatching reported in other studies was 5.5%, 15.6%, and 10.9%. In orchards, 27.3% of nests experienced total failure whereas no non-orchard nests failed completely. Thirty percent of orchard nests were completely successful compared with 75% for non-orchard nests. Results suggested that pesticides might be implicated in egg failures, but there was no evidence to support this. In British Columbia, 52 waxwings died and 27 were partially paralyzed after feeding in an orchard that had been sprayed with parathion (Witmer et al. 2020).

In New York, nest success depended upon nest-tree species and vegetation density. Although hawthorn was the preferred nest tree, nest success was not significantly higher in hawthorn than in other species; nests in white pine were most likely to fledge nestlings. Successful nests had greater canopy cover and more trees within 50 m than random sites (Murphy et al. 1997).

Nests initiated later in the season have a higher success rate than early nests. In Ohio, only 22% of 45 nests built before 20 June were successful compared with 51% of 51 nests initiated later. Loss of early nests appeared to be due in part to inattentiveness by the adults. Storms were also common during the early period and heavy rain and wind accounted for 10 of 29 early desertions (Putnam 1949).

The Cedar Waxwing is highly likely to desert the nest if it is disturbed by humans, particularly early in the nesting process (Crouch 1936; Saunders 1911; Witmer et al. 2020).

The Cedar Waxwing is highly vulnerable to being killed by vehicles. It frequently feeds along roadsides and its habit of descending from a perch to the fruit source and returning to the perch to eat it frequently exposes it to on-coming traffic. Dowler and Swanson (1982) reported high mortality associated with highway plantings in Texas. Fruit-bearing shrubs were planted in the median, at the edge of the highway, and along ramps. As vehicles passed, feeding flocks flew up, crossed the highway, and returned immediately with several birds being struck on each occasion. All 298 mortalities were associated with shrubs planted in the median of the highway.

Forestry practices are beneficial to the Cedar Waxwing. Forest management creates openings and edges that improve nesting habitat. Forest thinning and clearing also promotes the growth of fruit-bearing shrubs (Shaffer and Tardif in Gauthier and Aubry 1996; Witmer et al. 2020). In selectively thinned northern hardwood stands near Sault Ste. Marie, it increased in abundance 3-4 years after

harvest. It was much more common in thinned than control stands. It was associated with thinned stands supporting few hardwood saplings, but preferred sugar maple regeneration to small shrubs (Holmes and Pitt 2006). In the Carolinian Forest Region of southern Ontario, there was no difference in its abundance in uncut forests and those where selective thinning or diameter-limit cuts had occurred (Holmes et al. 2004). In the Canadian Shield of Ontario, there was no difference in its abundance in early successional and mid-successional clear-cuts than in burns in the same seral stages. It was significantly more abundant in early successional than mature stands but equally abundant in mid-successional and mature stands (Zimmerling et al. 2017).

In Pennsylvania and New Jersey over a 15-year period, the basal area of hemlock declined from 56% of the total basal area to 46% due to the hemlock woolly adelgid, and coverage by understorey deciduous shrubs increased. The Cedar Waxwing increased over this period, probably due to the increased coverage by shrubs and more openings in the canopy (Toenies et al. 2018).

In Alberta, there was no significant difference in the Cedar Waxwing's abundance at seismic lines, pipelines, or well pads than in forest interior adjacent to these structures (Bayne et al. 2016).

Status

The Cedar Waxwing has always been a common breeder in Ontario. It probably increased in response to deforestation associated with European settlement and with clear-cutting in extensive forests. Baillie and Harrington (1937) considered it a common summer resident, breeding north to at least the southern end of James Bay and west to Lake of the Woods. During the first atlas, its range was determined to cover essentially the entire province. It was widespread and common in southern Ontario but less abundant in the far north (Mountjoy and John in Cadman et al. 1987). James (1991) considered it a common summer resident north to at least Big Trout Lake and Attawapiskat, and probably rare to the north coast in the west and to Sutton Lake in the east.

The second atlas demonstrated that there had been no change in the distribution of the Cedar Waxwing. There was no significant change in its probability of observation province-wide but significant declines occurred in the Great Lakes–St. Lawrence Forest Region, both in and south of the Canadian Shield. Possible reasons for declines include natural succession from shrublands to forest and destruction of hedgerows. Highest abundance occurred south of the Shield, especially in a broad band along Lake Erie from Rondeau to Long Point, on the Bruce Peninsula, west of Toronto, and in another broad band between the Shield and Lake Ontario from Lake Simcoe to the Kingston area. Scattered areas of high abundance occurred in the Shield portion of the Great Lakes–St. Lawrence Forest Region and the Boreal Forest Region. It became less abundant northward (Kits in Cadman et al. 2007).

Surveys were undertaken in Illinois in the 1900s, 1950s, and 2007-09. The Cedar Waxwing was not detected during the 2 earlier periods. It is now common and rapidly increasing there, most likely because of the large increase in food availability. Fruiting trees, shrubs, and evergreens are common landscape plants in developed areas and these are preferred foraging and nesting substrates (Walk et al. 2011).

Long-term (1970-2021) Breeding Bird Survey data indicate annual decreases of 0.233% in Canada and 0.529% in Ontario. The short-term (2011-21) trends were annual decreases of 3.64% in

Canada and 5.09% in Ontario. The Ontario short-term trend was of medium reliability; the other trends were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young leave the nest when they are 14-18 days old and are fully capable of flight. They remain near the nest for 2-8 days and may return to the nest the day after fledging but not again. In some cases, fledglings may remain near the nest for as long as a month, but most disperse much sooner. Young are fed completely by the adults until 7-8 days after fledging and are independent by the time they are 21-30 days old (Witmer 2020).

After independence, young form small flocks that fly about feeding on fruit and catching flies. Flocks occur in the latter part of July and early August and are joined by adults in late August. These flocks grow in numbers and remain evident until autumn migration. During the postbreeding period, waxwings are found most frequently in areas with fruit-producing shrubs, including riparian areas. In Michigan, all juveniles were caught in riparian habitat, which was in a mix of alder, honeysuckle, and mature trembling aspen, rather than in 100-year-old upland trembling aspen stands. Most adults were also caught in riparian habitat. In Pennsylvania, family groups were seen on a hydro right-of-way through forested habitat but not in the forest. During the postfledging period in Pennsylvania, 22 adults and 22 juveniles were captured in clear-cuts compared with 1 adult and 0 fledgling in adjacent mature forest habitat (Akresh et al. 2009; Crouch 1936; Putnam 1949; Stoleson 2013; Yahner et al. 2002). In Minnesota, Streby et al. (2001b) did not capture any waxwings in regenerating clear-cuts during the breeding season, but caught 16 fledglings and 37 adults during the postbreeding period. In Quebec, Major and Desrochers (2012) caught Cedar Waxwings in regenerating clear-cuts during the postfledging period.

MIGRATION

Although some overwinter in the breeding range, most Cedar Waxwings are migratory. Migration is poorly understood because of low levels of philopatry and the difficulty of distinguishing between nomadism and true migration. In spring, some birds may still be migrating while others are nesting. Spring migration is prolonged and begins for all age classes in March, but birds do not arrive on the breeding grounds until late May. Breeding populations may not stabilize until mid- or late June, or even early July north of Lake Superior. At Prince Edward Point, there was a tendency for third year and older birds to arrive earlier in spring. The difference in timing between alpha and other birds was significant in 1985 but not in 1984 (Mountjoy and Robertson 1988). In Ontario, true spring migrants arrive after mid-May and the peak of spring migration is in late May and early June. In autumn, wandering flocks of juveniles and postbreeders are difficult to distinguish from migrants. Autumn migration may be prompted by cold fronts or depletion of fruit supplies. Most migratory flocks form in August and leave the northern part of the range in late August and September. Adults migrate southward about a month earlier than juveniles. In Muskoka and Parry Sound districts, waxwings begin flocking in August. Some years they are locally scarce by the end of that month but flocks sometimes linger if the fruit crop is good. Large flocks have been documented in mid-August in Algonquin Park. The main autumn movement in the south is from August through October with peak numbers from late August until mid-September; stragglers may still be moving through in early December (Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

Ontario birds have been recovered in Alabama, Oregon, Texas, Guatemala, and Mexico. Five birds banded in autumn in Iowa, Wisconsin, or Ontario were recovered in spring or summer in British Columbia, California, or Oregon 1-4 years later. Two birds banded within 5 days of each other in St. Thomas were recovered in Alabama and Oregon. Individuals may winter in widely separated areas in different years, so there is limited site fidelity during migration. Most migration occurs during the day, but mortalities at Florida television towers suggest that some nocturnal migration occurs (Baillie and Hope 1943; Brewer et al. 2018; Brugger et al. 1994; Mountjoy and Robertson 1988; Weir 2008; Witmer et al. 2020).

During spring migration in Pennsylvania, Smith and Hatch (2008) detected the Cedar Waxwing 5.7 times more often in shrubs than in forest habitat. During migration, it frequents open forests that support fruiting trees and shrubs (Witmer et al. 2020). In British Columbia, it occurs in many open-forest habitats during migration, but is most numerous in anthropogenic areas such as roadside thickets, orchards, urban parks, shrubby gardens, residential yards with berry trees, hedgerows, sewage lagoons, and shrubbery along hydro rights-of-way. In natural areas, it frequents second-growth forests; forested margins of tidal flats; riparian thickets of willow, red-osier dogwood, and elderberry; riparian cottonwood stands; juniper groves; beaver ponds; burns; and spruce and tamarack muskegs (Campbell et al. 1997).

During autumn migration in New York, approximately 20% of fecal samples contained Bella honeysuckle fruit, 10% contained fruit of red-osier and gray dogwoods, and 35% contained common buckthorn berries (Mudrzynski and Norment 2013). From mid-September to mid-October, flocks of juveniles appear at local concentrations of fruit in New York, moving on once crops are depleted (Witmer et al. 2020).

During migration, some Cedar Waxwings are killed by television towers and other tall structures, but the incidence of this is relatively low because it is predominantly a diurnal migrant. It is commonly killed by striking windows. This may occur in seasons other than migration whenever fruit is available near residences (Witmer et al. 2020).

McClure et al. (2013b) created a phantom road by playing traffic noise in an otherwise undisturbed forest during autumn migration. The Cedar Waxwing appeared to avoid the noise and was virtually absent when noise levels reached 55 dB(A).

The Cedar Waxwing is a common to locally abundant migrant. Daily high counts of approximately 200-4,000 have been recorded in both spring and autumn (Curry 2006; LaForest 1993; Weir 2008). At the Port Burwell Hawk Watch in Elgin County, 3-hour counts included 280 on 1 October, 188 on 9 September, and 185 on 19 September (Lancaster et al. 2004).

WINTER

Historically, the winter distribution of the Cedar Waxwing was probably confined to areas where red cedar occurred. It now has a much wider distribution due to planting of ornamental fruit-bearing trees and shrubs (Anonymous 2006). Throughout its range, presence of red cedar is still the primary factor defining where it occurs in high densities. Many small abundance peaks are associated with large river valleys (Root 1988). In winter, it occurs in areas with fruit-bearing trees or shrubs in open

woodlands, parks, gardens, second-growth forests, forest edges, and suburban areas (Witmer et al. 2020).

In winter, the Cedar Waxwing is nomadic, staying in an area rich in fruit until the resource is depleted and then moving elsewhere. Fidelity to wintering areas in subsequent years is low at 5.5%. In the Hamilton area, some birds remain into winter if there is a good berry crop; these birds usually dissipate in February and March. In other years, birds do not appear until February and March. These are likely birds that have wandered there after depleting fruit crops elsewhere. Christmas Bird Count (CBC) results for Ontario are irregular, with marked irruptions at unpredictable intervals. Large irruptions in the eastern United States are believed to result from fruit-crop failure at higher latitudes. In some years, peak numbers coincide with those of the Northern Mockingbird, Northern Cardinal, and especially the American Robin (Curry 2006; Freedman and Riley 1980; Hamilton 1997; Witmer et al. 2020).

In Ontario, wintering Cedar Waxwings have been documented feeding on the fruit of common buckthorn, red cedar, mountain-ash, and pokeweed. It has fed on female white-marked tussock moths that were frozen in fissures in the bark of red oaks (Crins 2002; Curry 2006; McIlwraith 1894; Weir 2008).

McPherson (1987) studied the winter fruit preferences of the Cedar Waxwing in Oklahoma. It consumed 3 species of hollies, 2 types of crabapples, mistletoe, red cedar, hackberry, and juniper. The order of preference for consumption of fruit was abundance, caloric content, and fruit size. Fruit 7-8 mm in diameter was highly preferred. It showed no preference for fruit colour. In late winter when fruit became scarce, it fed on elm seeds and flowers of hackberry, white elm, and cottonwood. In Texas, it fed on whichever fruit was most abundant, primarily juniper and mistletoe. During a winter of low fruit production, it was completely absent (Chavez-Ramirez and Slack 1996). Most authors concur that the staple winter foods of the Cedar Waxwing are berries of the red cedar (and other juniper species) and mountain-ash; buckthorn is important in the Ontario diet. Other fruits it has eaten in winter are those of barberry, cotoneaster, arbutus, crabapple, hawthorn, hackberry, and privet (Allen 1939; Campbell et al. 1997; Crouch 1936; Leighton et al. 2002; Tyler in Bent 1950).

The Cedar Waxwing seldom visits feeding stations. It may be attracted to feeders if fruits that it is already feeding on are put out. It is readily attracted by water and may accept raisins and apple slices (Dunn and Tessaglia-Hymes 1999).

Prior to a severe winter storm in Illinois, the density of Cedar Waxwings per km² was 31.6 in bottomland forest, 193.8 in upland forest, and 0 in urban residential areas. After the storm, none were present. Graber and Graber (1979) found no evidence of mortality and concluded that it emigrated from the area. Its nomadic habits may allow it to cope with adverse winter weather better than species that are more sedentary in winter.

James (1991) considered the Cedar Waxwing a common winter erratic in the south that occasionally occurred to northern Lake Superior. It is rare in winter in Algonquin Park (Tozer 2012) and possibly may not persist there all winter. It was detected on 8 of 13 Brighton CBCs, but sighted in only 2 winters at Presqu'ile (LaForest 1993). In Elgin County, large flocks gather where fruit is

abundant and there are flocks of about 100 birds most winters in the Aylmer Wildlife Management Area (Lancaster et al. 2004).

Freedman and Riley (1980) examined data from southern Ontario CBCs beginning in 1929 and found that the trend was toward more frequent irruptions and a higher overall population since about 1952. They concluded that the increase may have been a response to increasing availability of winter food due to planting of fruit-bearing shrubs. CBC data for Ontario indicate an annual increase of 2.77% 1970-21 and an annual decrease of 6.22% 2009-2021 (National Audubon Society 2022).

Red-breasted Nuthatch

Sitta canadensis

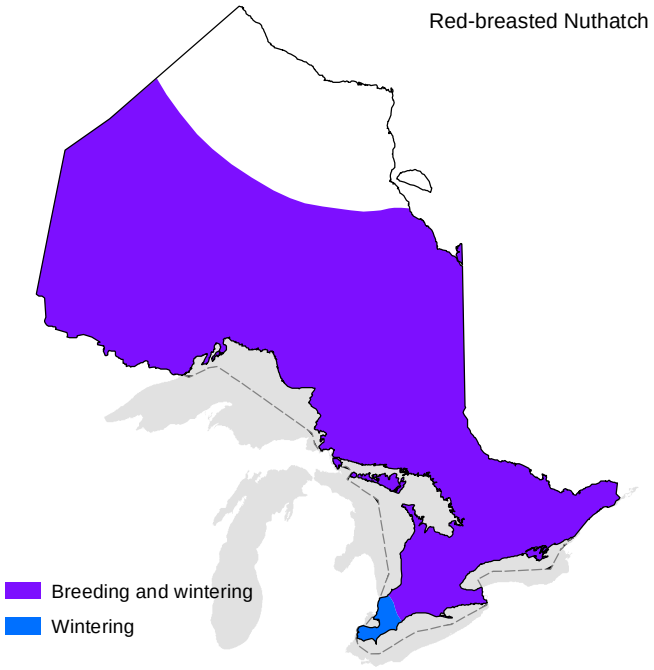
BREEDING SEASON

Habitat Requirements

In Ontario, the Red-breasted Nuthatch usually nests in mixed woods, occasionally in coniferous forests, and rarely in deciduous stands. More nest sites were in wet than dry habitats, possibly due to greater availability of dead trees for nesting. Some nests were at beaver ponds and most were near water, woodland edges, clearings, and roads, suggesting a preference for open areas near the nest (Peck and James 1987). Cheskey (1990) reported it nesting successfully in a backyard in the city of Waterloo. Although the yard was well wooded and part of a well-treed neighbourhood, it was not forest with most trees occurring in hedges and small groups.

In the Boreal Forest Region, the Red-breasted Nuthatch was associated with older, closed, mixed-wood forests and with areas with little interspersion of young and old forests. It and other species in this guild were associated with low amounts of edge and more intact forests (Rempel 2007; Rempel et al. 2007). Near Pickle Lake, highest densities occurred in mixed and coniferous forests (McLaren and McLaren 1981).

In the Canadian Shield in the Great Lakes St. Lawrence Forest Region, the Red-breasted Nuthatch commonly nests in mature and old-growth white pine forests. Its abundance in these forests is significantly correlated with the total basal area and the basal area of conifers (Kirk et al.



2012). It was rare in jack pine stands near Gogama, with the managed forests providing few nesting opportunities. It was absent until pines reached about 6 m in height. It was present in mixed forests because deciduous snags probably offered more potential nest sites (James and Peck 1995a). It occurred in 2 of 5 plots in jack pine forests in Parry Sound. Both were open stands with 25-50% crown closure and mixed with species such as trembling aspen, white birch, white pine, sugar maple, white spruce, and tamarack (James 1979a). In Algonquin Park, Martin (1960) considered it characteristic of hemlock. In wetlands, it nested in black spruce–white cedar stands, but was absent in pure black spruce and in bogs. In upland stands, it was present in white pine, fir-pine-hardwoods, hardwoods, and hemlock, and absent in poplar-birch, poplar-birch-fir-spruce, and fir-spruce. In immature white pine stands, it was tied for third in abundance with the Dark-eyed Junco.

In Durham Region in the Great Lakes–St. Lawrence Forest Region south of the Shield, the Red-breasted Nuthatch nested in an open-canopy young forest with poor drainage and a mature pine plantation. Speirs and Orenstein (1975) considered it a late-succession species associated with pine. During the first atlas in the Kingston region, breeding was reported only in squares containing coniferous and mixed woods where it particularly favoured white pine and red pine (Weir 2008).

The Red-breasted Nuthatch is strongly associated with coniferous tree coverage throughout its range. It typically nests in mature, diverse stands dominated by spruce, fir, pine, hemlock, tamarack, and cedar, and less frequently in pure stands of pine or hemlock. It also breeds in mixed forests, particularly where the dominant conifers are mixed with poplar or oak. It rarely nests in pure aspen stands. In the northeast, it regularly nests in coniferous plantations, northern hardwoods, lowland hardwoods, aspen-birch, natural pine forests, upland spruce-fir stands, lowland conifers (black spruce, tamarack, and white cedar), and mixed woods. In the Boreal Forest Region, it is most frequently associated with balsam fir stands, but is also present in stands dominated by spruce, pine, tamarack, and hemlock. In Quebec, it prefers mixed forests and deciduous woodlands with scattered conifers. In British Columbia, 44% of nests were in coniferous forests, 26% in mixed woods, and 11% in deciduous stands; 6% were in logged forests. It also occurred in lakeshores, riparian bottomlands, gardens, and parks; 13% were in treed urban, suburban, and rural areas (Back 1979; Bielefeldt and Rosenfield 1994; Campbell et al. 1997; Capen 1979; Crawford and Titterington 1979; Dawson 1979; Erskine 1977; Flack 1976; Ghalambor and Martin 2020; Hoffman 1989a; Niemi and Pfannmuller 1979; Noon et al. 1979; Rail in Gauthier and Aubry 1996; Samson 1979; Temple et al. 1979; Webb et al.

1977). The Red-breasted Nuthatch has variously been reported preferring pine, hemlock, spruce, and fir. This may be more a function of availability of coniferous species in different geographic areas. Spruce may be preferred wherever it is available and balsam fir may also be selected in the Boreal Forest Region. In certain areas, such as the Great Lakes–St. Lawrence Forest, pines are preferred and these are the dominant conifers. Hemlock is widely used, but may not be preferred where other conifers are present. In New Hampshire and Maine, it was associated predominantly with coniferous stands. It was most abundant in forests codominated by spruce and balsam fir, followed by those dominated by white pine and finally by balsam fir. In New Jersey, it was a facultative hemlock species. Approximately 5% of the population nested among hemlocks. The remainder nested in coniferous plantations dominated by Norway spruce. It may occasionally nest in tamarack and white cedar stands but these are not preferred species (Benzinger 1994; DeGraaf et al. 1998; Erskine 1977; Sinclair et al. 2003; Speirs and Orenstein 1975; Temple et al. 1979).

Near White River, the Red-breasted Nuthatch was significantly more abundant in mature forests than in clear-cuts 3-25 years old (Venier and Pearce 2005). In Pennsylvania, it was positively associated with old-growth forests. It occurred in 72.7% of old-growth forests compared with 4.1% of forests statewide and 6.4% of forests in the Appalachian Plateau (Haney 1999). In Alberta aspen stands, it was significantly associated with the density of coniferous species and was significantly more abundant in old-growth than in mature aspen stands. It was absent in young aspen stands (Schieck et al. 1995). In British Columbia, 76% of nesting habitats were mature stands (Campbell et al. 1997; Capen 1979; Erskine 1977; Kirk et al. 1996; Sinclair et al. 2003).

In New Hampshire and Maine, abundance of the Red-breasted Nuthatch was positively correlated with deciduous trees larger than 10 cm diameter at breast height (DBH), woody stems per ha, and total foliage volume of coniferous trees 2-10 cm DBH. It was negatively correlated with total foliage volume of deciduous trees (DeGraaf et al. 1998). In boreal forest habitat in New York, Vermont, Maine, Nova Scotia, and Newfoundland, it was positively correlated with the number of dead snags, canopy cover, and presence of deciduous trees. It occurred in a wide variety of spruce-fir habitat types (Ralston et al. 2019).

The Red-breasted Nuthatch is considered an area-sensitive species in Ontario (Coleman et al. 2000), but it requires relatively small woodlots of 10 ha or larger. In some cases, smaller woodlands may be used. Presence of suitable nest sites may be more limiting than forest size, and it may not actually be area sensitive in Ontario. It nested in a Waterloo backyard (Cheskey 1990) and a wooded area smaller than 0.5 ha in Aurora (personal observation), suggesting that it is not area sensitive in Ontario. In Minnesota, Howe (1979) observed it on 2 islands that were 0.9 and 1.1 ha in area, but did not positively confirm breeding. In Michigan, the presence of the Red-breasted Nuthatch was positively correlated with forest size (Crozier and Niemi 2003).

The Red-breasted Nuthatch is often considered a forest-interior species. In California, it showed a nonsignificant but substantial tendency for lower density close to forest edge. Density 400 m from edge was 1.71-2.64 times that at forest edge (Brand and George 2001). In Saskatchewan, it was more common in large forest fragments and in contiguous than fragmented forest. Hobson and Bayne (2000) considered it a forest-interior species. In Ontario, it is not a forest-interior species, frequently nesting along edges and near forest openings (Peck and James 1987) and even in urban yards

(Cheskey 1990). Strauss (2007) reported a Red-breasted Nuthatch nesting in a nest box on the eaves of a city residence in Victoria, British Columbia. In Newfoundland balsam fir stands, Whitaker and Montevecchi (1997, 1999) considered the Red-breasted Nuthatch a forest-interior specialist. It was significantly more abundant in forest interior than in riparian and nonriparian forest edges. In intact forests, it occurred in riparian areas 20-50 m from edge, but was absent in similarly sized buffer strips left adjacent to clear-cuts. In northeastern Quebec balsam fir–white cedar stands, there was no significant difference in its density in riparian and nonriparian stands (LaRue et al. 1995). Lindell et al. (2007) reviewed studies that examined abundance of the Red-breasted Nuthatch in relation to forest edge. One study found no response to edge; the other found that it avoided edge.

During incubation and brooding, the male and female roost together in the nest cavity. Females continue to roost overnight with the young until they fledge. Resident birds may use cavities for roosts year round (Ghalambor and Martin 2020).

The Red-breasted Nuthatch usually excavates its own nest cavity, but occasionally uses old woodpecker nests and natural cavities such as knotholes. Most Ontario nests were near the top of a dead tree stub, 3 were in dead or dying branches, and 2 were in living trees, one of which was dying. The DBH of 4 nest trees was 12.5-20.5 cm (average 15.8 cm). No preference was shown for nest orientation. It is a weak excavator, so most nests are in soft-wooded deciduous trees. Over 70% of nests were in deciduous trees, with poplar, birch, and spruce trees used most often. Nests were 1.5-15 m from the ground, with most 3-9 m up (Peck and James 1987). Cheskey (1990) reported a nest in a 20 cm diameter apple tree stump that was only 80 cm from the ground, one of the lowest ever reported. Two Ontario nests were in boxes designed for Black-capped Chickadees in white and red pine plantations near Long Point (Dunn et al. 1975).

Most nest cavities are excavated, with a few nests in old woodpecker and chickadee nests; use of nest boxes is rare. In Montana 52% of nests were in old sapsucker nests. Nest reuse is rare, but in British Columbia, 3 of 11 available old nests (27.3%) were used again. Most nests are in dead trees or dead portions of trees, but a few are in living trees and some are in posts and poles. Aspens and birches are the dominant nest trees, with lesser numbers of firs and pines and a variety of infrequently used species. The optimum DBH of nest trees has been estimated at 30 cm, but smaller trees (12.5 cm DBH) may be used and larger ones are often used. Nest heights of 0.5-36.6 m have been reported, with a mean of 10.2 m (Aitkin et al. 2002; Campbell et al. 1997; Evans and Conner 1979; Ghalambor and Martin 2020; Gunderson 1939; Leighton et al. 2002; Li and Martin 1991; Michael 1934; Sinclair et al. 2003; Tyler in Bent 1948).

The Red-breasted Nuthatch is highly aggressive early in the nesting season, particularly during excavation and nest building. During this period, any species that approaches the nest is attacked. Breeding territory sizes are variable, averaging from as small as 0.2 ha in Quebec hemlock forests to 10 ha in subalpine forests in New Hampshire. In the latter area, the large territory sizes appeared to be related to the scarcity of dead trees and suitable nesting cavities. In Algonquin Park, territory size averaged 0.49 ha (range 0.08-1.29 ha). In many areas, breeding territories are 1-3 ha, but snag density may affect territory size and breeding density. In Maine white spruce stands, mean territory size was 1.34 ha (Ghalambor and Martin 2020; Martin 1960; Morse 1977; Rail in Gauthier and Aubry 1996; Sabo 1980). No information on home range size is available.

No information is available on natal philopatry. Resident birds may maintain the same territory for years. It is not known if migratory or irruptive birds return to the same area to nest (Ghalambor and Martin 2020).

Limiting Factors

Eggs have been reported in Ontario nests from early May until mid-June, with most present from mid-May through the first week of June (Peck and James 1997). In Algonquin Park, nest cavity excavation occurs from mid-March to late May, nestlings are present from early June until early July, and dependent fledglings have been observed from early July to mid-August (Tozer 2012).

The time required to excavate a nest cavity varies depending upon hardness of the wood. Cavity excavation may take less than 5 days or as long as 18 days. As many as 4 cavities may be dug before the female selects one. Eggs are laid at the rate of 1 a day. At 1 nest, incubation began with laying of the penultimate egg; no other information is available. The incubation period at 1 Ontario nest was 13 days and it has been reported elsewhere as 12-13 days. Young left an Ontario nest at age 19 days, consistent with the overall reported range of 18-21 days. Young may leave the nest when they are as young as 15 days if the nest is disturbed (Cheskey 1990; Ghalambor and Martin 2020; Gunderson 1939; Kilham 1973; Michael 1934; Tyler in Bent 1948).

One brood is typically raised in a year. There is 1 record of a second brood in Ontario from Nipissing District; the second brood was raised in the same cavity. A pair of yearlings raised 2 broods in captivity in New Hampshire. In British Columbia, 6 pairs each raised 2 broods during years of outbreaks of the mountain pine beetle. Renesting occurs, usually in a newly excavated cavity. Clutches of 1-7 eggs have been reported in Ontario, mostly 5-6 eggs. Overall, clutches of 2-8 eggs have been reported (mean 5.8 eggs). In British Columbia, most clutches contained 6 or 7 eggs. Six-egg clutches were most common overall. During a year of high beetle abundance, some 9-egg clutches occurred (Campbell et al. 1997; Ghalambor and Martin 2020; Kilham 1973; Norris and Martin 2014; Peck and James 1987, 1997; Tyler in Bent 1948).

Both sexes first breed when they are 1 year old and birds breed every year thereafter. The mating system is monogamous. Resident birds remain mated for more than 1 year. Migratory and irruptive birds may only have seasonal pair bonds. Ontario residents may pair as early as December; nonresidents pair after spring return, usually in March and April (Ghalambor and Martin 2020; Kilham 1973).

Foraging occurs mostly in coniferous trees, primarily in live trees and less frequently in snags. The Red-breasted Nuthatch commonly forages in white cedar, balsam fir, hemlock, pine, and spruce. Most foraging was in live conifers in Oregon but live and dead trees were used according to their availability in Washington. In spring, it selected snags for foraging. Old-growth trees were selected in winter and second-growth trees were used for foraging in summer. Although foraging occurred in large-diameter trees (greater than 50 cm DBH) more than expected, smaller diameter trees (11-50 cm DBH) were used year-round. In mixed forests, foraging also occurs in deciduous trees such as poplars, basswood, beech, birches, and maples. It may use all portions of a tree for foraging, but usage of tree areas may vary seasonally. In winter, it forages significantly lower and closer to the trunk than in other seasons. Most foraging occurs on tree trunks and the upper and lower portions

of branches from their tips to the trunk. It walks up or down tree trunks and large branches and probes crevices in the bark for insects. It also forages on small branches by probing beneath flakes of bark, at bases of needle clusters on conifers, and on conifer cones where it extracts seeds. Foraging on twigs and foliage is common during the breeding season; foraging in winter is predominantly on bark of trunks and large limbs. Less commonly, it forages in leaf litter on the ground for arthropods and fallen seeds, in rocky outcrops, and on undersides of leaves. It occasionally flycatches and there is 1 record of it foraging on the back of a live white-tailed deer (Adams and Morrison 1993; Ghalambor and Martin 2020; Lundquist and Manuwal 1990; Sabo 1980; Tyler in Bent 1948; Weikel and Hayes 1999).

Nestlings are fed arthropods exclusively; young at 1 nest were fed large quantities of flying ants. Adults eat mostly arboreal arthropods in summer and large numbers of conifer seeds in autumn and winter. In Ontario in spring, it may feed on sugar maple sap icicles. In Oregon, the Red-breasted Nuthatch ate mostly weevils, leaf beetles, and other beetles during the breeding season; weevils, leaf beetles, ants, leaf bugs, earwigs, scarab and click beetles, and other insects postbreeding; and leaf beetles, weevils, sedge seeds, bark beetles, leaf bugs, and other insects during winter. It eats a wide range of beetles, but also caterpillars, spiders, ants, bugs, and flies. Its density is related to spruce budworm density in the Boreal Forest Region and northern New England. At low budworm density, it eats few budworms, but consumption increases exponentially as budworm numbers increase. In New Brunswick, there was no relationship between its abundance and budworms. During a spruce budworm outbreak in Maine, 16 stomachs contained 39% budworm larvae and pupae by volume (Crawford and Jennings 1989; Erskine 1977; Ghalambor and Martin 2020; Mitchell 1952; Morris et al. 1958; Simpson 2025; Sinclair et al. 2003; Tyler in Bent 1948). During bark beetle outbreaks in British Columbia, it excavated more new cavities instead of using existing ones, maintained a constant clutch size of about 6 eggs throughout the breeding season, and fledged as many as 100% more young than when beetles were scarce (Norris 2012). Norris and Martin (2014) studied the effects of an outbreak of the mountain pine beetle on the Red-breasted Nuthatch in British Columbia. Although this beetle does not occur in Ontario, infestations of the emerald ash borer have the potential to have the same effect. In areas and years where beetles were abundant, some second broods were produced, clutch size of replacement nests were as large as first nests instead of being smaller, and the number of fledglings produced per nest increased. Matseur et al. (2019) conducted a similar study on its response to forest disturbance by the mountain pine beetle and wildfires in South Dakota and Wyoming. Its abundance was negatively correlated with the coverage by 3-5-year-old wildfires. Densities increased as the percent cover of beetle-killed trees increased from 0% to 16%.

Brown-headed Cowbird parasitism of Red-breasted Nuthatch nests has not been reported in Ontario. There are only 2 records of parasitism in North America: one from Saskatchewan and one from Montana (Ghalambor and Martin 2020).

Logging or other factors that remove dead or diseased trees may have negative effects on breeding populations of Red-breasted Nuthatches. Results vary depending on the composition of the forest. In the Boreal Forest Region, its abundance did not change significantly when 30% or 50% of trees were removed, but it declined when 70% of trees were removed. It experienced a 25%

decrease when 50% of trees were removed, a 50% decrease when 70% of trees were removed, and a 75% decrease when 98% of trees were removed (Vanderwel et al. 2007, 2009). In the Canadian Shield of Ontario, there was no difference in its abundance in early successional and mid-successional clear-cuts compared with burns in the same seral stages. It was significantly less abundant in early successional and mid-successional stands than in mature stands (Zimmerling et al. 2017). In Algonquin Park, there was no difference in its abundance in control areas and sites where single-tree selection harvest had occurred. In California, burned coniferous forests supported vagrants only but unburned plots supported breeding pairs. In Montana, it continued to nest in areas that had been burned, but was absent in burns where salvage logging occurred. In Oregon, it decreased in response to fire but densities still remained higher in the forest that was burned than in the control forest. In New York northern hardwoods, it appeared to be unaffected by forestry operations, but it was rare overall due to the predominantly deciduous cover. In Vermont, it incorporated both logged and unlogged areas into territories. In Minnesota, it exhibited no significant response to timber harvesting in buffer strips, although its trend was positive. In Alberta, it decreased significantly in deciduous woodlands that were clear-cut and increased significantly when 25% of trees were removed in coniferous woodlands (Bock and Lynch 1970; Ghalambor and Martin 2020; Hanowski et al. 2005; Harrison et al. 2005; Hutto and Gallo 2006; Jobes et al. 2004; Lent and Capen 1995; Siegel and De Sante 2003; Stephens et al. 2015; Webb et al. 1977). In northern Ontario, Rempel et al. (2007) predicted a decline of the Red-breasted Nuthatch for all forest management scenarios: under silvicultural guidelines for replanting, tending, and harvest volume objectives; silvicultural guidelines plus application of timber management guidelines for marten, moose, caribou, and fish habitat; and silvicultural guidelines plus natural composition targets.

In Minnesota, blowdown of spruce-fir forest reduced canopy cover by 80% and increased shrub coverage by 100%. The Red-breasted Nuthatch bred in control plots, but was only a visitor to the blowdown area (Burris and Haney 2005).

In Quebec, abundance of the Red-breasted Nuthatch was not adversely affected by high densities of white-tailed deer. Its abundance was correlated with the amount of coniferous coverage (Cardinal et al. 2012).

Blewett and Marzluff (2005) studied the effects of urban sprawl on cavity-nesting birds near Seattle. Higher densities of Red-breasted Nuthatches occurred in areas with higher dispersion of land cover (more fragmented landscapes with less forest cover). Densities in built and forest areas combined were about 6 times less than those in natural woodlands. Productivity was highest where the percent of forest was low but aggregated, and where snag densities were high. Along the Michigan north shore of Lake Superior, it was significantly less abundant on cottage lots than in forest on the other side of the cottage road (Ford and Flaspohler 2010).

In Edmonton, noise was the second-most important factor in determining abundance of the Red-breasted Nuthatch. It has a low minimum song frequency that may be masked by anthropogenic noise, particularly from roads. It was less common in noisy areas (Proppe et al. 2013). In Alberta, it was significantly more abundant at quiet well pads than at noisy compressor stations. Sites distant from each of these structures supported significantly more nuthatches than sites close to them (Bayne et al. 2008). McClure et al. (2013b) created a phantom road during autumn migration

by playing traffic noise in an otherwise undisturbed forest. The Red-breasted Nuthatch declined with increasing noise activity. At 37 dB(A), 3.5 nuthatches were detected compared with less than 1 at 57 dB(A).

In Alberta, the Red-breasted Nuthatch was significantly more abundant at seismic lines than in adjacent forest interior and significantly less abundant at well pads than in adjacent forest interior (Bayne et al. 2016). There was no difference in its abundance at pipelines and adjacent forest interior.

Price (2004) concluded that the Red-breasted Nuthatch could disappear as a breeding species in southern Ontario if the average summer temperature increased by 2°C. In central Quebec and Labrador, it was strongly associated with stands having the warmest summer temperatures (DesGranges and LeBlanc 2012). This suggests that temperature increases may be beneficial near the northern extent of its breeding range.

Status

The Red-breasted Nuthatch undoubtedly bred throughout southern Ontario prior to forest clearing by European settlers. It probably was relatively uncommon in the south due to the predominance of deciduous tree cover. With forest clearing, it was locally extirpated as a breeding species in the south. McIlwraith (1894) knew of it only as a migrant in southern Ontario. In southern Quebec, populations declined after the 1850s due to extensive logging and it was a rare breeder there at the turn of the 20th century (Rail in Gauthier and Aubry 1996). In the Kingston area, there were only 3 summer records until 1968. It now breeds there regularly wherever red and white pines are common (Weir 2008). In Hamilton, the first documented nest was in 1956 and by the 1980s it was a regular breeder, predominantly in coniferous plantations (Curry 2006). Baillie and Harrington (1937) considered the Red-breasted Nuthatch a fairly common summer resident in nearly all of Ontario and certainly from Wellington, Peel and Renfrew counties north to southern Kenora District and Moose Factory. They had no records from more southerly areas of the province. Dunn et al. (1975) reported 2 nests at the St. Williams Forestry Station, and this was the southernmost breeding record for Ontario. At that time, the nearest breeding record was from Erindale from about 1950, about 130 km northeast of St. Williams. It is now a common and regular breeder in the St. Williams forest. In Elgin County, it was only a migrant in 1891 and 1954. By 2000, it was a rare breeder with records only from conifer plantations 60-70 years old (Lancaster et al. 2004). During the first atlas, it was widely distributed in the north to Attawapiskat and the Big Trout Lake area. It was well distributed in the south, but absent from many squares and all of Essex County. Breeding in Kent, Elgin, Middlesex, Huron, and Oxford counties occurred during the first atlas only in 1985 after a southward irruption (Mills in Cadman et al. 1987). James (1991) considered it an uncommon summer resident north to Big Trout Lake and Moosonee, but rare and local south of the Canadian Shield.

The second atlas indicated that the range of the Red-breasted Nuthatch was much the same as during the first atlas, except that it had become much more common and widespread south of the Canadian Shield. Its probability of observation increased significantly province-wide and in all regions. Largest increases occurred in the south, probably due to maturation of coniferous plantations. It was most abundant in the Great Lakes–St. Lawrence Forest Region in the Shield, and in the southwest portion of the Boreal Forest Region in Kenora District. Highest densities occurred

in the central and upper Ottawa valley, the Algonquin Highlands, and from the northwest shore of Lake Superior north to the Berens River and Sandy Lake (Cheskey in Cadman et al. 2007).

Long-term (1970-2021) Breeding Bird Survey data indicate annual increases of 2.1% in Canada and 2.3% in Ontario. The short-term (2011-21) trends were annual increases of 2.03% in Canada and 3.06% in Ontario. All results were of medium reliability except that the short-term Canadian trend was highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Most young are fully independent about 2 weeks after fledging, but others remain with their parents for extended periods and possibly all winter (Ghalambor and Martin 2020).

MIGRATION

The Red-breasted Nuthatch has a mixed migration strategy. Northern birds undertake regular migration and southern birds tend to be resident. All populations are irruptive and may move considerably south of their normal breeding and wintering ranges during irruption years. It is at least partially migratory in Ontario, but southern and central Ontario populations may be resident. Major irruption corridors occur at Point Pelee and along the northern shore of Lake Ontario, with birds flying south to Ohio and west toward Michigan. Significant migration movements are associated with fair weather, westerly winds, and high pressures. Movements are inhibited by adverse weather, low pressure, and fog (Ghalambor and Martin 2020).

Spring return flights are never as strong as autumn flights, but perhaps birds move on a broader front and are less concentrated. In the south, migrants appear in late April and are present until mid-May, with some stragglers remaining into early June. Timing of autumn migration varies depending on whether it is a normal migration year or an irruption year. In normal years, southward movement begins in late July or August and may continue into November. Most birds arrive south of the breeding range between the end of September and early November. Birds may appear along the southern shore of Lake Erie in Ohio as early as 20 August in a normal migration year. In Elgin County, autumn migrants arrive in late August some years, September other years, and often not until October. During irruptions, the timing of autumn migration is unpredictable, but it occurs much sooner than in normal migration years. Movement may start in early July; 1 family appeared to start southward migration the day after the young fledged. In the Kingston area, the average autumn departure date for irrupting birds is 19 October (Curry 2006; Ghalambor and Martin 2020; Lancaster et al. 2004; Weir 2008).

Irruptions of Red-breasted Nuthatches are frequent and fairly regular. Irruptive movements usually occur every other year, but may occur every 2-3 years, 2 years in a row, or with a 3-year gap. Southward invasions may coincide with irruptions of 7 other northern conifer seed-eating birds. Between 1901 and 1920 and 1951-80, there was high synchrony in the irruptions of the Red-breasted Nuthatch, Redpoll, and Pine Siskin, but no evidence of synchrony 1921-50. Invasion years are typically preceded by 1-2 years of bumper conifer seed crops, often resulting in exceptional reproductive success, followed by a collapse in seed production. In areas where Red-breasted Nuthatches do not breed, Christmas Bird Count (CBC) data show almost perfect cycles of abundance and absence. In Tennessee and Pennsylvania, cycles in peaks did not correspond to other areas and

may have been affected by local supplies of conifer seeds. Ontario CBC counts do not correspond well with irruption cycles, with peak numbers only 50% higher than lows. This is probably due to the presence of residents and migrants during normal migration years (Bock and Lepthien 1972, 1976b; Davis and Morrison 1988; Davis and Petersen 1995; Freedman and Riley 1980; Ghalambor and Martin 2020; Larson and Bock 1986; Yunick 1988).

During migration, the Red-breasted Nuthatch may occur in a variety of habitats, but it still prefers coniferous trees. In the nonbreeding seasons in British Columbia, it occurred in a diversity of habitats, but was most prevalent in older second-growth and old-growth forests dominated by conifers (Campbell et al. 1997; Ghalambor and Martin 2020). In oak savannahs in the Midwest, its abundance was correlated with tree density and was highest at tree densities of 500-600 per ha (Grundel and Pavlovic 2007b).

The Red-breasted Nuthatch begins caching food in autumn and continues throughout winter. Where it is resident, caching is probably critical to its winter survival. Most food items cached are conifer seeds, but it may cache some insects. Most caches are in crevices under bark, but occasionally in sapsucker wells, and rarely in the ground. About half of caches are covered with pieces of lichen or bark, and 1 ground cache was covered with small pebbles. In many cases, stored food is hammered into a crevice or pushed under a flake of bark. During autumn and winter in areas outside its normal range, it appears to be a short-term cacher. Food stored in the morning may be eaten in the afternoon of the same day or the next day. No information is available on how long food is stored by resident birds before it is retrieved (Dunn and Tessaglia-Hymes 1999; Ghalambor and Martin 2020; Grubb and Waite 1987; Hendricks 1995; Kilham 1974, 1975; Tyler in Bent 1948).

In autumn, the Red-breasted Nuthatch's diet consists of a mix of arthropods and seeds of conifers, but mostly conifer seeds. Seeds of pine, spruce, and hemlock are particularly favoured, as they are in winter. There is 1 record of nuthatches feeding on the entrails of a deer that had been dressed by a hunter. They may have been feeding on the tallow; suet is a favoured winter food (Ball 1945; Ghalambor and Martin 2020).

James (1991) considered the Red-breasted Nuthatch an uncommon to locally common migrant. Abundance varies considerably depending on whether or not it is an irruption year. At Prince Edward Point, none are seen during migration some years; hundreds may be seen other years (Weir 2008).

WINTER

The Red-breasted Nuthatch is associated with snow in winter. Length of the snow season is an important predictor of its presence (Keyser et al. 2022). For most populations, winter habitat is similar to breeding habitat, but a wider variety of habitats may be used. In addition to its typical habitat of coniferous and mixed woods, it may occur in deciduous forests, orchards, shrubby areas, riparian woodlands, parks, and shade trees and gardens in suburban areas. In winter, it is slightly more regular and abundant at rural than urban feeders. Data from Ontario Winter Bird-Population Studies revealed that it was associated with forests. The number of birds documented per km^2 was: 0 in farm, mixed rural, urban natural areas with open water, and city; 0.7 in urban natural areas, 1.0 in natural small urban areas, and 12.5 in forested areas. In suburban habitat in northern California, it

was positively associated with tall trees and negatively associated with roads and other human structures (Dunn and Tessaglia-Hymes 1999; Ghalambor and Martin 2020; Kalinowski and Johnson 2010; Smith 2003).

Resident pairs may maintain territories over winter. Migratory birds often join flocks of chickadees and other species and are nonterritorial. Some birds maintain winter home ranges of about 4 ha in winter, although these areas are not defended. In Ohio, where the Red-breasted Nuthatch does not breed, winter home ranges in deciduous forests were 0.9-4.5 ha. Home ranges may overlap; range overlap in Ohio for 2 males was 15%, but overlap was 50-60% for a group of 2 males and 1 female. As many as 3 male-male-female groups occurred in 1 woodlot. Some birds formed loose groups; others were solitary. Some emigrants set up home ranges and others do not, so that occasionally as many as 10 may visit a winter bird feeder. This number of nuthatches at a feeder is rare, with most northern feeders supporting a maximum of 2 birds compared with 1 in the south (Dunn and Tessaglia-Hymes 1999; Ghalambor and Martin 2020; Matthysen et al. 1992).

In winter, the Red-breasted Nuthatch relies heavily on conifer seeds and cached food, which is also predominantly conifer seeds. Northern populations rely more on cached foods than southern populations. Winter foods are mostly seeds of pine, spruce, and hemlock. It may eat insect eggs and larvae, bits of rotten apples and other fruit, sap from trees and stumps, and seeds of dock and giant ragweed as well as other weeds that extend above the snow. Feeding on hemlock seeds is affected by weather because hemlock cones open in dry, cold, and windy periods and close on warmer and more humid days. It often forages on conifer seeds that fall to the ground and this becomes more common as winter progresses (Ghalambor and Martin 2020; Kilham 1975; Tyler in Bent 1948).

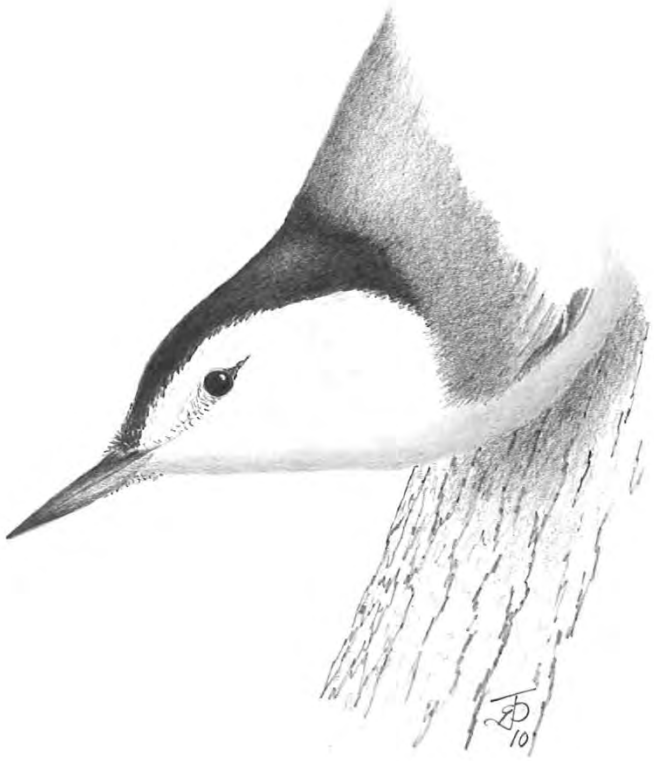
The Red-breasted Nuthatch frequently visits winter bird feeders, but the percentage of feeders visited declines steadily throughout winter. Frequently consumed feeder foods include suet, sunflowers, hulled peanuts and hearts, peanut butter mixes, and bird puddings. Infrequently consumed foods include mixed seeds, safflower, corn, niger, peanuts in the shell, meat scraps, baked goods, water, and oats (Dunn and Tessaglia-Hymes 1999). Participants in Canada and the United States recorded 7,258 Red-breasted Nuthatch foraging bouts. It preferred black oil sunflowers, 0.3-mm and 0.5-mm sunflower chips, and platform feeders (Horn et al. 2014).

James (1991) considered the Red-breasted Nuthatch rare to locally common in winter in the south, and occasional and rare in the north to Thunder Bay and Manitouwadge.

CBC data for Ontario indicate that the Red-breasted Nuthatch increased at annual rates of 5.03% 1970-2021 and 2.82% 2009-21 (National Audubon Society 2022).

White-breasted Nuthatch

Sitta carolinensis



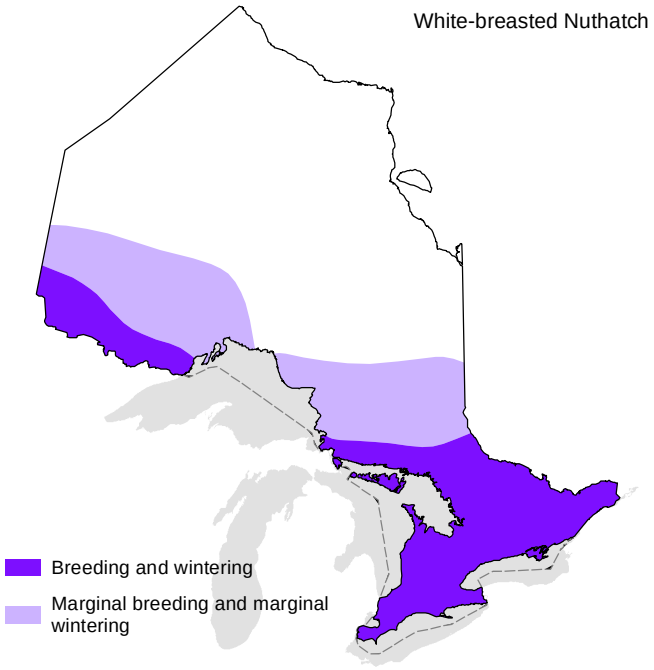
BREEDING SEASON

Habitat Requirements

In Ontario, the White-breasted Nuthatch nests mostly in mature deciduous woodlands, less frequently in mixed woods, and rarely in coniferous stands and residential areas. Forest edges are greatly preferred over interior. Most nests are near open areas such as watercourses or water bodies, roads, clearings, and fields (Peck and James 1987).

In eastern boreal forests, Erskine (1977) considered the White-breasted Nuthatch characteristic of transitional sugar maple–beech forests, but sometimes extending far into the Boreal Forest Region in mixed or deciduous habitats. Highest densities occurred in sugar maple or white ash stands, with low densities in poplar and birch stands. It was characteristic of deciduous forests in Algonquin Park. It occurred in hardwood stands but was absent in wet and dry bogs; coniferous forests dominated by pure or mixed stands of black spruce, white cedar, balsam fir, and hemlock; and birch-poplar stands and birch-poplar stands mixed with conifers (Martin 1960). In Durham Region, Speirs and Orenstein (1975) considered it a late-succession species. It was most abundant in mature beech–sugar maple and sugar maple–oak stands followed by a sugar maple–riparian area

of conifers, sugar maple and cedar-elm swamp, and a deciduous stand heavily damaged by a hurricane.



In the east, the White-breasted Nuthatch breeds most frequently in deciduous and mixed stands and is rare to uncommon in coniferous stands. In the west, it may be common in coniferous forests. In the western Boreal Forest Region, it was mostly associated with mesic mixed or deciduous forests and was absent in black spruce and species-poor jack pine stands (Kirk et al. 1996). In British Columbia, 78% of breeding records were from open but fairly contiguous forests, 20% were from human-influenced forests, and 2% from grasslands with scattered trees. In California, it was significantly more abundant in oak savannahs with grass and in montane hardwoods than in savannahs with shrubs. Its abundance in oak woodlands was intermediate between these habitat types. In eastern northern hardwoods, it was found on 90% of plots in mature, undisturbed habitats and 17% of plots in disturbed and successional areas. There are occasional records of it nesting in suburban areas throughout its range. It appeared to reach its highest densities in mesic stands and was least abundant in xeric stands in Wisconsin. Most authors concur that the White-breasted Nuthatch is usually associated with mature forest. In Quebec, clear-cuts in mixed or coniferous forest regenerating to hardwoods provided suitable habitat as did regenerating old fields. In Pennsylvania, it was negatively associated with old-growth forests. It occurred in 54.5% of old-growth forests compared with 82.8% of forests statewide, and 84.0% of forests on the Appalachian Plateau (Bancroft 1987; Beals 1960; Bent 1948; Bond 1960; Campbell et al. 1977; Capen 1979; Duyck and McNair 1991; Faanes and Andrew 1983; Haney 1999; Lanoue and Rail in Gauthier and Aubry 1996; McEllin 1979; Noon et al. 1979; Samson 1979; Temple et al. 1979; Wood et al. 2013).

At the landscape level, the White-breasted Nuthatch preferred areas that were 59-75% forested in North Dakota and 58-82% forested in New York. There were no areas with greater than 75% forest cover in North Dakota (Cunningham and Johnson 2019). In North Dakota 400-m landscapes, it increased with increasing tree cover within 100 m in landscapes with less than 30% tree cover, but its probability of occurrence declined when tree coverage exceeded 60% in landscapes with more than 30% tree cover. In wooded areas, it selected more edge-rich sites than in open landscapes (Cunningham and Johnson 2016).

Some information is available on microhabitat preferences of the White-breasted Nuthatch. In Tennessee, the most important habitat variables were related to understorey biomass (foliage, branch, and bole biomass of trees 1.2-8.4 cm diameter at breast height [DBH]) and the number and

size of trees in the lowest woody vegetation layer. It was present where there was lower biomass in the understorey layer and smaller than average understorey tree sizes (Anderson and Shugart 1974). In Michigan riparian swamps, it was most common in swamps closest to a river, with densities declining further from the river, and even fewer in upland forest beyond the riparian swamp (Inman et al. 2002). In Tennessee, there were more territories within 268 m of edge than 268-488 m from edge, but the difference was not significant (Kroodsma 1984). In Maryland, its presence was positively correlated with tree height (Lynch 1987). In Iowa, it was positively associated with sapling and tree richness and presence of deciduous trees (Stauffer and Best 1980). In the mid-Atlantic states, it was positively associated with forest area, number of trees, forest slope, and canopy height, and negatively associated with the percentage of forest cover within 2 km, the number of trees larger than 3 cm DBH, and the percent canopy cover by coniferous trees. Robbins et al. (1989) concluded that it was most likely to occur in greatly isolated and moderately isolated forests. In Vermont, it was associated with mid-successional habitats, increasing coverage by deciduous species, moderate density of dead trees, moderate amounts of poplar and white pine, low amounts of red maple, and abundant hophornbeam, sugar maple, and beech (Lent and Capen 1995).

The White-breasted Nuthatch was considered an area-sensitive species by some authors. In the mid-Atlantic states, it reached its maximum probability of detection in 300-ha forests. The size of forest at which detection decreased by 50% was 3.0 ha. The 3 smallest forests where it was detected on 2 or more visits were 4.2, 3.0, and 1.6 ha (Robbins et al. 1989). Blake and Karr (1987) considered it area sensitive in Illinois because its presence was positively associated with woodlot size, but gave no minimum forest size for it. In Missouri, Hayden et al. (1985) concluded that it required woodlands a minimum of 2.2 ha, but it reached 100% occurrence in forests 42-54 ha in size. Minimum size requirements were estimated at 4.7 ha in Illinois and 2.0 ha in New Jersey. Stauffer and Best (1980) concluded that it was restricted by patch size in Iowa and found that the minimum plot width for occurrence in riparian areas was 17 m. In Ontario, the White-breasted Nuthatch is occasionally considered an area-sensitive species requiring woodlots a minimum of 10 ha in area (Coleman et al. 2000). In southern Ontario, Austen et al. (2001) determined that the probability of observation of the White-breasted Nuthatch was negatively correlated with amount of forest 100 m or more from edge, amount of forest within 2 km, and amount of regional forest. It was negatively correlated with forest size. These relationships were not significant. Keller and Yahner (2007) found no relationship between forest size and its presence in Pennsylvania. In South Dakota, Gentry et al. (2006) found that its density was significantly lower in small (0.7-3.5 ha) isolated woodlots than in large riparian woodlands. It is likely that many of these woodlots were smaller than the typical territory size of this species. The White-breasted Nuthatch has a relatively large territory size and it seems unlikely that it is truly area sensitive. Its scarcity in woodlands smaller than 10 ha may simply be because these woodlands are smaller than the area required for a territory. In Ontario, it occasionally nests in isolated trees in non-forested areas (personal observation) and residential areas (Peck and James 1987).

Roosts are an important habitat component of the White-breasted Nuthatch. It uses roosts year-round, but they are most critical in winter. Winter roosts are frequently cavities excavated by Downy Woodpeckers. Roosts used throughout the winter by males may ultimately be taken over by the

female and used as the nest cavity. Nuthatches appear to prefer holes that are 2-3 times the size of their bodies for roosting. Although most roost in cavities in dead stubs, one roosted in a curl of bark hanging from a high, dead maple limb. Roosts are 2-12 m from the ground (Kilham 1971; Tyler 1916).

One pair of nuthatches was observed excavating or enlarging a cavity, but all other Ontario nests were in existing cavities, predominantly in trees. Two were in tree stumps and 4 were in bird boxes. Natural cavities were greatly preferred (87.1% of nests) to cavities previously constructed by woodpeckers or other species. Most nests were in living trees and, except for 2 nests in branch cavities, all were in trunks of trees. The DBH of 3 nest trees was 25.5-35.5 cm. Natural-cavity nests were in splits and knotholes and faced in random directions. Nests were occasionally used in successive or subsequent years. Eight-five percent of nests were in deciduous trees of 10 species compared with 2 species of conifers. The most frequently chosen nest trees were maples (18 nests), oaks (11), elms (7), and pines (5). Nests were 0.5-20 m from the ground, with most 1.8-9.0 m up (Peck and James 1987, 1997).

Most authors consider the White-breasted Nuthatch a secondary cavity nester, relying on natural cavities and old woodpecker holes for nest sites. In British Columbia, it is considered a primary excavator and has been observed excavating nest cavities elsewhere. In some areas, particularly the west, it readily uses nest boxes; usage of nest boxes in the east is less frequent. Most Ontario nests were in living trees, but use of snags and dead and living trees is variable elsewhere. In some areas, most nests are in snags; in others they are mostly in live trees or live portions of trees that are predominantly dead. Usage of type of tree is probably more dependent on availability of suitable nesting cavities rather than whether the tree is alive. Tree species used for nesting include elms, black cherry, pines, silver maple, hackberry, black walnut, aspens, oaks, and apple. Nest tree species may be defined by cavity availability; aspens were actively selected in an Arizona study area. One common characteristic of nuthatch nests is that they tend to be fairly low and in the main trunk of a tree. In Colorado, most nest entrances were immediately above a large branch and all entrances faced southward, away from the prevailing wind. Natural cavities appear to be preferred over woodpecker holes, with a high percentage of nests in knotholes where a dead branch has fallen off or in a cavity created by a lightning strike. The White-breasted Nuthatch has been known to evict chickadees from their nest and then use it. Most nests are 3-9 m from the ground. A wide range of tree sizes is used for nesting, with a minimum DBH of 25-30 cm. Abundance of nests appears unrelated to snag availability in most areas and, in Missouri, nests are highly correlated with increasing size and soundness of the nest tree (Bancroft 1987; Bent 1948; Bock and Fleck 1995; Brawn et al. 1984; Campbell et al. 1997; Cunningham et al. 1980; Duyck and McNair 1991; Evans and Conner 1979; Grubb and Pravosudov 2020; Lanoue and Rail in Gauthier and Aubry 1996; Li and Martin 1991; McEllin 1979; Rand 1972; Stauffer and Best 1980, 1982).

The White-breasted Nuthatch is territorial year-round, although boundaries of the winter and breeding territories may not be the same. Breeding occurs within the winter territory, but often at its edge. Evans and Conner (1979) reported a territory size of 0.8 ha, which is probably an underestimate. In New York, pairs nesting in wooded habitat had territories averaging 9.7 ha and in New Hampshire most territories were approximately 15 ha. In semi-wooded areas, territories may be as large as 20 ha. Certain density estimates and size of woodlands that it has been reported

breeding in suggest that territories may occasionally be as small as 3-5 ha. Territory size is probably determined by the amount of forest cover and the availability of suitable cavities for nesting (Butts 1931b; Grubb and Pravosudov 2020; Kilham 1972, 1981).

Nothing is known about natal philopatry, but it may be almost zero. Young leave their parents and the natal territory in July. In New York, young spent the winter near a feeder 0.8 km from their natal territory, but disappeared prior to the next breeding season. Adult site fidelity is extremely high. Once an adult breeds, it maintains the same territory for the rest of its life (Butts 1931b; Grubb and Pravosudov 2020).

Limiting Factors

Eggs have been reported in Ontario nests from the last week of April until the end of May, with most present in the first half of May (Peck and James 1987). In Algonquin Park, nests are under construction from early to mid-May, eggs are present in mid-May, nestlings are present from mid-May to late June, and dependent fledglings have been observed from mid-June to late July (Tozer 2012).

Nest building may continue a few days after the first egg is laid. Eggs are laid at the rate of 1 a day. The incubation period is 12-15 days. The nestling period is 21-26 days, and adults continue to feed the young for about 2 weeks after they fledge (Bent 1948; Butts 1931b; Duyck and McNair 1991; Grubb and Pravosudov 2020).

One brood is raised annually. Renesting usually does not occur after clutch loss, but there is 1 record of renesting from North Carolina. Ontario egg dates suggest that renesting does not occur, or is rare. Clutches of 5-8 eggs have been reported in Ontario, with most containing 6-8 eggs. Overall, clutch sizes of 5-10 eggs have been reported, but 6-9-egg clutches are typical with 8 eggs most frequent. Clutches may be smaller in the west, with most British Columbia nests containing 5-7 eggs. The average clutch size in North America was estimated at 7.3 eggs. The North Carolina pair that renested had an initial clutch of 7 eggs and a replacement clutch of 6 eggs (Bent 1948; Campbell et al. 1997; Duyck and McNair 1991; Grubb and Pravosudov 2020).

The age at first breeding is 1 year and birds apparently breed every year thereafter. The mating system is monogamous, and the pair bond is usually for as long as both birds remain alive. Due to the high mortality rate, only a few pairs remain mated for even 2 years. When a bird disappears, the survivor remains in the territory until a new mate shows up, regardless of the sex of the survivor. New mates usually appear within a week. In 1 pair, the male disappeared early in the breeding season and was replaced, and the new male nested with the female. The female disappeared during incubation and was replaced by a second female. This new pair nested together the following year (Bent 1948; Butts 1931b; Grubb and Pravosudov 2020; Kilham 1972).

Both members of a pair usually forage close together. The White-breasted Nuthatch typically forages on the bark of trees, either by moving upward on trunks or, more often, head-first downward. It chips the bark away with its beak to uncover food hidden in crevices. In a laboratory study, nuthatches were supplied with branches 0.5, 1.0, 2.5, 5.0, 10, and 20 cm in diameter. Branches 20 cm in diameter were used significantly more than expected; branches 1.0 cm in diameter and smaller were avoided. Males preferred to forage on the bottoms of branches; females preferred the

sides. In Ohio, no differences in foraging preferences of the sexes were evident. Both sexes relied on tree trunks and major limbs for foraging with the mean branch or trunk diameter used by males being 13.0 cm compared with 11.0 cm for females. Each bird in the pair mimicked their partner's foraging behaviour. As 1 bird moved higher, used larger branches, or branched further out from the trunk, so did the other. Birds started foraging high up in trees in the morning, descended toward midday, often searching the leaf litter for beechnuts, and moved up into the canopy again in late afternoon. In ponderosa pine forests in Colorado, there were significant differences in foraging behaviours between the sexes. Females foraged significantly higher (7.7 m) than males (2.8 m) with females foraging mostly on limbs and males feeding predominantly on trunks. Ground foraging may occur regularly, particularly if there is an abundant food source available. In Algonquin Park, foraging occurred from the ground to a height of 10 m; canopy height was 30 m. In Vermont, 55% of foraging was by gleaning, 43% by hammering, and 2% by hanging. Substrates used were 2% foliage, 40% branches, 56% trunks, and 2% twigs. Nuthatches rarely hawk for insects (Bent 1948; Brackbill 1950b; Grubb 1982; Grubb and Pravosudov 2020; Lent and Capen 1995; Martin 1960; Pierce and Grubb 1981).

The food brought to nestlings consists predominantly of invertebrates such as miscellaneous winged insects, caterpillars, grubs, moths, and spiders. During the breeding season, the White-breasted Nuthatch feeds almost exclusively on invertebrates, although it may drink from sapsucker wells in spring. The proportion of seeds in the diet has been estimated at 48% in spring, 0% in summer, 29% in autumn, and 68% in winter. During the breeding season, it feeds on stink bugs, beetles (weevils, and leaf, click, and metallic wood-boring beetles), earwigs, flying and wingless ants, book lice, adult and larval moths, spiders, millipedes, treehoppers, jumping plant lice, scale insects, gall midge larvae, aphid eggs, fall cankerworm eggs, and gypsy moth and forest tent caterpillars. One removed an egg from a Blue-gray Gnatcatcher nest and flew away with it. About 2 minutes later, it returned and took a second egg (Bancroft 1987; Bent 1948; Brackbill 1950b; Butts 1931b; Coggins 2002; Duyck and McNair 1991; Grubb and Pravosudov 2020; Lanoue and Rail in Gauthier and Aubry 1996). In New Brunswick, it did not exhibit any increase in populations associated with increasing numbers of spruce budworms (Morris et al. 1958).

White-breasted Nuthatch nests are rarely parasitized by the Brown-headed Cowbird. One of 26 Ontario nests (3.8%) was parasitized. No parasitized nests have been found in British Columbia. Parasitism has been documented in Illinois, but there are no records of any cowbirds being fledged (Campbell et al. 1997; Grubb and Pravosudov 2020; Lowther 1997; Peck and James 1997). Bent (1948) knew of only 4 cases of parasitism.

Extensive breeding habitat for the White-breasted Nuthatch was undoubtedly lost when European settlers cleared southern Ontario forests. It is still vulnerable to forest clearing and habitat fragmentation, with many residual woodlots being too small to support a pair. Some habitat is being regained as abandoned farmland evolves into forest.

The response of the White-breasted Nuthatch to timber harvesting and fire varies depending upon the intensity of the treatment. In the Boreal Forest Region, with special reference to Ontario, Vanderwel et al. (2009) reported no change in its abundance when 30, 50, or 70% of trees were removed. In the Carolinian Forest Region of Ontario, Holmes et al. (2004) found no significant

differences in its abundance in woodlots with no recent harvesting history and those where selection thinning and diameter-limit cuts had occurred. In New York, there were no differences in its abundance between control forests and forests where 25%, 50%, 75%, or 100% of merchantable trees were removed. These forestry practices left young trees and older trees with no value and are not comparable to clear-cuts (Webb et al. 1977). In Minnesota, it exhibited no significant response to tree removal in riparian strips along small watercourses (Hanowski et al. 2002). In Pennsylvania, it was significantly more common in cuts where snags were retained than in areas where snags were removed (Stribling et al. 1990). In the California Sierra Nevada, it occurred in both burned and unburned forest and was more abundant in the burned area. In the burn, it nested in burned stubs but foraged mostly in live trees that had been spared by fire (Bock and Lynch 1970). It is likely that nuthatch abundance would decline in burns where most trees were killed. In the Midwest, its density was highest where the frequency of fire was 0 within a 15-year period. It disappeared once the frequency of fires within 15 years reached 6 (Grundel and Pavlovic 2007b). In Montana, it was absent in burns where salvage logging occurred, but was present in unlogged burns; the difference in abundance was significant (Hutto and Gallo 2006). Fires or timber harvesting that remove a high proportion of snags and most of the canopy are detrimental to the White-breasted Nuthatch.

In North Carolina, the White-breasted Nuthatch increased in abundance with increasing numbers of houses and buildings within 200 m of the centre of the forest stand, but not significantly (Lumpkin and Pearson 2013).

In New Jersey and Pennsylvania over a 15-year period, hemlock declined from 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The White-breasted Nuthatch responded favourably to hemlock decline, possibly due to the increased prevalence of snags (Toenies et al. 2018).

Price (2004) predicted that the range of the White-breasted Nuthatch would contract in southern Ontario if the average summer temperature increased by 2°C. In Quebec, DesGranges and Morneau (2010) concluded that it was not very sensitive to climate change.

Status

McIlwraith (1894) considered the White-breasted Nuthatch a common resident. Baillie and Harrington (1937) reported it as a fairly common resident north to at least Temagami and Sudbury and had 1 record from the Lake of the Woods area. They concluded that it was much more common in the southern part of its range, becoming uncommon north of Parry Sound District and Ottawa. Mills (1981) stated that it reached the northern limit of its range in Muskoka and Parry Sound districts, becoming uncommon in the latitude of Lake Nipissing. During the first atlas, it was widespread in southern Ontario except for in Essex and Chatham-Kent, but was sparse in distribution in the Algonquin Highlands and south of Lake Nipissing. It occurred further north near Sudbury, Temagami, Sault Ste. Marie, Thunder Bay, and in the Kenora area (Mills in Cadman et al. 1987). Weir (2008) reported no change in status in the Kingston area since the 19th century, where it remains a common breeder and permanent resident. James (1991) considered the White-breasted Nuthatch an uncommon permanent resident in the south and occasional and rare in the north to Kenora, Thunder Bay, and Timiskaming District.

The second atlas indicated that the White-breasted Nuthatch had increased in abundance and extended its range somewhat since the first atlas. Its probability of observation increased significantly province-wide and in the Great Lakes–St. Lawrence Forest Region. The increase in the Boreal Forest Region was not statistically significant. There was a nonsignificant decline in the Carolinian Forest Region. Its range extended further north in northwestern Ontario and around Lake Nipigon. The greatest increase was in the southern Canadian Shield from Algonquin Park to Sault Ste. Marie, possibly due to increases in deciduous forest and canopy cover in this area. It also became more widespread in Essex County. It was most abundant in a wide band along the southern edge of the Canadian Shield from Kingston and Ottawa west to Georgian Bay (Bavrlic in Cadman et al. 2007).

Breeding Bird Survey data indicate annual increases of 1.76% in Canada and 1.65% in Ontario for 1970-2021. For 2011-21, there were annual increases of 0.417% in Canada and 0.428% in Ontario. The long-term trend for Ontario and the short-term trend for Canada were highly reliable; the other estimates were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

During the postbreeding period in Michigan, 60% of birds, including 75% of juveniles, were found in mature upland trembling aspen stands; 40% of birds and 25% of juveniles were found in riparian habitat that was a mix of alder, honeysuckle, and aspen (Akresh et al. 2009).

AUTUMN

The White-breasted Nuthatch is a predominantly permanent resident, with most birds remaining on their first breeding territory for the remainder of their lives. Birds may be found at the northern extreme of the range every winter. A 3-year study at Ithaca, New York, found no evidence of migration. The number of birds present remained the same and in most cases it was known that they were the same individuals. Over the course of the study, 3 birds were recorded only once, and these may have been migrants or wanderers without a territory. Portions of western and northern populations occasionally are irruptive. In Pennsylvania, 300 passed by a hawk watch in autumn 1968 compared with a total of 53 the 7 previous years. Irruptions may be very localized, with few birds observed in other areas near concentration sites. No information is available on the age of irrupting birds but it is possible that they are predominantly juveniles. There is little evidence of a return spring flight so it is unknown if wanderers breed near their natal area or elsewhere. At Point Pelee, numbers are small, with migrants arriving irregularly from the end of August until mid-September. Southern Ontario Christmas Bird Counts (CBC) indicated irregular cycles of abundance, with major irruptions in 1930 and 1961 and smaller numbers in 1937, 1942, and 1969. Rare irruptions have been documented in the Hamilton area between mid-September and 20 October. Numbers involved were typically 30-50, but there are 2 records of about 150 birds, 1 of 234 birds, and 1 of 275. Irruption years were 1966, 1968, 1975, 1977, 1989, and 1999. At Prince Edward Point, the White-breasted Nuthatch exhibited regular migration in spring and autumn in 1971 and 1972, with daily maxima of 10 in spring and 25 in autumn. The reasons for these irruptions are unknown. Data from Long Point Bird Observatory suggest occasional autumn irruptions and return movements in spring. A review of New York CBCs from 1960 to 1980 showed that there was little synchrony in the irruptions of the 2 nuthatch species. An analysis of CBCs over a more widespread area from 1931 to 1981 found that

the irruption patterns of White-breasted and Red-breasted nuthatches were similar. Until 1944, the fluctuations were irregular; from 1950 to 1964 there were 2 peaks at 3-year intervals and 4 peaks at 2-year intervals; the fluctuations became irregular again after 1970. From 1950 to 1955, the dates of high and low counts for White-breasted Nuthatch were close to those of the Red-breasted Nuthatch, and they were identical 1955-65 (Bent 1948; Brewer et al. 2018; Butts 1931b; Curry 2006; Davis and Morrison 1988; Freedman and Riley 1980; Grubb and Pravosudov 2020; Mills 1981; Weir 2008; Yunick 1988).

Autumn habitat is similar to that of the breeding season, although residents may shift their home ranges to include more open areas than those used during the breeding season. The White-breasted Nuthatch may appear in suburban areas or at rural residential lots, particularly if a feeder is available. In Pennsylvania, it was most abundant in forest interior, forest edge, and suburban forests followed by forest-agricultural edges and shrub-sapling stage forest. It was not observed in pole-stage forests (Rodewald and Brittingham 2002). During the nonbreeding season in British Columbia, it typically occurs in forested habitats, but may also be present in orchards, urban gardens, and where there are bird feeders (Campbell et al. 1997).

In autumn, the White-breasted Nuthatch maintains a territory that is retained throughout the winter. The nonbreeding territory is often a bit larger than the breeding territory and is in the same general area. Breeding and nonbreeding territories may be the same, but usually they are in slightly different locations with some overlap. Some authors stated that the autumn-winter territory was actively defended. Others stated that territories were not defended but that pairs had mutual respect for each other's territories. Occasionally territories overlap. Both members of a pair usually travel together within the territory but they occasionally split up. Members of a pair have been seen as far as 1 km apart. The territory and home range are often the same during autumn and winter, but birds may occasionally leave the territory to visit a distant feeder or other plentiful food source. The size of nonbreeding territories is variable and was only 2.9 ha in Ohio. In New York, 31 pairs had an average territory size of 19.4 ha. Where territories were entirely forested, they were 10.1-11.3 ha. Birds inhabiting territories that were only partially forested ranged over about 20 ha. In addition to territorial birds, there appear to be single birds without established territories that may range over a wider area (Bent 1948; Butts 1931b; Grubb 1982; Grubb and Pravosudov 2020; Tyler 1916).

Autumn and winter foraging techniques are similar to those used during the breeding season. During the nonbreeding season, nuthatches may forage in flocks led by chickadees and titmice. Nuthatches often follow other birds and supplant them from food sources. As a flock moves along, nuthatches drop out of the flock at the edge of their territory and are replaced by nuthatches in the adjoining territory (Grubb and Pravosudov 2020).

The diet changes in autumn with less reliance on invertebrates and greater consumption of mast. The winter diet is similar to that of autumn, but with more mast consumed as fruit and invertebrates become scarcer. Autumn and winter diet includes lesser amounts of animal foods (orthopterans, bugs, beetles, caterpillars, hymenopterans, and spiders) and more soft and hard mast (corn, cherry pits, sunflowers, hawthorns, wheat, grapes, beechnuts, acorns, hickory nuts, and walnuts). By winter, almost all food consists of hard mast but nuthatches also eat pine and hemlock seeds (Bent 1948; Grubb and Pravosudov 2020; Lanoue and Rail in Gauthier and Aubry 1996; Root

1988; Tyler 1916). It prefers acorns of pin oak and white oak over those of black oak. Black oak acorns have harder shells and it may have difficulty cracking them (Richardson et al. 2013).

During autumn and winter, the White-breasted Nuthatch is a scatter hoarder, storing food 10-100 m from where it is obtained, but mostly within 30 m. Food items are taken singly and stored individually. Virtually all caches are in trees where they are wedged under bark or into a furrow or crack in the bark. In Ohio and Arkansas, 69% of caches were on tree trunks larger than 8 cm DBH and 30% were on branches. Food was cached on the bottom of branches more than expected. No compass orientations were selected for caches on tree trunks. Eighty-one percent of caches were in the inner portions of trees, 12% in the middle, and 5% in outer portions. Forty percent were in a furrow or crack, 57% under bark, and the remainder at the end of a branch or in a bud, between 2 branches, or on a leaf. Males usually store food on the trunk of a tree but females may use a variety of sites for caching. Only 6-7% of caches were in trees with a DBH less than 15 cm, 10% in 15-23 cm DBH, 12% in 23-38 cm DBH, 20% in 38-53 cm DBH, and more than 30% in trees larger than 53 cm DBH. Caches averaged 8.0 m above ground (range 1-23 m). Caches are covered with bark or rotted wood (81%), lichens (15%), snow (3%), or moss (1%; Bent 1948; Grubb and Provosudov 2020; Kilham 1974; Petit et al. 1989).

In the United States, the White-breasted Nuthatch was among the most vulnerable species for striking residences 1-3 stories tall; it was 25.0 times more likely to suffer a collision than birds on average. It was not on the lists of the 20 most vulnerable species for striking low-rises or high-rises (Loss et al. 2014).

WINTER

Cold winter weather may affect White-breasted Nuthatch foraging strategies. In Ohio, the height at which it foraged was not significantly related to temperature or wind, but the distance that birds occurred from the windward side of woodlots was. It appeared to be wind sensitive when the temperature dropped below –6°C. On more than 62% of winter visits, it foraged only in the leeward half of woodlots, suggesting the potential for food depletion over winter. In other areas during cold and windy weather, it foraged significantly lower and on larger branches, used less exposed portions of the home range, and spent more time stationary (Dolby and Grubb 1999; Grubb 1982; Grubb and Pravosudov 2020). In New Jersey, it continued to be most common in oak woods even during cold, snowy weather, even though this cover type provided less shelter than some other habitats. It may have continued to use oak stands during adverse weather due to its high dependence on acorns for food (Brush 1989). In Missouri, temperature had a positive effect on its detection probability; wind had a negative effect. Its density increased 17% over the range of stocking from savannah to woodland to forest. It was essentially equally abundant at all levels of tree stocking (Kendrick and Thompson 2013).

Williams and Batzli (1979) examined the contents of 20 stomachs collected in winter in Illinois. The diet was comprised of 71.8% vegetable matter and 28.2% animal matter. The vegetation eaten consisted of 49.7% corn, 6.6% mast (mostly acorns), 5.7% wheat, 5.5% sunflowers, 3.8% unknown, 0.3% hawthorn, and 0.1% each grapes and other. The animal food included 7.2% adult hymenopterans, 6.5% adult beetles, 3.3% unknown, 3.3% bugs, 2.9% orthopterans, 2.7% caterpillars, 1.1% hymenopteran larvae, 1.0% spiders, and 0.2% other. The authors considered the White-

breasted Nuthatch moderately specialized in its winter diet. In New Jersey pine barrens, wintering birds were partly granivorous and ate acorns but not pine seeds. They were restricted to habitat with acorns and were common only in areas of tall oaks (oak and oak-pine forests); pine swamps and cedar swamps were not used (Brush 1989).

The White-breasted Nuthatch is a regular visitor to winter bird feeders, but the number using feeders declines as winter progresses. In some areas, it appears to prefer natural foods to feeders, but in other areas access to feeders improves the nutritional condition of birds. In Pennsylvania, feeders were provided at heights of 2, 4, and 6 m. Nuthatches foraged on 40.3% of visits at 6 m, 32.1% at 4 m, 27.6% at 2 m, and 0% on the ground. It was the only species that did not forage on the ground (although this often occurs elsewhere). Food taken consisted of 63.2% sunflowers, 35.3% corn, and 1.5% niger seed. No canary seed or millet was taken. According to Project FeederWatch, favourite foods at feeders were suet, sunflowers of any type, hulled peanuts or hearts, peanut butter mixes, and bird puddings. Infrequently taken foods included mixed seed, safflower, whole or cracked corn, niger, peanuts in the shell, meat scraps, baked goods, water, and oats (Bent 1948; Butts 1931b; Dunn and Tessaglia-Hymes 1999; Grubb and Pravosudov 2020; Nastase and Linville 1995). A total of 17,581 observations of White-breasted Nuthatch feedings were made by participants in Canada and the United States. It preferred black oil sunflowers, medium-sized (0.5 mm) sunflower chips, striped sunflowers, and whole peanuts. Tube and platform feeders were preferred over hopper feeders (Horn et al. 2014).

Forest fragmentation affected wintering White-breasted Nuthatches in Alberta and Quebec. They were unwilling to cross wide gaps (200 m) and presence of narrow hedgerows did not facilitate their movement among forest patches (St. Clair et al. 1998).

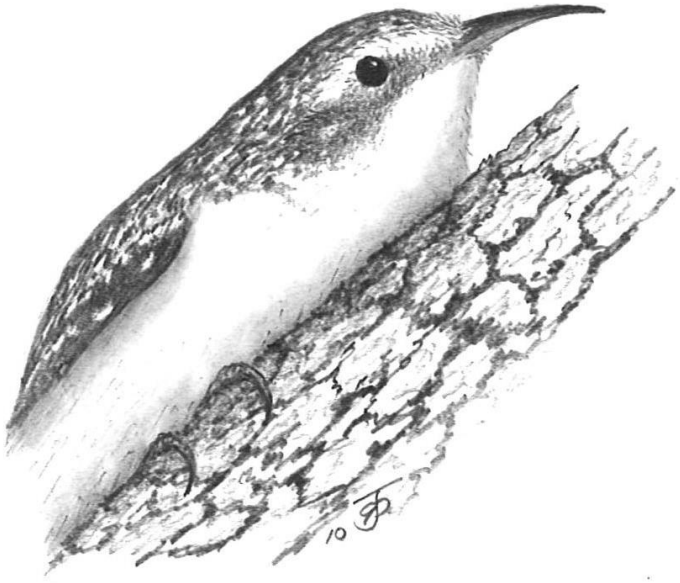
Severe winter weather may result in direct mortality of the White-breasted Nuthatch. In New Hampshire, populations declined sharply between the summers of 1969 and 1970. Holmes and Sturges (1975) attributed this to severe weather in the intervening winter and early spring. In Pennsylvania, Overlease and Overlease (1987) correlated local population fluctuations with severe weather and suggested that it was vulnerable to depth and length of snow cover, especially when accompanied by cold weather. In Illinois, Graber and Graber (1979) found no evidence of mortality after a particularly severe and prolonged winter storm. There was no overall change in density of birds, but many apparently moved from bottomland forests to upland forests.

Invasion by the emerald ash borer is having a positive effect on the White-breasted Nuthatch. The larvae of this beetle provide an abundant food source and the dead ash trees they leave behind supply potential nesting cavities (Bonter 2013; John 2013).

Southern Ontario CBCs indicated a significant increase from 1929 to 1977 (Freedman and Riley 1980). CBC data for Ontario indicate that the White-breasted Nuthatch increased at annual rates of 1.73% 1970-2021 and 3.84% 2009-21 (National Audubon Society 2022).

Brown Creeper

Certhia americana

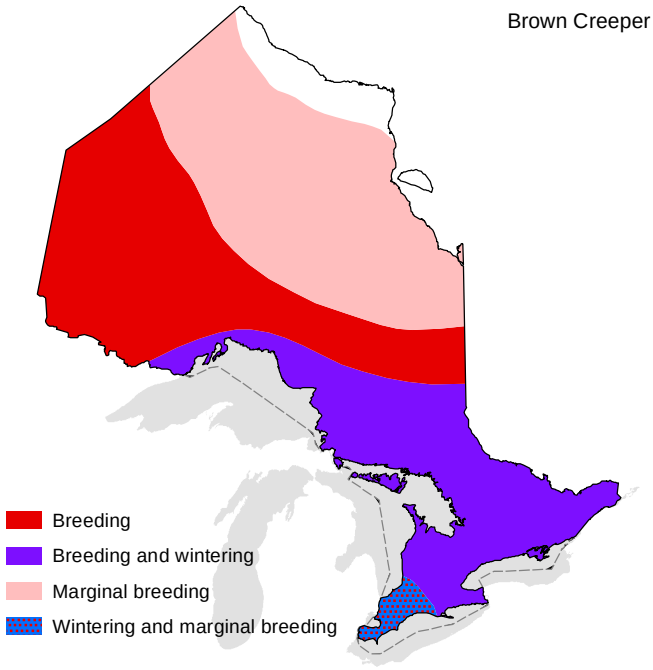


BREEDING SEASON

Habitat Requirements

In Ontario, the Brown Creeper breeds mostly in forests (72.5% of nests), including 33.3% in mixed woods, 25.4% in deciduous forests, and 13.7% in coniferous forests. Other habitats where nests occurred were beaver ponds with standing dead trees (15.7%), spruce bogs (7.8%), and edges of shrubby fields (3.9%). Most nests were found in wet rather than dry habitats which may be a reflection of the greater abundance of dead trees in wet areas (Peck and James 1987).

In the Boreal Forest Region of Ontario, the Brown Creeper was associated with older, closed, mixed-wood forests with little interspersion of young and old forest and a greater proportion of intact forest older than 80 years. It was not significantly correlated with average stand age, the percentage of hardwoods in stands, the amount of edge, or the percentage of total forest that was more than 80 years old (Rempel 2007; Rempel et al. 2007). Erskine (1977) considered it one of the most typical boreal species, characteristic of black spruce stands. In the Boreal Forest Region in western Canada, it was associated with dry, moderately rich, older, conifer-dominated stands. Kirk et al. (1996) considered it an old-forest species. In the Ontario portion of the Clay Belt, it was associated with mesic to wet stands with moderate to rich nutrient levels. It was most frequent in white or black spruce and jack pine stands, occasional in poplars, and was absent in tamarack and



cedar (Welsh and Lougheed 1996). From Pickle Lake north to the Manitoba border, McLaren and McLaren (1981) found it only in coniferous and mixed forests.

In the Canadian Shield in the Great Lakes–St. Lawrence Forest Region, the Brown Creeper nested in both mature and old-growth white pine stands. Its abundance was significantly correlated with stand age and density of pines larger than 40 cm diameter at breast height (DBH). It was 1.5 times more abundant in old-growth stands than in mature stands. Its probability of occurrence was 33% with 62 stems per ha (11.6 m^2 per ha) of medium-sized and large pine trees (Kirk et al. 2012). In Quetico Park, it was most common in 112-year old forests where it was the dominant species in the timber-gleaner guild. It occurred in nearly all communities from early succession following fire to old growth (Apfelbaum and Haney 1985). It was essentially absent in managed jack pine stands near Gogama, but occurred in adjacent pine stands that were more than 100 years old. Managed pine stands probably do not provide suitable nest sites until they are 70-80 or more years old when some larger dead or dying trees might occur (James and Peck 1995a). In jack pine stands in Parry Sound District, James (1979a) found the Brown Creeper along 1 transect of 10-15-m tall pines mixed with 5-15-m tall white birch, white pine, trembling aspen, white spruce, and tamarack; it was absent on 4 other transects. In Algonquin Park, Martin (1960) reported it in stands dominated by black spruce and white cedar, white pine, hardwoods, and hemlock. It was absent in bogs, white birch–poplar stands, and balsam fir–black spruce stands.

In Durham Region in the Great Lakes–St. Lawrence Forest Region south of the Shield, the Brown Creeper occurred in a young open-canopy forest, a black spruce bog with a fringe of red maple–poplar swamp, an open swamp, a mature white cedar–elm swamp, a mature sugar maple–oak forest, and a hilltop dominated by sugar maple with a swamp of white cedar–balsam fir–spruce at the toe of the hill. Speirs and Orenstein (1975) considered it characteristic of white cedar forest.

The Brown Creeper does not appear to favour any particular forest cover type but seems to use the cover types that are most prevalent in the landscape. In the north, it is most strongly associated with coniferous and mixed forests because these are the dominant types available. South of the Boreal Forest Region, it is found mostly in mixed and deciduous stands and even further south, mostly in deciduous forests. In northern hardwoods, it is most abundant in old stands dominated by sugar maple and yellow birch, with balsam fir snags. In western North America, it nests predominantly in coniferous stands. It has been reported nesting in sugar maple forests, maple–yellow birch–hemlock stands, white pine–white oak stands, red maple swamps, cedar swamps,

hemlock forests, white and black spruce stands, mixed swamps, flooded timber, aspen-dominated mixed woods, and balsam fir stands (Betts 1909; Chadbourne 1905; Golet et al. 2001; Hall and Laitsch 1963; Higgelke and MacLeod 2000; Inman et al. 2002; Kennard and McKechnie 1905; Mossman and Hoffman 1989; Palmer-Ball and Haag 1989; Poulin et al. 2020; Thompson et al. 1999).

The most critical habitat component for the Brown Creeper is presence of large trees and snags for feeding and nesting. Consequently, it is typically associated with mature or old-growth forests, or younger or more open habitats that have residual old trees. These latter areas may include early-succession forests with scattered large trees and snags that persist after a fire or, less frequently, a clear-cut. In these more unusual circumstances, nests may be in fairly open habitat, although it typically nests in closed-canopy forests. Near White River, it was significantly more abundant in mature forests than in clear-cuts 3-25 years old. It was only observed once in early successional habitats. In Alberta, at least 3 ha of mature to old-growth forest were required around the nest site. In Alberta aspen stands, it occurred only in old-growth forest and preferred areas with coniferous cover. In Quebec, it nested in recent burns with saplings shorter than 2 m, but with numerous snags; in young forests with saplings 5-11 m tall; and in mature forests 120 and 200 years old. It was not detected in clear-cuts where saplings were less than 5 m tall. It was significantly more abundant in mature forests than recent burns, but its abundance in young forests was not significantly different from either burns or mature forests. In New Brunswick, the probability of finding a nest declined significantly when there were fewer than 127 stems per ha of trees that were 30 cm DBH or larger. Stand structure (large trees and snags) and the presence of mature or old forest patches within a 250-m radius had a significant influence on the probability of the presence of a Brown Creeper nest. In black spruce forests, it is most common in stands older than 120 years. In burns, it is most frequent in moderate and severe burns in coniferous forests that leave a high number of snags and adjacent live trees for foraging. In the east, it is twice as abundant in old-growth forests as in mature second-growth forests. In the Appalachians in Pennsylvania, it occurred in 100% of old-growth forests compared with 23.1% of forests statewide and 32.4% of forests on the Appalachian Plateau. It was considered an obligate old-growth species. In eastern deciduous forests, it is seldom detected in woodlands younger than 60 years. In Washington, nests were found only in stands 60-120 years old and in old-growth forest; in British Columbia it was most abundant in stands older than 200 years (Bock and Lynch 1970; Campbell et al. 1997; Haney 1999; Higgelke and MacLeod 2000; Imbeau et al. 1999; Poulin 2008; Poulin et al. 2020; Schieck et al. 1995; Shaffer and Alvo in Gauthier and Aubry 1996; Tyler 1914; Venier and Pearce 2005; Wiggins 2005; Zarnowitz and Manuwal 1985).

Presence of breeding Brown Creepers appears to be correlated with the amount of forest habitat in the general area. In Alberta and the mid-Atlantic states, it was positively associated with the amount of forest within 2 km. In New York, it was found mostly in areas with at least 50% forest cover (Higgelke and MacLeod 2000; Robbins et al. 1989; Shaffer and Alvo in Gauthier and Aubry 1996). In Ontario, it regularly breeds in landscapes with 20-30% forest cover. In southern Ontario, its probability of detection was positively correlated with the amount of forest cover 100 m or more from edge, but negatively correlated with woodlot size, amount of forest cover within 2 km, and amount of regional forest cover; these relationships were not significant (Austen et al. 2001).

Several studies identified microhabitat requirements of the Brown Creeper. Many authors concluded that it needs a closed-canopy forest. In Alberta, canopy closure less than 20% was unsuitable habitat and 80-100% canopy closure was optimum (Higgelke and MacLeod 2000; Poulin et al. 2020; Thompson and Capen 1988; Wiggins 2005). It may require openings in the canopy to allow light penetration to the nest (Shaffer and Alvo in Gauthier and Aubry 1996). In a Michigan study area, light penetrated to each nest site due to the presence of dead trees, a road opening, swamp clearing, or the position of the nest tree on a stream bank (Davis 1979). In Idaho, canopy height and density were important predictors of Brown Creeper occupancy. Density of the upper canopy was the most important variable, although mean tree height and height variability were also important. The upper canopy was twice as dense at occupied sites as unoccupied sites (26.38 compared with 13.78 light detection and ranging hits). Mean tree height was almost 50% higher at occupied sites (12.17 m) than unoccupied sites (8.20 m; Vogeler et al. 2013). In northeastern mixed woods, the Brown Creeper's abundance increased with abundance of yellow birch and sugar maple (Temple et al. 1979). In South Dakota and Wyoming, its abundance was highest where spruce was the dominant tree. Its density increased as the percentage of spruce in the canopy increased from 0% to 80% (Matseur et al. 2019). In the mid-Atlantic states, its presence was positively associated with basal area (BA) and negatively associated with the density of trees smaller than 3 cm DBH and the number of trees near the detection site (Robbins et al. 1989). In Vermont, microhabitat characteristics included 42.7% ground cover, 9.1% of ground covered by slash, 84.4% canopy closure, 26.3 m canopy height, 14.5 m canopy depth, 12.6 m^2 BA of deciduous trees, 8.8 m^2 BA of coniferous trees, average DBH of deciduous trees 15.4 cm, and average DBH of coniferous trees 19.1 cm. Thompson and Capen (1988) considered the Brown Creeper typical of forest cover with moderate understorey coverage.

Presence of water may be a habitat requirement. Many nests have been in beaver ponds or flooded swamps, or close to a watercourse. All nests found in a Michigan study area were either in swamps with standing water or within 60 m of a stream. Wet conditions are more conducive to producing snags, so the Brown Creeper's affinity with water may be more a function of availability of nest sites. It does appear to prefer cool, moist microclimates (Davis 1979; Higgelke and MacLeod 2000; Palmer-Ball and Haag 1989; Poulin et al. 2020; Shaffer and Alvo in Gauthier and Aubry 1996).

The Brown Creeper is an area-sensitive species. In southern Ontario, anecdotal information suggests that it requires forests that are a minimum of 30 ha. It is possible that smaller woodlands may be used in heavily forested landscapes. Minimum forest sizes have been defined as 50 ha in Connecticut and 100 ha in Wisconsin and Wyoming. In Kentucky, the only known breeding area was in a 200-ha swamp, the largest swamp of its type in Kentucky (Palmer-Ball and Haag 1989; Poulin et al. 2020). In the Seattle area, it was most abundant at the 3 study sites with the highest percentages of forest cover and largest forest patches, and its abundance was correlated with snag density (Blewett and Marzluff 2005).

Most researchers consider the Brown Creeper a forest-interior species that avoids forest edges and openings. In Alberta, Higgelke and MacLeod (200) concluded that it was sensitive to the presence of clearings within 100 m of the nest, and reported that its probability of detection was inversely related to the amount of early successional habitat within 1 km. In California, it reached

highest densities 400 m from edge. It was estimated that the edge width for it was 85 m. In Oregon, it stayed further from forest edge (average 252 m) than any other cavity-nesting species. Another California study found that it was more abundant in sites with less high-contrast edges. It avoided soft edges (edges between patches of differing habitat quality for the species) and moderate edges. Average distance of nests from different edge types was 62 m for soft edges, 87 m for moderate edges, and 80 m for hard edges. Successful nests were in large-diameter trees and snags in forests with lower canopy volume and further from moderate and hard edges than unsuccessful nests. It showed clear negative responses to edges in terms of abundance, nest location, and nest survival. Nesting at forest edge has been observed in Ontario and Massachusetts (Brand and George 2001; Chadbourne 1905; Inman et al. 2002; Peck and James 1987; Poulin et al. 2020; Purcell et al. 2012; Wiggins 2005). Lindell et al. (2007) summarized studies that determined the abundance of the Brown Creeper in relation to forest edge. Two studies found that it demonstrated no response to edge; a third study found that it avoided edge. Nichols (1948) reported nesting in an unusual area in New York. Nests were in trees 1.8 m from the edge of a frequently used driveway. The habitat was an open area surrounded by lawns and scattered ornamental trees such as Norway spruce.

The habitat of the Brown Creeper may be summarized as large mature to old-growth forests with a closed canopy and numerous large trees and snags. There are exceptions including burns and clear-cuts where there are residual snags among new growth and some retained larger trees.

Limited information is available on Brown Creeper roost sites. In Michigan, a group of recently fledged creepers roosted on a tree trunk that was sheltered by other trees. They roosted in a tight circle with their bills pointing inward. A different tree was used as a roost each night and adults roosted separately from the young. Winter roosts may be used more permanently and human-made structures may be used as well as trees. In Colorado, creepers roosted during winter in groups of 2 or 3 in a Russian olive, where they squeezed into a crack or scar in the bark. The same tree was used 2 consecutive winters (Davis 1979; Poulin et al. 2020). In New York, 2 roosted for over a month beside the chimney of a house. The birds roosted beside a wasp nest that afforded protection, and pushed their bills straight up into the wood of the overhanging roof (Stone 1950). Other winter roost sites include on the rough stucco of a house near the front door (this roost was used by 2 birds for 2 winters); 1 roosted for 1 night in the rough bark of a large white ash; 11 roosted in a hollow beam at the end of a barn; 4 roosted regularly on the side of a building a short distance from a door and subsequently moved to the bole of a hollow elm 40 m away (Fitch 1958; Tyler in Bent 1948).

Most Ontario nests were in dead trees and stubs, although 1 was in a living tree, 2 were in fence posts, and 1 was behind a piece of tin under the roof logs of an outhouse. Most nests (91.3%) were in loose bark of trees, with 5.2% in cavities in tree trunks and 3.4% in splits in tree trunks. All but 1 nest were placed against the main trunk of a tree, with the other against a large limb. Most nests were built between loose bark and the tree trunk. Slightly more nests (54.9%) were in deciduous trees than conifers. The most common nest trees, in order of abundance, were elms, spruces, balsam fir, and pines. The DBH of nest trees was 15-41 cm. Nests were 0.6-12 m from the ground, with most 1.4-3.7 m up (Peck and James 1987, 1997). In Algonquin Park, small-diameter trees are occasionally used for nesting and nests are sometimes placed in cracks in tree trunks (Tozer 2012).

Of 248 North American nests, over 95% were in dead trees, nest height ranged from 0.2 to 22.5 m, and nest tree DBH varied from 15 to 103 cm. Of 273 New Brunswick nests, 72% were in balsam fir, 12% in maple, 6% in yellow birch, 5% in beech, 4% in spruce, and 1 was in white cedar. Ninety-eight percent of nests were in snags and the mean DBH of nest trees was 32.3 cm. In addition to the tree species used in Ontario, the Brown Creeper has nested in white cedar, large-toothed aspen, red and silver maple, and chestnut, black and white oak. It rarely uses bluebird boxes. In British Columbia, it uses artificial structures built especially for it, consisting of slabs of wood attached to a tree to create a cavity. Most natural nests are attached to bark that has pulled away from a tree trunk, but a few are in natural cavities created by lightning strikes or other stresses, or abandoned chickadee or woodpecker holes. Unusual nest sites include behind a wooden grill, in a stack of concrete blocks, under loose roof shingles, beneath a piece of channel iron on a wooden utility pole, and behind window shutters. These latter nests demonstrate that it does not always nest in forested habitat. It has been observed nesting in the same tree in 5 consecutive years, but all were in different locations. In California, 12 nest sites were reused in a subsequent year, but it was not stated if old nests were reused (Base 1989; Betts 1909; Bradbury 1919; Campbell et al. 1997; Chadbourne 1905; Cunningham et al. 1980; Davis 1979; Hall and Laitsch 1963; Higgelke and MacLeod 2000; Kennard and McKechnie 1905; Li and Martin 1991; Meyer 1913; Nichols 1948; Palmer-Ball and Haag 1989; Poulin et al. 2020; Purcell et al. 2012; Tyler 1914; Tyler in Bent 1948; Wiggins 2005; Zarnowitz and Manuwal 1985). In the Seattle area, the Brown Creeper nested in snags that were more decayed than random snags, and nested in snags with any kind of fungus less often than expected by chance (Blewett and Marzluff 2005).

Little information is available on territory size, on what areas are defended, or if territories are exclusive. In Ontario, average territory size was 1.0 ha (range 0.73-1.29 ha) in coniferous forest dominated by balsam fir and black and white spruce north of Lake Superior. Few observations were made of individual birds, and territories may have been as large as 2 ha. Territory size of 1 pair in Quebec was 0.47 ha. In northeastern Minnesota and adjacent Ontario, average territory sizes were 0.01-0.025 ha in postfire, mature, and old-growth mixed-woods. Small territories were related to high densities. In red spruce forests in Maine, mean territory size was 1.34 ha. In Michigan, territories were 2.3-6.4 ha. In northern hardwoods, the mean territory size was 4.2 ha (range 2.3-9.4 ha). In Massachusetts, adults rarely moved more than 10 m from the nest to obtain food for nestlings (0.03 ha), but in Michigan, territories were expanded as adults moved as far as 150 m to obtain food for nestlings. After fledglings leave the nest, the family may range 150-500 m from the nest, but it is unknown if any of this area is defended. No information on home range size is available (Chadbourne 1905; Kendeigh 1947; Morse 1977; Poulin et al. 2020; Shaffer and Alvo in Gauthier and Aubry 1996; Wiggins 2005).

No information is available on natal dispersal or philopatry, or on adult site fidelity to breeding or wintering sites (Poulin et al. 2020).

Limiting Factors

Eggs have been reported in Ontario nests from the last week of April until mid-July, with most present from the last week of May until mid-June. Young were present in a Nipissing District nest on 9 August, suggesting a later egg date (Peck and James 1997). In Algonquin Park, nests are under

construction from early May to late June, eggs are present from mid-May to early July, nestlings are present from late May to late July and rarely to early August, and dependent fledglings have been observed from early June to late July (Tozer 2012).

The female may take 6-30 days to build the first nest, but usually 7-14 days. Nests for second or third attempts are usually built in 6 or 7 days. Eggs are laid at the rate of 1 a day; laying may start the morning after the nest is completed. Incubation begins with the laying of the last egg. The incubation period at 1 Ontario nest was 13-14 days. Elsewhere, the incubation period has been reported as 11-17 days, with 15 days most frequent. All eggs typically hatch on the same day. The young fledge when they are 13-20 days old, but mostly at age 15-17 days (Davis 1979; Peck and James 1987; Poulin et al. 2020; Shaffer and Alvo in Gauthier and Aubry 1996; Tyler in Bent 1948; Wiggins 2005). Nesting activities within a given area may be highly asynchronous. In a small Michigan study area, 1 female had just finished building her nest while another was laying eggs, 1 female was incubating, and 1 nest contained 14-day-old nestlings (Davis 1979).

A single brood is raised annually. Earlier records of second broods were based on unmarked birds and probably represented different pairs. Renesting may occur about a week after the loss of the initial nest. Clutches of 4-8 eggs have been reported in Ontario, with most containing 4-6 eggs. This is typical throughout the Brown Creeper's range. The average size of North American clutches was 5.48 eggs; the mode was 6 eggs in Michigan (Campbell et al. 1997; Davis 1979; Nichols 1948; Peck and James 1997; Poulin et al. 2020; Tyler in Bent 1948; Wiggins 2005).

The age at first breeding has not been confirmed, but is thought to be 1 year. The mating system is monogamous and no cases of polygyny have been reported. Resident birds may remain paired year-round but migratory birds pair in early spring (Poulin et al. 2020; Wiggins 2005).

The Brown Creeper forages almost exclusively on the trunks of large trees and, to a lesser extent, on large branches. It occasionally forages on medium-sized and small branches and rarely on the ground. Although it forages on a wide range of tree sizes, larger trees are actively selected. Large tree trunks are more deeply furrowed and support a higher density of arthropods than smaller trees. Energy intake may be increased by foraging on 1 large tree instead of several small ones. In Washington, it was estimated that it would have to forage on 13 young trees (29 cm DBH) or 3.3 mature trees (67 cm DBH) to obtain the same amount of spiders as present on 1 old-growth tree (112 cm DBH). It was estimated that a minimum of 100 stems per ha of trees at least 25 cm DBH are required to support foraging Brown Creepers, but 500 stems per ha or more are necessary to support maximum densities. Its typical foraging strategy is to land at the base of a tree trunk and move upward either in a spiral pattern or straight up. When a branch is encountered, it may either move around it, or forage on the underside. Bases of dead limbs are favoured for foraging because they often support high densities of invertebrates. Most foraging occurs at heights of 9 m or less, but occasionally to the treetop. Once 1 tree has been scaled, it usually flies to the base of another large tree and repeats the process. Live and dead trees are typically used in proportion to their availability, and limbs that are used for foraging are usually larger than 5 cm in diameter. Tree species does not appear to be of importance, with tree size being more critical. In western North America, most foraging occurred on conifers. In Pennsylvania and Illinois, oaks, hackberries, elms, and pines are widely used, as are spruces and maples in Ontario (personal observation). It obtains most of its food

by probing, pecking, and gleaning. It rarely hawks insects (Adams and Morrison 1993; Franzreb 1985; Higgelke and MacLeod 2000; Lundquist and Manuwal 1990; Poulin et al. 2020; Tyler in Bent 1948; Weikel and Hayes 1999; Wiggins 2005).

Nestlings are fed small invertebrates exclusively. Ten-day-old nestlings in Michigan were fed click beetles, harvestmen, and mayflies. Invertebrates provided to young included ants, beetles, moths, spiders, and mayflies. Nestlings in New Brunswick were fed lepidopterans (mostly moths), spiders, and fly larvae, although smaller items could not be identified. During the breeding season, adults feed solely on invertebrates, especially insects, spiders, and pseudoscorpions. Most food items are less than 3 mm in length. In California, 62.8% of the diet consisted of beetles, 12.9% was unidentified, 9.7% was pseudoscorpions, 7.5% bugs, 1.0% flies, and 0.4% hymenopterans. Insects consumed included stink bugs, beetles (weevils and long-horned, bark, and leaf beetles), dark-winged fungus gnats, lepidopterans including caterpillars and codling moth pupae, lacewings, caddisflies, aphids, leafhoppers, scale insects, ants, sawflies, katydid eggs, and leaf skeletonizers (Davis 1979; Franzreb 1985; Poulin et al. 2020; Tyler in Bent 1948; Wiggins 2005). Crawford and Jennings (1989) examined 2 Brown Creeper stomachs in New Hampshire and Maine and found that they had not ingested any spruce budworms. In New Brunswick, there was no relationship between the abundance of the Brown Creeper and spruce budworms (Morris et al. 1958).

In 2005, a nest was found in Norfolk County that was parasitized by the Brown-headed Cowbird. This was the first record of cowbird parasitism of the Brown Creeper in Ontario. Parasitism is rare, with only 3 reports previous to the Ontario record (Davis 1979; Peck and James 1987; Peck and Peck 2006; Poulin et al. 2020).

Forest fragmentation and timber management may be the greatest limiting factors to the Brown Creeper. Due to its area sensitivity, it is vulnerable to forest fragmentation. In Wyoming, forest fragmentation resulted in greater declines of the Brown Creeper than any other species known to be old-growth specialists. It is sensitive to almost all types of forest management. Abundance decreases with decreasing canopy closure, lower density of large mature trees, and lower density of snags. Almost all types of logging, including fuelwood removal, have negative effects on all these factors. There may even be negative effects with selective thinning where snags are retained. In Pennsylvania, its density was higher in timber stand improvement areas where snags were retained than areas where snags were removed. No comparison was made to densities in areas where thinning did not occur. Without exception, paired comparisons of its abundance or presence in logged versus nearby unlogged forests indicated strong negative impacts from logging. Retaining large patches of forest with old-growth characteristics significantly increases habitat suitability. Patches of residual trees in clear-cuts are typically not used. Past logging may have affected populations and its distribution in eastern North America. The current range may be limited by where logging occurred between 1880 and 1930 (Franzreb 1985; Higgelke and MacLeod 2000; Poulin et al. 2020; Shaffer and Alvo in Gauthier and Aubry 1996; Stribling et al. 1990; Wiggins 2005). In the Canadian Shield of Ontario, there was no difference in its abundance in early successional clear-cuts and burns, but it was significantly less abundant in mid-successional clear-cuts than in mid-successional burns. It was significantly less abundant in early successional and mid-successional stands than in mature stands (Zimmerling et al. 2017). Vanderwel et al. (2007, 2009) summarized

studies that examined the effects of partial timber harvest in the Boreal Forest Region. Abundance of the Brown Creeper decreased when 30% and 50% of trees were removed, and it became locally extirpated when 70% of trees were removed. It experienced a 25% decrease when 20% of trees were removed, a 50% decrease when 35% of trees were removed, and a 75% decrease when about 50% of trees were removed. It was the second-most sensitive species to tree removal to the Ovenbird. Rempel et al. (2007) modelled the response of the Brown Creeper to forest harvesting in the Boreal Forest Region of Ontario. They predicted a population decline over 100 years even if all current forest management guidelines were implemented. They concluded that boreal forest management should create clustered areas of high edges separated by large areas of intact forest matrix to support the full suite of birds that inhabit the Boreal Forest Region. Intact areas are required to maintain Brown Creeper habitat. In Algonquin Park, Tozer et al. (2010) found that typical and intensive group-selection harvesting of trees had no effects on the Brown Creeper. Jobes et al. (2004) also found no significant effects on it due to partial harvesting in Algonquin Park. Geleynse (2013) observed contrasting effects of logging on the Brown Creeper in Algonquin Park. Its density was significantly lower in 4 silvicultural treatments, including intensive group-selection, typical group-selection, old single-tree selection, and recent single-tree selection. Nest trees were significantly closer to forested wetlands than randomly selected trees in all stands. In unlogged stands, it nested further from forested wetlands and in greater numbers in upland hardwoods than in logged stands. Densities declined in harvested upland hardwood forests due to loss of nesting habitat. In the Carolinian Forest Region of Ontario, the Brown Creeper was the only species that responded negatively to partial harvesting. It was absent in heavy cuts and rare in standard cuts (Holmes et al. 2004). In the Seattle area, its density in forests managed for timber production was 2.2 times higher than in suburban forests. Productivity was greatest where the percentage of forest was low but aggregated, and where snag densities were high (Blewett and Marzluff 2005).

The Brown Creeper often responds positively to fires that leave large snags, insect and disease outbreaks, and windthrow provided that these are not too severe. The positive response is usually short-lived and is related to bark-retention times on dead and dying trees. Overall, the loss of large trees to exotic insects and diseases and the eventual loss of snags could be a significant limiting factor in the east (Burris and Haney 2005; Mossman and Hoffman 1989; Poulin et al. 2020; Wiggins 2005). In South Dakota and Wyoming, its abundance was positively correlated with the percent area of 4-5-year-old wildfires. It also increased as the density of trees killed by beetles increased from 0 to 16% (Matseur et al. 2019).

Cold, wet weather during the breeding season may reduce reproductive success and some nests may become weakened and fall during prolonged rain. During the 1950s, the Brown Creeper was adversely affected by spraying of DDT to control Dutch elm disease, but there are no recent known impacts from pesticides or other contaminants (Davis 1979; Poulin et al. 2020; Wiggins 2005).

Status

It is probable that the Brown Creeper population declined with European settlement and subsequent forest fragmentation and lumbering. McIlwraith (1894) reported that it was observed in all seasons, but was rare during the breeding season. Baillie and Harrington (1937) stated that it bred sparingly from Middlesex and Welland counties north to the transcontinental railway line and

westward to Lake of the Woods. In Elgin County, it was only observed during migration in the 1890s, but was a rare breeder in 1954 and 2000 (Lancaster et al. 2004). During the first atlas, its distribution in the south was discontinuous due to its habitat requirements, and it was uncommon where it did occur. In the north, it appeared to be fairly common (Blomme in Cadman et al. 1987). James (1991) considered it a rare and local breeder in the agricultural south, uncommon north to Big Trout Lake and Moosonee, and rare north to Sutton Lake.

The second atlas revealed that there had been a range expansion and increase in abundance of the Brown Creeper since the first atlas. Its range extended much further northward to cover almost all of the Hudson Bay Lowland. It is uncertain if this represented a true range expansion or was an artifact of better coverage during the second atlas. Its probability of observation increased significantly province-wide and in the Canadian Shield and Hudson Bay Lowland. There was a nonsignificant increase in the Great Lakes–St. Lawrence Forest Region south of the Shield. There was a nonsignificant decline in the Carolinian Forest Region. In the south, there were noticeable increases in the number of squares occupied in the Sudbury to Sault Ste. Marie area and in the agricultural areas of Bruce, western Grey, Perth, and Middlesex counties. It was most abundant in Algonquin and Quetico parks, the Algoma highlands, and in northwestern Ontario from Woodland Caribou to Wabakimi parks. These are parks where logging is not permitted or are north of where logging occurs, so they support more mature trees (McLaren in Cadman et al. 2007).

Breeding Bird Survey data for 1970-2021 indicated annual increases of 0.74% in Canada and 1.71% in Ontario. Short-term (2011-21) trends included annual decreases of 0.828% in Canada and 2.01% in Ontario. All trends were of medium reliability except that the short-term trend for Ontario was of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings often split into 2 groups, with one following each parent. Parents continue to feed young 17-26 days after fledging. In Michigan, fledglings remained within 500 m of the nest site for at least 17 days postfledging. The family unit breaks down before autumn migration (Davis 1979; Poulin et al. 2020).

MIGRATION

In the east, the Brown Creeper is highly migratory. In the west, it tends to be a resident with seasonal movements related to changes in altitude. It occurs in Ontario during winter, but it is unknown if wintering birds are those that remained on their breeding grounds or those that retreated from more northerly sites. Northern populations appear to migrate longer distances than more southerly ones. Migration is known to occur at night, but it is possible that daytime movement may also occur (Poulin et al. 2020; Wiggins 2005). Banding records suggest that birds may fly directly over Lake Erie (Brewer et al. 2018).

Spring migration begins in Ontario in early April or very late March and continues until mid-May. Autumn migrants appear in the first week of September. Autumn migration is much more leisurely and birds may still be moving south in mid-November (Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981, 2005b; Weir 2008).

During migration, the Brown Creeper still prefers wooded areas, but has less stringent habitat requirements. While migrating, it may occur in most wooded areas that have intermediate-aged to mature trees, in suburban woodlands and treed lots, and in rural lots with large trees. When large numbers occur at Presqu'ile during migration, it may occur almost anywhere, including on the beach and in marshes. Small numbers (usually 1 or 2) may occur in flocks of chickadees, nuthatches, and kinglets (Campbell et al. 1997; LaForest 1993; Lancaster et al. 2004; Poulin et al. 2020). In Pennsylvania during autumn migration, it occurred at low densities with no significant differences among habitats. In order of decreasing abundance, it occurred in forest interior, suburban forest, forest edge, and forest-agricultural edge. It was absent in shrub and sapling-stage forests (Rodewald and Brittingham 2002). During autumn migration on 2 islands in the Gulf of Maine, it was significantly more abundant on a forested island than on one dominated by shrubs (Suomala et al. 2010).

Tall buildings and communication towers may be a significant source of mortality during migration. From 1993 to 1998, 434 collisions with Toronto office towers were reported, with 147 resulting in death. The Brown Creeper is one of the more common species that collides with Toronto office buildings. Collisions with tall towers are also common; 12 deaths occurred in an hour at 1 Illinois television tower (Poulin et al. 2020; Wiggins 2005). In the United States, the Brown Creeper was among the 20 most vulnerable species for striking any type of building, being 26.2 times more likely to suffer a collision than species on average. It was on the top 20 list of most vulnerable species to collide with each type of building: 81.1 times more likely than average to strike a residence 1-3 stories tall, 44.8 times more likely to strike a low-rise, and 44.3 times more likely to strike a high-rise than average (Loss et al. 2014).

Mills (2005b) examined spring and autumn migration timing for the Brown Creeper at Long Point 1975-2000 in relation to global warming. It arrived significantly earlier during this period at a rate of 4.1 days per decade and significantly delayed autumn migration at a rate of 5.8 days per decade.

In most of the province, the Brown Creeper is uncommon to common during migration, but it may be locally abundant in key migratory stopover areas. Daily spring counts may be as high as 500-650 at Prince Edward Point and Presqu'ile (James 1991; LaForest 1993; Weir 2008).

WINTER

The Brown Creeper is one of about only 45 species that winters in the Boreal Forest Region in Canada. Winter habitat is similar to breeding habitat, although younger forests, suburban forests, and treed rural and residential lots may be visited (Erskine 1977; Poulin et al. 2020). Densities of Brown Creepers per km^2 reported on Winter Bird-Population Studies in southern Ontario were 8.1 in rural forests, 3.8 in mixed rural habitats, 1.6 in urban natural areas and urban natural areas with open water, 0.4 in urban natural areas smaller than 10 ha, and 0.1 in cities. It was not reported from open farmland (Smith 2003). At Presqu'ile, it occurs most frequently in coniferous plantations (LaForest 1993). In California, wintering Brown Creepers were positively associated with tall trees and negatively correlated with human structures and roads (Kalinowski and Johnson 2010). In Missouri, its density increased with increased tree stocking. It was present in savannahs, woodlands, and forests, but its density increased 75% from the more open savannah habitats to forest cover

(Kendrick and Thompson 2013). In New Jersey pine barrens, it was more common in pine-dominated habitats than in those dominated by oaks, but not significantly (Brush 1989).

During autumn migration and shortly after arrival in the wintering area, the Brown Creeper may be gregarious. As winter progresses, it becomes solitary and agonistic and may defend a territory. Once settled into an area for the winter, individuals remain in the general vicinity and may be seen in the same tree for periods of days or weeks (Dunn and Tessaglia-Hymes 1999; Fitch 1958; Poulin et al. 2020).

Winter foraging may occur singly or in small monospecific flocks, but often in mixed flocks. The Brown Creeper frequently occurs in flocks of woodpeckers, chickadees, titmice, nuthatches, and kinglets. It is strongly associated with the Red-breasted Nuthatch and the Golden-crowned Kinglet (Fitch 1958; McIlwraith 1894; Poulin et al. 2020; Tyler in Bent 1948; Wiggins 2005). Webber (1986) studied winter foraging sites of the Brown Creeper. All tree species present were used for foraging, but not in proportion to their availability. Ash, oak, and walnut were selected over hackberry and maple. The size of trees it used was negatively correlated with temperature. As temperatures decreased, larger diameter trees were used almost exclusively for foraging; smaller trees were used as temperature increased. Birds ascended trees in the typical spiral pattern regardless of temperature and wind velocity. Kendrick and Thompson (2013) reported similar results in Missouri and found that its detectability increased with temperature and was negatively affected by wind.

The Brown Creeper's winter diet is similar to that of the breeding season, with a heavy reliance on insects. In Illinois, the diet consisted of 80% animal material, including 57.2% bugs, 12.4% adult beetles, 4.4% ants, 11.6% spiders, and 2.8% other groups. Vegetation consumed included corn and fragments of acorns. Small amounts of pine seeds and grass seeds may be eaten in winter (Poulin et al. 2020; Tyler in Bent 1948; Williams and Batzli 1979).

Only about 20% of winter bird feeders are visited by the Brown Creeper, and rural feeders are visited most frequently. Most food taken from feeders consists of tiny crumbs of seeds, including niger or suet that other birds have left behind. Favourite feeder foods are suet, bird puddings, and peanut butter mixes. Infrequently consumed items include pieces of sunflowers, water, and possibly peanut hearts and baked goods (Dunn and Tessaglia-Hymes 1999; Mills 1981; Tyler in Bent 1948).

Food caching appears to be a rare winter behaviour. Lima and Lee (1993) observed Brown Creepers caching small bits of sunflower kernels taken from a feeder. This occurred on 5 different dates and more than 1 bird was involved. Food items were carried singly to a nearby tree with a trunk diameter of 20-30 cm and carefully pushed upwards into a crevice in the bark. Caches were scattered 4-6 m from the ground in a single tree or a set of adjacent trees. Birds typically cached 3-10 items in rapid succession at the end of a visit to the feeder. No attempt was made to cover caches, but they were well concealed. This is the only case of caching that has been reported.

The Brown Creeper appears to be vulnerable to severe winter weather, which may result in poor overwinter survival and reduced populations the next breeding season. After a severe winter storm in Illinois, populations declined by 15.8% in bottomland forests and 38.1% in upland forests. Although no carcasses were found, it was suspected that higher than normal mortality occurred.

Declines in abundance in some habitats were not compensated for by increases in other habitats (Graber and Graber 1979).

James (1991) considered the Brown Creeper a rare winter resident in the south that occurred west to Thunder Bay.

Christmas Bird Count data indicate that the Brown Creeper increased in Ontario at annual rates of 0.41% 1970-2021 and 2.81% 2009-2021 (National Audubon Society 2022).

Blue-gray Gnatcatcher

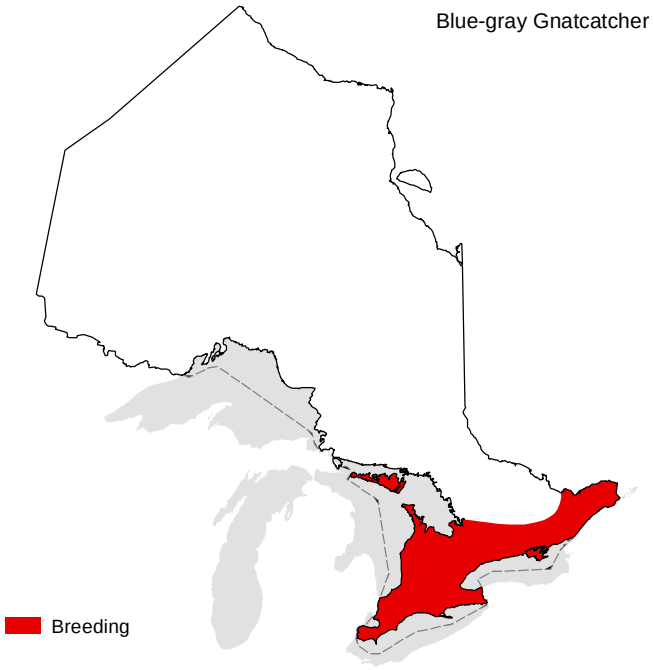
Polioptila caerulea

BREEDING SEASON

Habitat Requirements

In Ontario, the Blue-gray Gnatcatcher nests most frequently in deciduous forests (55.8% of nests) and mixed woods (27.9%), and less often in riverbank groves (9.3%), shrubby fields (4.7%), and swales (2.3%). It exhibits no apparent preference for upland or wetland habitat. Nests were often (41.9%) near openings such as paths, roads, clearings, streams, and lakes (Peck and James 1987). Lancaster et al. (2004) reported that it nested throughout Elgin County in woodlands, particularly along watercourses and in wooded swamps. McCracken (in Cadman et al. 2007) stated that it seemed to favour open-canopied deciduous swamps and floodplain forests.

Throughout its range, the Blue-gray Gnatcatcher nests predominantly in forested areas, but also in shrubby areas and rarely in suburban areas. It often nests in open shrubby habitat and forages in denser areas. It greatly prefers deciduous cover, but occurs in mixed woods less frequently. Conifers tend to be avoided except in the southeastern states where it may occur in pine stands. In the southeast, it is most abundant in forested river bottoms and upland pine woods with an understorey of oaks. In New Jersey, it was equally abundant in oak-pine forests and hardwood swamps. In Indiana, Illinois, and Kansas, it inhabits open shrub and woodland areas as well as lowland forests. In the northeastern states, it exhibits a marked preference for tall, mature trees in closed-canopy forests



along river floodplains. In the Midwest, its abundance was significantly associated with tree height. Its maximum density was at tree heights of 16 m, declining to about 70% at 22 m. In Illinois, it is most prevalent in riparian woods where it usually occupies the first level above the floodplain. Similar preferences were noted in Michigan where it was most abundant in the forested band adjacent to rivers. Densities decreased toward the upland forest further from the riparian habitat. When populations declined in Illinois, upland forests were deserted but densities in riparian woodlands remained constant suggesting that upland habitat was marginal. Kansas birds showed a preference for more open, drier situations, nesting in large honey locusts and elms in fields, in shrubby growths of chinquapin oaks and dogwoods, and less frequently in oak-hickory woodlands. In much of the mid-Atlantic states, it is strongly associated with oak and oak-hickory forests, predominantly white oak. Other habitats it has used for nesting include green ash and silver maple swamps in Vermont, silver maple–black ash and swamp white oak–black ash swamps in Wisconsin, white birch–basswood stands in Pennsylvania, red maple swamps in Rhode Island, and pine and oak barrens on river terraces in Wisconsin. Breeding habitat in Quebec included a silver maple–black ash swamp adjacent to a lake, a red oak stand beside a lake, a floodplain stand of swamp white oak, and a mature gray birch thicket in a field reverting to forest (Darveau in Gauthier and Aubry 1996; Fitch 1958; Golet et al. 2001; Graber et al. 1979; Grundel and Pavlovic 2007b; Inman et al. 2002; Kerschner and Ellison 2020; Mossman et al. 1991; Raynor 1964; Rich et al. 1994; Root 1967; Weston in Bent 1949).

Some studies documented microhabitat requirements of the Blue-gray Gnatcatcher. It appears to prefer more open-canopied forests with an open understorey layer. In Illinois, vegetation species composition, stem density, and basal area did not correlate with population abundance (Graber et al. 1979). In Utah, Whitmore (1977) considered the Blue-gray Gnatcatcher a habitat generalist, preferring moderate numbers of trees, shrubs, and ground cover. In Kansas, it was least frequent in oak-hickory woodlands that had a dense leaf canopy (Fitch 1958). In Vermont, it showed nonsignificant tendencies to select sites with lower basal area and tree density than in adjacent parts of the territory. Site characteristics were apparently more important than tree species (Kerschner and Ellison 2020). In Tennessee, Anderson and Shugart (1974) usually observed it in the upper canopy, but it selected habitat on characteristics of understorey biomass (foliage and branch biomass of trees 1.2-8.4 cm diameter at breast height [DBH] and bole biomass of trees 8.5-22.8 cm DBH) and the average size of canopy trees (foliage, branch, and bole biomass of trees larger than 22.8 cm DBH and stump biomass of trees 8.5-22.8 cm DBH). It occurred most frequently in areas with

an open understorey and large trees forming a canopy of approximately average biomass. Both conditions had to be satisfied for habitat to be suitable. In the mid-Atlantic states, its presence was positively correlated with canopy height and negatively correlated with slope and the number of dead standing trees larger than 3 cm DBH (Robbins et al. 1989). In Maryland, its abundance was negatively correlated with canopy closure and forest isolation (Lynch 1987). In Wisconsin, it occurred most frequently in intermediate stands on a moisture gradient and was not common in either mesic or xeric stands. This study was conducted entirely in upland areas. As the size of woodlots increased, its peak of abundance occurred in more xeric stands suggesting that there was a delicate balance between its response to woodlot size and vegetational conditions. It had a broader amplitude of habitat conditions than most species (Bond 1957). In California, it was significantly more abundant in oak savannahs with shrubs and montane oak stands than in oak savannahs with grass. Its abundance in oak woodlands was intermediate between these habitats. It was positively associated with coverage by hardwoods, shrubs, and conifers and negatively correlated with herbaceous cover and tree size (Wood et al. 2013).

The Blue-gray Gnatcatcher is typically considered an area-sensitive species, but not all studies support this. Hayden et al. (1985) did not consider it area sensitive, but had very few detections of it. In South Carolina, Kilgo et al. (1997) found no significant differences in detection rates in different-sized woodlots. Its probability of detection was 71% in hardwood stands as small as 0.5 ha. In Wisconsin upland stands, it was at least 50% more common in large than small woodlots and Bond (1957) concluded that it showed a preference for large woods. Frequency of occurrence was 6.2% in 6.1-14.2-ha woodlots, 17.4% in 16.2-32.4-ha woodlots, and 23.0% in stands larger than 32.4 ha. In Pennsylvania, its abundance was positively associated with larger woodlands. Robbins et al. (1989) considered it area sensitive in the mid-Atlantic states. Its probability of occurrence was greatest in forests larger than 3,000 ha and the probability dropped to 50% in 15.0-ha woodlots. The 3 smallest woodlots in which it was detected at least twice were 6.8, 10.1, and 23.0 ha. Kerschner and Ellison (2020) concluded that it may have specific microhabitat needs in upland forests, such as stream valleys and canopy openings that limit numbers rather than the species having requirements for large forests. They concluded that the area sensitivity of the Blue-gray Gnatcatcher needed further study.

Hodges and Krementz (1996) studied the abundance of the Blue-gray Gnatcatcher in riparian forests of different widths in Georgia. It was more abundant in medium-sized than narrow or wide corridors, but these differences were not significant. Its probability of observation was 82% in 50-m wide corridors, 83% in 100-m wide corridors, 86% in 200-m wide corridors, 92% in 500-m wide corridors, and 94% in 1,000-m wide corridors.

Somershoe and Chandler (2004) considered the Blue-gray Gnatcatcher a forest-interior species, but other authors considered it an edge or a forest edge–interior species (Golet et al. 2001; Harrison and Kilgo 2004; Hayden et al. 1985; Mossman and Hoffman 1989). In South Carolina, it was 6-7 times more abundant in small forest gaps or at forest edges during the spring migration, breeding, and postbreeding seasons than in forest. It occurred exclusively in edge and gaps during autumn migration. Bowen et al. (2007) considered it a forest edge species. In Tennessee, it exhibited regularly spaced peaks and lows of densities in relation to edge indicating that territories lined up parallel to

the edge of the forest. The density of territories was not significantly greater near edge than in deeper forest, although 18 territories were found within 268 m of edge compared with 6 territories 268-488 m from edge (Kroodsma 1984). Kerschner and Ellison (2020) concluded that it often occurred at or near habitat edges. In Ontario, the Blue-gray Gnatcatcher is not confined to forest interior. It may occur throughout forested habitat but is more prevalent at edges and forest openings, and may also occasionally breed in shrubby areas or small groves of trees (Peck and James 1987).

Most Ontario nests were in trees but 2 were in vines. Deciduous trees were selected for nest sites (94.1% of nests) over conifers and all but 1 nest tree was alive. Nest-tree species in descending order of abundance were oaks, ashes, maples, and birches. Nests were usually saddled on horizontal or near-horizontal branches (64.3%) and less frequently in crotches (35.7%). Eight nests were at knots, branch junctions, and vertical branches, or were under overhead branches or leafy twigs. The supporting limbs of 7 nests were dead. Nest limbs were 2.2-7.6 cm in diameter. One nest was at the trunk of the tree; 8 were 0.1-3.0 m distant, mostly 1.8-2.7 m from the trunk. Nests were 0.6-26 m from the ground, with most 6.7-12 m up (Peck and James 1987, 1997). Peck and James (1997) and Crins (2001) documented 4 instances of materials being taken from an old nest to build a new one. The nest reported by Crins (2001) was in a crack willow. A nest near London was 2 m from the ground on a branch close to the trunk of a hawthorn (Scott 1963).

Throughout its range, the Blue-gray Gnatcatcher nests predominantly in deciduous trees and occasionally in shrubs, rarely in conifers or dead snags. In Illinois, 98.6% of nests were in deciduous trees but in Florida pines may be selected over other tree species. In other areas in the north, oaks and elms are preferred nest trees, but nests have been reported commonly in sugar maple, sycamore, black walnut, sassafras, and honey and black locust and infrequently in ash, willow, hickory, hophornbeam, black cherry, crabapple, and alder. Most nests are saddled on horizontal branches (76% of Vermont nests), often built against a twig or side branch and also around a twig or knot for support. It also nests in outer branch forks but trunk forks are avoided as nest sites except in California. Nests are usually on limbs 2-5 cm in diameter, but occasionally on larger ones. Occasionally, nests may be among the forks of 3 or more branches. This is most likely to occur when the nest is in a shrub. In California, the height at which nests were situated was related to the height of the nest tree. Nests in oaks were always at least 0.9 m below the top of the tree; nests in shrubs were near the top. Individuals may build nests in very different situations. A female in California built nests in deciduous oaks, oaks that retained their leaves year round, and in shrubs, and nests were in shaded and unshaded locations and in vertical and horizontal nest forks. Nests have been reported at heights of 0.96-24 m with most 6-10 m up where trees are used for nesting. The same nest is not used again for replacement clutches or second broods, but the same nest site may be used later in the season or in subsequent seasons (Fitch 1958; Graber et al. 1979; Kerschner and Ellison 2020; Kershner et al. 2001; Nice 1932a; Nickell 1956; Raynor 1964; Root 1967, 1969b; Scott and McKinney 1994; Weston in Bent 1949). In Illinois, nest sites had significantly higher leaf density around nests than random sites at 1-m radius but there was no significant difference at 4-m and 11-m radii. Nest-tree species selection did not differ from availability. Nest height, distance to trunk, and leaf density did not differ significantly between first and subsequent nesting attempts (Kershner et al. 2001).

Early in the nesting season, the Blue-gray Gnatcatcher defends a territory. The entire territory is defended initially and boundaries become stable once nesting is underway. Later on, only favoured foraging areas are defended and there is a gradual decrease in territorial behaviour. Disputes later in the season are associated with shifts in territorial boundaries due to renesting activities. There is often a lack of synchrony in the nesting cycle of adjacent birds that allows pairs to move through undefended portions of neighbours' territories. It responds aggressively toward most vertebrates that approach within 6 m of the nest. In Illinois, territories were small and averaged 0.37 ha for 25 pairs observed within 26 ha of habitat. Nine territories in California averaged 1.8 ha (range 0.9-3.0 ha). Territories that contained large areas of open woodland tended to be larger, suggesting that territory size was related to the amount of tree foliage present. Four Vermont territories averaged 0.7 ha (range 0.5-1.1 ha). In Kansas, the territory used by 1 pair while feeding young was 0.49 ha, but outlying parts of the territory were rarely visited; another pair feeding young had a territory of 0.89 ha. Florida territories were 0.4 ha. In California, territorial boundaries were extended early in the fledgling period to include brood habitat and preferred foraging areas (Fitch 1958; Graber et al. 1979; Kerschner and Ellison 2020; Root 1967, 1969b).

Few data are available on home range size. Most pairs remain within 50 or 60 m of the nest once it is built. Others may forage as far as 150 m away in undefended areas. For the first few days, adults may forage near the brood which may be outside of the territory, or the territory may be extended to include these areas. In Florida, the home range size was 4.0 ha (Graber et al. 1979; Kerschner and Ellison 2020; Root 1969b).

No information is available on natal philopatry or dispersal. Very little is known about adult site fidelity. One instance of breeding site fidelity was reported in northern Florida (Kerschner and Ellison 2020).

Limiting Factors

Eggs have been found in Ontario nests from 6 May until 1 July, with most reported 25 May to 9 June (Peck and James 1997). The pair bond is established once pairs reach the breeding ground, but nesting may be delayed until arthropods become abundant. In Illinois, nest building began about a week after arrival. The time required to build a nest varies depending upon geographic location, whether it is a first or subsequent nest, and if material is used from a previous nest. One Kansas nest was built in a single day. Twenty-five Illinois nests took 3-5 days to build. In New Mexico, pairs averaged 4.8 days between abandoning parasitized nests and laying an egg in the next nest. In California, first nests took an average of 13.6 days to build (range 12-15 days), but only 8-10 days in Vermont. Second nests and replacement nests took an average of 4.8 days in California (range 3-6 days) and 5 or 6 days in Vermont. Second nests are started immediately after first nests produce young. In Illinois, the first egg was laid within 24 hours of completion of the nest. In the southeastern states, 5-10 days may elapse between nest completion and laying of the first egg. Nests are completed there before there is sufficient food to raise a clutch. Eggs are laid at the rate of 1 a day. Incubation starts with laying of the last egg, although full incubation may not begin until the next day. The incubation period of Ontario nests was 12 days at 2 nests and 15 days at another. Elsewhere, incubation periods of 11-15 days have been reported (mean 13 days). Young leave the nest when they are 10-15 days old, usually around 12-13 days, and the entire brood typically leaves the nest

within an hour. In Illinois, the nesting cycle from initiation of nest building until fledging was 33-38 days (Fitch 1958; Goguen and Mathews 1996; Graber et al. 1979; Kerschner and Ellison 2020; Peck and James 1997; Root 1967, 1969b; Scott 1993; Weston in Bent 1949).

In most areas, the Blue-gray Gnatcatcher raises only a single brood. Ontario egg dates suggest that second broods are not reared. In the southern states and California, second broods may be raised, but most pairs raise a single brood even in the south. In northern Florida, 1 of 22 pairs (4.5%) attempted a second brood and 1 of 60 pairs (1.7%) attempted a second brood in New Mexico. In Illinois, 69% of pairs that failed in their first brood renested and 21% of pairs attempted a second brood but only one was successful. In Vermont, 5 of 23 pairs (21%) attempted a second brood with only 3 pairs (13%) being successful in raising young in both broods. In Vermont, only pairs that started nesting the earliest attempted second broods. The gnatcatcher is a persistent renester and may make as many as 6 attempts in a year to raise a brood. In southern Illinois, renesting attempts ceased in early July. Ontario clutches contained 3-5 eggs, mostly 4 or 5. Mean size of 182 North American clutches was 4.5 eggs (range 3-6 eggs); 3- and 6-egg clutches are rare (Chamberlin 1901; Goguen and Mathews 1996; Kerschner and Ellison 2020; Kershner et al. 2001; Peck and James 1997; Root 1969b; Weston in Bent 1949).

Both sexes breed in their first year. The mating system is monogamous with no documented cases of polyandry or polygyny. Males and females share winter ranges and follow similar migration schedules suggesting the possibility of multi-year pair bonds, but there is no strong evidence that this occurs (Kerschner and Ellison 2020).

While foraging, the Blue-gray Gnatcatcher enters each tree that it encounters along a foraging route without exhibiting any avoidance or preference of any particular tree species. This study was done in California; it is uncertain if coniferous species are avoided in Ontario. An Illinois study determined that it was selective in the trees that it used for foraging. In order of preference, black gum, sycamore, pin oak, silver maple, shellbark hickory, and bitternut hickory were used more than their availability. In order of declining avoidance, pumpkin ash, red maple, blue beech, white elm, green ash, Shumard oak, and Manitoba maple were used less than their availability. Most foraging occurs near the tips of branches in broad-leaved foliage of trees and shrubs. Feeding is not confined to any particular level of trees and may occur in the herbaceous layer when adults are feeding young, where they search for grasshoppers and other large insects. It seldom forages around the trunk of trees or on large limbs where foliage is scarce. It typically forages on small-diameter horizontal twigs, but also on vertical twigs. It rarely perches on the upper surfaces of horizontal or diagonal limbs when twigs are absent. When feeding itself, the Blue-gray Gnatcatcher usually only gleans, but uses more varied tactics when feeding young. It hops rhythmically from perch to perch remaining only momentarily in 1 location (80 perches in 120 seconds counted) and fans its tail constantly which may assist in flushing prey. It rarely still-hunts by remaining in 1 location for more than 5 seconds. Three basic foraging techniques are used: surface gleaning, gleaning while hovering, and sallying after flushed prey. Hawking insects in flight or falling through the air is a rare foraging technique. Gleaning while hovering is used to capture prey on terminal sprigs of tree foliage or from tops of tall grasses and herbaceous plants (Gabbe et al. 2002; Kerschner and Ellison 2020; Root 1967).

Nestlings are fed larger food items than are consumed by adults. In California, grasshoppers were brought to young on nearly 20% of feeding trips but only 1 grasshopper was found in the stomach of an adult. In Florida, nestlings were fed mostly caterpillars. Optimal prey size appears to be 3-10 mm for adults; they rarely eat items smaller than 1 mm and larger than 10 mm. A sample of 287 stomachs from California revealed that the diet was predominantly insects but included spiders. Plants were found in stomachs on 3 occasions, but were thought to have been ingested incidentally. The diet consisted of 36.0% bugs, 32.3% beetles, 13.8% hymenopterans, 7.1% butterflies and moths, and 10.3% other. At least 70 families of arthropods were represented in the samples. In spring, plant bugs and lepidopterans formed a large proportion of the prey when these insects were abundant. In the summer, treehoppers and leafhoppers were more important in the diet. It avoided attacking late instar larvae of the tent caterpillar. In Vermont, half of 34 identifiable prey seen captured were adult and larval moths (Kerschner and Ellison 2020; Root 1967, 1969b).

The Blue-gray Gnatcatcher is one of the smallest regular hosts of the Brown-headed Cowbird. Parasitism rates vary considerably geographically. In Ontario, 4 of 33 nests (12.1%) were parasitized. Reported parasitism rates in other areas are 3.6% in Vermont, 27% in California, 56% in Illinois, 82% in Mississippi and Texas, and 77% in New Mexico. In New Mexico, parasitism was responsible for failure of 48 of 83 nests (58%). Individual pairs were inconsistent in their response to parasitism, both deserting and accepting parasitized nests. Nest desertion followed by renesting appeared to be an effective antiparasitism strategy but only 45% of nests parasitized during the egg-laying period were deserted. Two pairs buried a cowbird egg into the nest bottom. In both cases the cowbird egg was laid prior to completion of nest building before any gnatcatcher eggs were laid. Egg burying and nest desertion are the only rejection possibilities for the gnatcatcher because it is physically incapable of removing cowbird eggs. Cowbirds may remove gnatcatcher eggs and nestlings. Of 25 New Mexico nests where cowbird eggs were accepted during egg laying, 0 fledged gnatcatchers but 16 (64%) fledged cowbirds. Of 7 nests where cowbird eggs were laid during the incubation period, 2 were lost to predation, 3 fledged only gnatcatchers, 1 fledged only a cowbird, and 1 fledged 3 gnatcatchers and 1 cowbird. A later study in New Mexico found that no gnatcatchers fledged any of their own young in 54 parasitized nests. Gnatcatchers with a parasitized nest feed nestlings at the same rate as they would a normal clutch, but virtually all the food is consumed by the cowbird young. Brown-headed Cowbirds are able to fledge from gnatcatcher nests, but they do so at much smaller size and their survivorship to independence may be reduced. Gnatcatchers may exhibit an avoidance reaction to cowbirds when their populations are high. In Illinois in a bottomland forest that typically supported gnatcatchers, none were found in a year when the cowbird population was high (Ellison and Sealy 2007; Ellison et al. 2006; Goguen and Mathews 1996; Goguen et al. 2011; Graber et al. 1979; Kerschner and Ellison 2020; Kershner et al. 2001; Kilpatrick 2002; Peck and James 1997; Root 1969b; Scott and McKinney 1994; Weston in Bent 1949).

The response of the Blue-gray Gnatcatcher to forest management practices has been studied in Ontario, Pennsylvania, South Carolina, and Illinois. In Ontario in the Carolinian Forest Region, it was not observed in harvested woodlands. Holmes et al. (2004) concluded that it was a significant indicator of woodlands without a recent history of logging. In Pennsylvania, 1-ha plots were clear-cut in aspen and mixed-oak forests as part of a Ruffed Grouse management strategy. The Blue-gray

Gnatcatcher increased significantly due to this management, which resulted in a mosaic of forested plots of varying ages after the fourth cutting cycle (Yahner 2003). In South Carolina, Harrison and Kilgo (2004) compared its density in bottomland hardwood forests where patches of forest were left within a clear-cut with standard clear-cuts and leaving the forest intact. Densities in both types of clear-cuts were less than in control areas. Differences in density between standard clear-cuts and clear-cuts with patch retention were not significant. It was only 1 of 2 forest species that used clear-cuts in the second year of harvest. In Illinois, Robinson and Robinson (1998) cut openings of 0.02-0.4 ha in a 2,000-ha forest. The Blue-gray Gnatcatcher was significantly more abundant in recently cut compartments than in uncut areas and older cuts.

In Georgia, the Blue-gray Gnatcatcher increased in response to increasing fire severity. These responses were related to suppressed understorey, more open conditions, higher insect abundance, and improved foraging habitat (Klaus et al. 2010). In the Midwest, its greatest abundance occurred with fire frequency of 0 fires every 15 years, but this study was in oak savannahs where the canopy was already open (Grundel and Pavlovic 2007b). In North Carolina pine-oak forests, it responded positively to fire but only to those of high severity. Peak occupancy occurred 5-10 years after a severe fire. In this habitat, large patches of high-intensity fires may be needed to maintain populations (Rose and Simons 2016).

In urban woodlots in Chicago, the Blue-gray Gnatcatcher was positively correlated with coverage by nonnative honeysuckles and invasive-shrub stem density, particularly that of common buckthorn (Schneider and Miller 2014).

In New Jersey and Pennsylvania over a 15-year period, hemlock declined from representing 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The gnatcatcher responded favourably to hemlock decline and increased (Toenies et al. 2018).

The Blue-gray Gnatcatcher may be sensitive to severe winter conditions. Declines were observed in Maryland and North Carolina after the severe winters of 1977-78 and 1978-79 in the southeastern United States, with subsequent recovery (Kerschner and Ellison 2020).

In California, defoliation of trees by the tent caterpillar resulted in a general failure of nesting, probably due to the decline in food supplies (Root 1969b).

Status

McIlwraith (1894) concluded that the Blue-gray Gnatcatcher was a regular summer resident in southwestern Ontario, although it was locally distributed and not very abundant. In Elgin County in 1891 and 1954, it was considered a fairly common migrant that might breed; by 2000, it was an uncommon breeder (Lancaster et al. 2004). Baillie and Harrington (1937) considered it a very rare breeding species of extreme southern Ontario, south of Middlesex County and Durham Region. The most northerly records of its occurrence were Sault Ste. Marie, Goderich, and Sarnia. Curry (2006) reported only 4 records of the Blue-gray Gnatcatcher for the Hamilton area 1930-50. There were major flights of this species to the northeast in 1947 and 1954, and it has been observed in the Hamilton area annually since 1954 where it is expanding its range. Weir (2008) reported that the first birds appeared in the Kingston area as part of a major flight in 1953. Since then, it has been seen in

1954, 1958, and every year since 1959. Brewer (1994) noted that the Blue-gray Gnatcatcher was a regular but rather sparse breeder in southern Wellington County, but that it had become substantially more common in recent years. During the first atlas, Sutherland and Gartshore (in Cadman et al. 1987) concluded that it was an uncommon breeding species in southern Ontario. It was most abundant in the Carolinian Forest Region but absent from many squares there. Although there were some breeding records, it was still largely absent from southeastern Ontario. In the Great Lakes–St. Lawrence Forest Region south of the Canadian Shield, it was predominantly confined to the shores of Lake Ontario and the St. Lawrence River and in a band along the southern edge of the Shield. James (1991) considered it an uncommon summer resident in the Carolinian Forest Region; occasional and rare north to Bruce and Simcoe counties and the Ottawa area; and a vagrant to Manitoulin Island and in the north to Rainy River.

During the second atlas, the breeding distribution of the Blue-gray Gnatcatcher was similar to that reported during the first atlas. There was a bit of a northward range extension, with records from Manitoulin Island, the Bruce Peninsula, and considerably more records in the Great Lakes–St. Lawrence Forest Region south of the Shield. There was a significant increase in its probability of observation for the province as a whole due to infilling of its range in the Carolinian Forest Region and expansion in the Great Lakes–St. Lawrence Forest Region. It was most numerous along the north shore of Lake Erie with areas of moderate density near Grand Bend, along the north shore of Lake Ontario, and on the Frontenac axis (McCracken in Cadman et al. 2007).

Breeding Bird Survey data for Ontario indicate that the Blue-gray Gnatcatcher increased 1.78% annually 1970-2021 and decreased 3.37% annually 2011-21. The long-term trend was of medium reliability; the short-term trend was of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings may begin to feed themselves as early as 9 days after leaving the nest. Adults raising a second brood usually leave the young of the first nest to fend for themselves when they are about 18 days old. In California, fledglings start to move into areas unoccupied by territorial adults shortly after they are independent, but in the east family groups may remain together until mid-August (Kerschner and Ellison 2020).

Fledglings remain in dense foliage within 20 m of the nest for the first 3 days after leaving the nest. In California, young hatched in oak forest were led by their parents to shrub habitat when they were 1 or 2 days old. By the time fledglings are 4 days old, they begin to follow their parents. Adults raising a second brood may leave the brood in an area on the periphery or outside the territory while they attend to the second nest. The same stands of vegetation may be used by fledglings of different pairs at different times (Kerschner and Ellison 2020; Root 1967, 1969b).

In Missouri, Porneluzi et al. (2014) netted birds during the postfledging period in an oak-pine-hickory forest 2-15 years after it was clear-cut. The Blue-gray Gnatcatcher exhibited a significant curvilinear trend, peaking shortly after harvesting, declining to a low around 6-12 years after harvesting and then increasing somewhat.

MIGRATION

The Blue-gray Gnatcatcher is a diurnal migrant (Kerschner and Ellison 2020). Weir (2008) noted that gnatcatchers coming into the Kingston area appeared to be crossing Lake Ontario from the south. The sexes appear to migrate synchronously. Although loose aggregations may occur during migration, these seem to be fortuitous with gnatcatchers being more frequent as members of multi-species flocks (Kerschner and Ellison 2020).

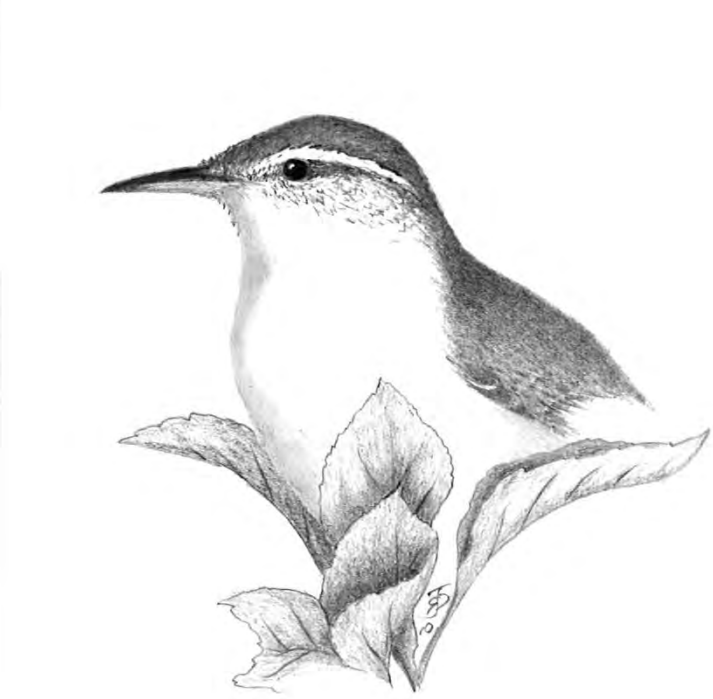
Spring migrants return to southern Ontario in mid-April with most moving through in the first 3 weeks of May. The Blue-gray Gnatcatcher appears to leave the breeding area shortly after the young are independent, usually in mid- to late August. Peak movement is in August. Most birds leave the province by the end of September, but stragglers may persist until late December (Cheskey 1985; Curry 2006; Lancaster et al. 2004; LaForest 1993; Weir 2008).

In Pennsylvania during autumn migration, the Blue-gray Gnatcatcher was most abundant at forest edge, followed by forest interior, suburban forest, forest-agricultural edges, and shrub-sapling-stage forest. It was not detected in pole-stage forest (Rodewald and Brittingham 2002). Also in Pennsylvania, it preferred larger woodlands during spring migration but had no relationship with forest size in autumn (Keller and Yahner 2007). In Minnesota and Wisconsin during spring migration, it was equally abundant in upland and floodplain forests (Kirsch et al. 2013).

James (1991) considered the Blue-gray Gnatcatcher an uncommon migrant in the province. Migration monitoring data from Long Point Bird Observatory indicated a significant increase of almost 5% per year since 1961, with the greatest rate of increase taking place since the late 1970s (McCracken in Cadman et al. 2007).

Bewick's Wren

Thryomanes bewickii



BREEDING SEASON

Habitat Requirements

In Ontario, the Bewick's Wren has nested only at Point Pelee National Park. All nests were in open habitat in wooded parkland and were in picnic pavilions or under a cottage (Peck and James 1987).

Where the Northern House Wren is absent, especially in the east, the Bewick's Wren prefers to nest near dwellings and outbuildings near shrubby or wooded areas. In the west, the 2 wren species may coexist but in the east the presence of house wrens forces Bewick's Wrens to nest in woodlands where there is dense shrub cover. The Bewick's Wren may nest in deciduous, mixed, and coniferous stands. Dominant tree species in breeding habitat include chestnut oak and other oaks, ashes, and pitch pine. In addition to open, brushy woodlots and suburban and rural residential areas, it nests in lowland riparian forests, shrubby thickets, hedgerows, orchards, and farmland at edges of forested areas. Forests with dense overhead canopy are usually avoided as are grassy areas devoid of shrubs. A Utah study concluded that it was a habitat generalist confined to areas of dense thickets; the Northern House Wren was associated with lower shrub density and increasing amounts of grass. In Washington, the Bewick's Wren nests in deciduous and riparian woodlands, shrubby thickets, parks, and gardens. It preferred higher foliage-height diversity and more complex and dense habitats than the Song Sparrow. In many areas, particularly in the west, the Bewick's Wren is strongly associated

with junipers (Bent 1948; Campbell et al. 1997; Gorton 1977; Graber and Graber 1963; Kennedy and White 2020; Kroodsma 1973; Miller 1941; Pogue and Carter 1995; Smiley and Stapleton 1976; Sutton 1930; Whitmore 1977). In grassland areas of Oklahoma, it was absent where there was no shrub cover and increased in abundance with increasing density of red cedar. It was associated with shrub and woodland cover (Chapman et al. 2004). In California, it was significantly more abundant in oak savannahs with shrub cover and montane hardwoods than in oak savannahs with grass cover and oak woodlands (Wood et al. 2013). In Texas, its highest probability of occurrence was at 40-60% woody canopy cover within a radius of 250 m (Plappert et al. 2024).

During the breeding season, adults roost individually in cavities in trees and posts, among vines and dense conifer foliage, and in buildings and nest boxes. Young roost together for about a month, sometimes in old nest cups (Kennedy and White 2020).

All Ontario nests were on or under buildings at Point Pelee. The first was on a beam under a cottage and the others were on beams under the eaves of picnic pavilions. Two nests were 1.8-2.4 m above ground (Baillie 1962; Peck and James 1987).

The Bewick's Wren is a secondary cavity nester that uses a wide range of natural and artificial sites. Nests in natural situations may be in tree cavities or old woodpecker holes. Less frequently, nests are in burrows in the sides of banks, in holes in the ground under shrubs or rocks, at the mouth of vacant rodent holes, in crevices of rock ledges, in interstices between small boulders, in holes in the floor of small caves, in upturned roots of fallen trees, and in the centre of dense brush piles. Most nests in artificial situations are in openings under, on, or in abandoned or occupied buildings. Nests have been reported in rock walls, piles of boxes, under roof tiles, in nest boxes, in tin cans at a landfill site, in old cow skulls in pastures, on beams under buildings or under eaves of open structures, in a truck glove compartment box (the truck was used daily), in empty cartons, among saddles and harness, in rubber boots, on plates or exposed shelves in buildings, in garage drawers and cupboards left ajar, behind a frying pan hanging on a post, in hay in barns, in holes in fence posts, in empty barrels, in discarded clothing hung in buildings, in baskets and empty flowerpots, in deserted automobiles and machinery, in oil wells, in mail boxes, in old phoebe and Barn Swallow nests associated with buildings, in old oriole and mockingbird nests, in a hanging sack, in woodpiles, in a paper bag half filled with nails, and in a fishing creel. In British Columbia, 47% of nests were in buildings, 5% in posts and poles, 4% in abandoned automobiles, and 40% in trees. Overall, 42% of

nests were in artificial cavities, containers, or nest boxes; 34% were in natural cavities or crevices; and 15% were in rafters or other supports in buildings. Nearly 80% of nests were in backyards, on farms, or in gardens. In West Virginia, 12% of nests were in natural or woodpecker cavities and the remainder were associated with buildings. It is much less inclined to nest in nest boxes than the Northern House Wren and Bewick's Wren's nests tend to be placed closer to the ground. Nests have been reported from below the ground to 10 m above ground, but most are 1-3 m up. In British Columbia, nests were 0.3-6.0 m from ground with most 0.9-1.8 m up. One California nest extended horizontally about 45 cm into a hillside (Beemer 1947; Bent 1948; Campbell et al. 1997; Kennedy and White 2020; Miller 1941; Pogue and Carter 1995; Root 1969a; Smiley and Stapleton 1976; Verner and Purcell 1999).

The male defends the territory and resident pairs may retain their territory year-round. Territories may overlap those of Carolina and Northern House wrens but in some areas Bewick's and house wren territories may be exclusive. In Oregon, 3 of 6 house wren territories were completely within Bewick's Wren territories and the other 3 overlapped Bewick's Wren territories. Bewick's Wren territories that did not overlap Northern House Wren territories averaged 2.0 ha (range 1.3-3.8 ha). Territories overlapping those of Northern House Wrens were larger and averaged 3.8 ha (range 2.5-4.8 ha). The larger territories may have been due to the extensive open areas in them or possibly due to interspecific competition. In northeastern Kansas, territories averaged 1.58 ha (range 1.17-2.14 ha); territories that overlapped those of Northern House Wrens in California averaged only 0.34 ha (range 0.17-0.45 ha). Territory size and shape vary with the distribution of vegetation and open space and the number of birds (Kennedy and White 2020; Kroodsma 1973; Miller 1941; Sutton 1930).

The rate of natal philopatry in migratory populations is uncertain. In resident populations, most young leave the natal territory at age 5 weeks, although some may remain until the following spring. Young males may establish a territory in July or August of their first year. One male established a territory at age 60 days and a female was mated to an adult male at age 75 days. Of 17 fledglings in a resident Oregon population, 11 males dispersed an average of 1.2 km (range 0.1-3.2 km), 2 females dispersed 0.8 km, and 4 females remained in the natal territory 10-27 weeks but did not breed there. In Kansas, 2 birds banded as nestlings returned to nest the following year (Kennedy and White 2020).

Resident adults may maintain their territory as long as they live. Limited evidence suggests that migratory adults have fairly high site fidelity. In Kansas, 2 males that bred in 3 successive years (4% of birds), and 3 males and 3 females that bred in 2 successive years (15% of birds) all returned to nest within 100 m of the nest where they were originally banded. It was thought that the percentage of returning birds was an underestimate. In California, 1 nest site was used in 10 consecutive years, but it was unknown if the same birds were involved (Kennedy and White 2020; Miller 1941).

Limiting Factors

Eggs have been found in Ontario nests from 9 to 24 May (Baillie 1962; Peck and James 1987). All Ontario nests failed; first nests that went full term would probably contain eggs into early June. In other areas, the Bewick's Wren may nest late into the season: a specimen taken 12 December in California exhibited evidence of breeding. In resident populations, the nest may be started very early in the season and construction may take as long as 1 month. The median time to build a nest is 7 days and 66% of nests are completed in less than 8 days. A pair renesting in a new cavity built a nest

in a single day. The first egg is usually laid sometime between the first and third morning after the nest is complete. One egg is laid per day, although a day may occasionally be skipped in larger clutches. Incubation is initiated with laying of the penultimate or last egg. Early studies reported the incubation period to be 10-14 days, mostly 14 days. It appears as though reports of shorter incubation periods are incorrect, and that the incubation period is 14-16 days. Second broods may have slightly shorter incubation periods. The nestling period is 14-22 days and appears to be shorter in the southern portion of its range. In British Columbia, the nestling period is 18-22 days compared with 14-17 days in the south where 14 days is most frequent. The young remain together and continue to be fed by the adults for about 2 weeks after fledging (Bent 1948; Campbell et al. 1997; Kennedy and White 2020; Koenig and Stahl 2007; Miller 1941).

Most pairs raise 1 brood annually, but 2 broods are commonly raised. Although most cases of second broods are from more southern portions of its range, second broods are common in British Columbia. Only birds with early first clutches (13 April to 15 May) initiate second broods, usually 1-10 days after the first brood fledges. One Oklahoma pair raised 3 broods in a season. Renesting occurs if loss occurs early in the season. Some birds lay 3 clutches in order to raise 2 broods: the initial clutch, a replacement clutch, and the second brood. Clutches of 4-6 eggs were found in Ontario. Clutches of 3-8 eggs have been documented, with a mean clutch of 5.6 eggs for clutches started prior to 1 June and 5.2 eggs for later clutches. Mean clutch sizes are larger in the east than west. Clutches of 9-11 eggs were reported historically, but clutches this large have not been documented recently (Baillie 1962; Bent 1948; Campbell et al. 1997; Kennedy and White 2020; Pearse et al. 2004; Peck and James 1987).

Both sexes breed in their first year and continue to breed in successive years. In some populations, many males remain unmated with as many as 24% not breeding. These males tend to have inferior territories. The mating system is predominantly monogamous. Rare cases of polygyny and polyandry have been observed or suspected. One polyandrous female laid the first egg of her second clutch when the young of the first brood were 15 days old, 2 days before fledging. Resident birds may remain paired long term. Migratory birds may pair early each spring (Kennedy and White 2020; Kroodsma 1972; Pearse et al. 2004).

The Bewick's Wren feeds primarily by gleaning invertebrates from leaves, branches, and twigs of the lower strata of herbaceous species, shrubs, and trees. Much foraging is done in dense vegetation, but it also ventures into open areas to forage on tree trunks. On small branches and twigs, it sometimes clings to the lower sides and hangs upside down. In dense vegetation, it moves quickly among the lower branches. On tree trunks, it usually begins at the base and hops upward, often in a spiral fashion similar to that of the Brown Creeper. It removes insects imbedded in bark by a rapid series of pecks resembling those of a woodpecker. Occasionally it hops on the ground and picks food from it or turns over leaves with its bill. It rarely hawks or hovers for food. In early spring, the sexes may segregate with the female foraging near the ground and the male in trees. After nest building and later in the season, there are no sexual differences in foraging. Seasonal differences in foraging techniques were observed in Arizona: 77-82% probing and 17-18% gleaning in May and June; and 35-46% probing and 54-64% gleaning in July. Gleaning in July was mostly on the ground, possibly in response to new plant growth. A New York pair foraged for food for nestlings in more

open forest; adults with fledglings foraged in dense undergrowth (Kennedy and White 2020; Miller 1941; Smiley and Stapleton 1976).

Males bring food to incubating females. Supplemental feeding experiments have demonstrated that food was limited to incubating females. Initially, 1-cm-long caterpillars are brought to nestlings but, as the young age, they are brought larger items (2-3 cm) that include butterflies and some hard-bodied arthropods. Food brought to Kansas young consisted of 51% caterpillars with some adult butterflies and moths, 13% spiders, 6% grasshoppers, 6% insect pupae, 4% beetles, and unidentified arthropods. An examination of 146 stomachs from all months in California determined that the adult diet consisted of 31% bugs, 21% beetles, 17% bees and wasps, 12% caterpillars with some adult butterflies and moths, 6% flies and other insects, less than 5% spiders, 4% grasshoppers and crickets, and less than 3% vegetation (fruit pulp, seeds, and plant rubbish). Most vegetable matter was eaten in December and January. The same study determined that nestlings were fed predominantly caterpillars, but also spiders, grasshoppers, insect pupae, and various small arthropods (Bent 1948; Kennedy and White 2020; Pearse et al. 2004; Smiley and Stapleton 1976).

The Bewick's Wren is rarely parasitized by the Brown-headed Cowbird. Only 15 cases of parasitism have been documented: 5 In Texas, 5 in British Columbia, and 1 each in Ohio, Tennessee, Missouri, Oklahoma, and Kansas. In most cases, wrens either deserted the nest or removed the parasitic egg. In 1 British Columbia nest, the adults raised 1 cowbird but none of their own young (Campbell et al. 1997; Kennedy and White 2020).

One of the greatest limiting factors to the Bewick's Wren is interspecific competition. Interspecific competition has been reported with the Northern House Wren, Carolina Wren, and Song Sparrow. The most significant competitor is the house wren. In some areas, the 2 species coexist peacefully with overlapping territories. In other areas, the 2 species coexist but with much territorial conflict with the house wren being dominant. In some areas, the house wren has resulted in local extirpation of the Bewick's Wren. Peaceful coexistence occurs mostly near the west coast where the 2 species have been in contact for a long time. In some areas, resident populations of Bewick's Wrens are often able to raise a brood before the migratory house wrens arrive. Once house wrens appear, Bewick's Wrens are frequently relegated to suboptimal habitats. Competition is most extreme in eastern populations where both species are migratory because the Bewick's Wren does not have the benefit of an earlier start to breeding. The house wren moved into much of this area fairly recently so that the 2 species have not adapted to coexistence. Where the 2 species compete, the house wren is more aggressive and dominant and excludes the Bewick's Wren from the best habitats. The house wren frequently punctures and removes Bewick's Wren eggs from nests, or covers up their nests with twigs; occasionally it kills Bewick's Wren nestlings. In Kansas, 35.6% of Bewick's Wrens' nests failed as a result of house wren activity and 81% of nest losses were due to the house wren. Nest-box programs for Bewick's Wrens usually fail where house wrens are present. Not all authors agree that declining Bewick's Wrens are a result of the house wren, but there is very strong circumstantial evidence for this being the case in the east where declines in the Bewick's Wren are strongly correlated with increases in the house wren. In winter, the Bewick's Wren avoids Florida and southern Louisiana and shows a depression in numbers in southern Texas. These are the locations where the house wren is most abundant. There is some evidence that the 2 species are

becoming more tolerant of each other. In West Virginia, the Bewick's Wren reoccupied areas where it was formerly common and subsequently disappeared after the arrival of the house wren (Bent 1948; Brooks 1947a; Kennedy and White 1996, 2020; Kroodsma 1973; Root 1969a, 1988; Sutton 1930; Verner and Purcell 1999; Whitmore 1977).

Occasionally territorial interactions occur with the Carolina Wren, but the 2 species often coexist with no apparent conflicts (Sutton 1930). In winter, the Bewick's Wren appears to avoid the southern grasslands and eastern part of the tree and shrub savannah habitat where the highest concentration of Carolina Wrens occurs (Root 1988).

In Washington, territories of Bewick's Wrens and Song Sparrows overlapped in forage behaviour, heights, and techniques. The Song Sparrow showed some territorial aggression to the Bewick's Wren, but this declined as the season progressed. The 2 species appeared to divide the habitat vertically. Presence of Song Sparrows does not appear to be a significant limiting factor to the Bewick's Wren (Gorton 1977).

Nest sites may be limiting in some parts of the Bewick's Wren's range. Addition of nest boxes in Arizona and Mexico significantly increased its density but nest boxes have the potential to increase local house wren populations (Kennedy and White 2020).

Near Seattle, the Bewick's Wren strongly avoided areas within forest patches that were rich in a single predator species, but co-occurred with nest predators at larger scales (Marzluff et al. 2007).

Severe winter weather may result in significant mortality. Significant declines occurred throughout the Bewick's Wren's range after severe winters in the 1970s. A localized decline of 62% occurred in California after the exceptionally cold winter of 1990-91 (Kennedy and White 2020; Verner and Purcell 1999).

DDT has been suggested as a potential cause of this species' decline. A possible significant limiting factor is the increased abundance of feral and domestic cats (Campbell et al. 1997; Kennedy and White 1996, 2020).

Price (2004) concluded that the breeding range of the Bewick's Wren might expand northward to include southern Ontario if the average summer temperature increased by 2°C.

Status

The first record of the Bewick's Wren nesting in Ontario occurred in 1950 when a nest was found at Point Pelee. Nesting occurred at the same location in 1956 and 1957. Five nests have been found in Ontario and all were at Point Pelee. There has been no evidence of breeding in the province since 1957 (Baillie 1962; James 1991; Peck and James 1987).

The Bewick's Wren has experienced large fluctuations in its abundance and range. It responded favourably to the extensive deforestation due to European settlement. Most of its initial range extension occurred from about 1890 to 1910. As early as the 1920s significant declines in breeding populations occurred, especially in the east at the same time that the Northern House Wren was extending its range. Despite this decline, in the 1940s the Bewick's Wren was steadily increasing its range northward into Illinois, Michigan, Pennsylvania, Ohio, and Indiana where it was unknown 50 years previously. It was near the end of this range expansion that it occurred in Ontario. The decline

of the Appalachian Bewick's Wren, the eastern subspecies that probably nested in Ontario, was first noted in the 1930s. The Bewick's Wren has declined steadily since the Breeding Bird Survey was initiated in 1966. It has declined significantly throughout its range, but has almost disappeared east of the Mississippi River. During the 1980s, it was estimated that there were only 20 breeding pairs in Maryland, Virginia, and West Virginia combined (Bent 1948; Kennedy and White 1996, 2020).

MIGRATION

West coast birds are resident whereas eastern birds are short-distance migrants. Spring migration in the east occurs from mid-March to mid-April. Males arrive a week prior to females. Autumn migration in the east extends from late September to early November. In Ontario, the Bewick's Wren has been recorded until late October (James 1991; Kennedy and White 2020; Miller 1941).

It is unknown whether the Bewick's Wren is a diurnal or nocturnal migrant. There are 4 records of it striking towers, suggesting some nocturnal migration. During migration it typically forages and travels singly, but may occasionally occur in mixed-species flocks (Kennedy and White 1996, 2020).

During migration, the Bewick's Wren occurred in lowland riparian forest in Colorado (Kennedy and White 2020). Campbell et al. (1997) summarized its nonbreeding season habitat in British Columbia, but the species is a permanent resident there. They described it as a species of edge habitats where shrubby areas abutted coniferous forest, and of shrubby areas at edges of fields, along power-line cuts, around swampy ponds and sloughs, along roads, and on shorelines of creeks and lakes. It also occurs in shrubby parks and residential gardens.

The Bewick's Wren is a vagrant in Ontario that exhibits no regular migration. It is absent in the province most years.

Carolina Wren

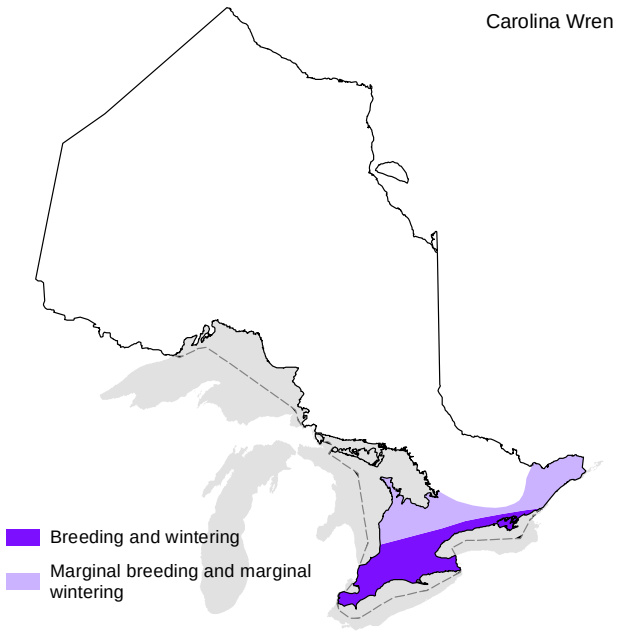
Thryothorus ludovicianus

BREEDING SEASON

Habitat Requirements

In Ontario, the Carolina Wren nests mostly in buildings in residential and wooded areas, but also in deciduous woodlands. There is 1 record of it nesting in duck-trap gear in a marsh (Peck and James 1987, 1997). In Elgin County, it occurs most frequently along Lake Erie, in shoreline woodlots, and in villages and towns (Lancaster et al. 2004). At Presqu'ile, all nesting records are from the campground (LaForest 1993).

The most important habitat requirement of the Carolina Wren is dense shrubs or brushy cover. It may frequent brush piles, fallen treetops, and rocky places in woods. In the northern portion of its range, it is most frequently associated with rural dwellings and residences in villages and towns, although it also inhabits woodlands. In the south, it tends to occur more frequently in woodlands than around residences. Within woodlots, it is often found along watercourses and in ravines with steep, bare banks. Areas with exposed tree roots or uprooted trees are preferred. It often occurs in disturbed woodlands and is more frequent in younger than older stands. In Tennessee, it selected areas with large numbers of canopy and subcanopy trees. These trees were smaller than those



found in the general area. It appears to prefer moist woodlands over upland hardwoods. In Alabama, it was most likely to occupy floodplain forests during the breeding season. It is not area sensitive and is more likely to be found in isolated woodlots than in areas of contiguous forest. Its presence is not associated with width of riparian forests. Although 1 study suggested it required 10 ha of forest cover, it used significantly smaller woodlands in South Carolina. Its probability of detection in South Carolina woodlots surrounded by fields was 84% in 0.5-ha woodlots, 90% in 1-ha woodlots, 98% in 2.5-ha woodlands, and 100% in 5-ha and 10-ha woodlots. Its probability of detection was lower in hardwood woodlots surrounded by pine forest: 14-15% in 0.5 ha, 21-22% in 1.0 ha, 43-50% in 2.5 ha, 70-94% in 5 ha, and 72-100% in 10 ha (Anderson and Shugart 1974; Bannon and Rail in Gauthier and Aubry 1996; Bent 1948; Fitch 1958; Haggerty and Morton 2020; Keller et al. 1993; Kilgo et al. 1997; Lynch 1987; McClure et al. 2013a; Noon et al. 1979; Robbins 1979; Sutton 1930).

In Texas pine and pine-hardwood forests, abundance of the Carolina Wren was positively correlated with the number of shrub species and stems, foliage density 1 and 3 m from the ground, and percent coverage by hardwoods 5-16 cm diameter at breast height (DBH). It was negatively correlated with percent coverage by pines 17-32 cm DBH and the number of tree stems 17-32 cm DBH (Conner et al. 1983).

In South Carolina, the Carolina Wren was most frequent in forest edge habitat during spring migration and the breeding and postbreeding seasons. Usage of forest gaps was consistent from spring through autumn and was typically lower than for other habitat types (Bowen et al. 2007). Kroodsma (1984) found no edge effect for it in Tennessee. It occurred in low density at forest edge to approximately 100 m from edge, was most abundant 100-220 m from edge, and occurred in low density beyond 220 m from edge. All birds seen were within 268 m of edge and none were present 268-488 m from edge.

Roosts are an important habitat component for the Carolina Wren. During the incubation period, the male roosts in shrubs, usually within 50 m of the nest. Both adults roost in shrubs during the nestling period. A Florida pair roosted together in a hanging plant basket 2.4 m from the nest during nest construction through laying of the first egg (12 nights) and also on the day that the fourth egg was laid. It is extremely vulnerable to cold, so roosts are important even on cool summer nights. There is 1 record of 4 fledglings roosting together in a newly constructed Northern Cardinal nest on a night when there was frost. In winter, roosts are critical in keeping wrens warm. Birds may roost in their own nests and 1 pair used an old Eastern Phoebe nest under the eaves of a building

as a winter roost. There are a few records of Carolina Wrens enlarging the hole in hornets' nests and using the nest as a roost site. Other reported roost sites include in bird boxes, old coat and shirt pockets, hanging ferns, garages, barns, squirrel dreys, vine tangles, decaying logs, small cavities in snags of trees, and on the ground under ferns. Members of a pair may roost together or singly (Bent 1948; Brooks 1932; Fitch 1958; Haggerty and Morton 2020; Jawor and Gray 2003; Labisky and Arnett 2006; Laskey 1948; Ramsay 1987).

Twenty-five percent of Ontario nests were in natural habitat, mostly in cavities in stumps and fallen trees; 1 was in a brush pile. Nests in buildings and other artificial sites were on shelves, electrical boxes, and beam ledges; in washbasins, 6-quart baskets, empty boxes, nail barrels, travel bags, funnels, hanging flower pots, bird boxes, and in duck-trap gear in a marsh; under eaves of a building; and under an overturned canoe between a seat and a seat-pad (LaForest 1993; Lancaster et al. 2004; Peck and James 1987, 1997). Nests are hidden at depth in a recessed area and may be used for subsequent nestings in the same year or in following years. Nests were 0.5-4.5 m from the ground, with most 1.2-2.2 m up (Peck and James 1987, 1997).

Nests in natural habitats elsewhere were under decayed wood among stump roots, among exposed roots of a walnut tree, between the divided stem of a young cedar tree, in a 3-point fork of a white elm in a woodland, in a hole in the ground, in tree cavities, in a black walnut on a partially broken-off limb, in tangles of vines, in conifer branches, and in a hole in a bank. First nests of the season are often on the ground under dense, fresh vegetation. Most reported nests are in or on artificial features, but these nests are much easier to find and may be over-represented in the sample. Many nests are in buildings; wrens may gain access through very small openings such as a hole in a cracked window pane or a partially open window. Ledges and eaves around buildings are favoured nesting areas. Nests have been in hanging baskets and flower pots, in a paper bag on a shelf, between the rafters of a porch, on the top of a cupboard in a bedroom, in hornets' nests, behind a picture in a bedroom, in bluebird boxes, on shelves among cans and jars, in a sack of old clothes, in a sack of seeds, in the fold of a hanging quilt, in a crevice between a house wall and a downspout, in a mail box, in a tin cylinder for newspapers, in a dust mop, in window boxes, in cardboard boxes, in a pair of pants hanging from a hook, in glove compartments of abandoned cars, in grain sheaves, in a cavity in a stone wall, in old shoes, in tin cans, on top of propane tanks, in the back of a sofa in a house, and in discarded hats. One successful nest was on a tractor that was used daily. Nest height extremes of from below the ground to 9 m have been reported but most nests are 1-2 m up; the mean height of 393 nests was 1.8 m (Bent 1948; Brooks 1932; Chapman 1947; Grzybowski 1995; Haggerty and Morton 2020; Laskey 1948, 1950a; Luther 1974; McGaha 1998; Nice and Thomas 1948; Ramsay 1987; Sanborn 1932; Sutton 1930; Tinker 1909; Turcotte 1989).

The Carolina Wren is territorial year-round, and territorial aggression is highest outside the breeding season. The size of the territory is defined by resources required for winter survival rather than breeding. Territory size decreases with increasing wren density, but boundaries may overlap slightly and shift with changes in density. All nesting, foraging, and feeding of young occurs within the territory. In Illinois, the mean size of 3 territories was 0.12 ha (range 0.049-0.25 ha). In Tennessee, mean territory size was 4.1 ha (range 2.1-8.1 ha); mean territory size was 1 ha in North Carolina. The year-round range of Alabama birds averaged 0.7 ha (range 0.38-1.72 ha). In Kansas, 1 territory

measured 2.3, 3.7, 1.6, and 3.1 ha over 4 years. Although this territory was occupied in 6 years, the individuals using it changed (Brewer 1955; Fitch 1958; Haggerty and Morton 2020; Haggerty et al. 2001; Morton and Shalter 1977).

The Carolina Wren is nonmigratory and very sedentary. Some limited diurnal movement may occur. Little information is available on natal philopatry and juvenile dispersal. In most cases, juveniles are precluded from breeding in their natal territory due to the territorial activities of their parents. In Alabama, 4% of fledglings remained to breed in the study area. All nested on or very close to a territory adjacent to the natal territory and within 150 m of their natal territory. Once a bird establishes a territory, which may be in the autumn after fledging, it typically remains in the same territory for its lifetime. Exceptions may be females that lose their mates and are unable to continue to defend the territory. These females may be forced to move and find an unmated male holding a territory (Haggerty and Morton 2020; Laskey 1948, 1950a).

Limiting Factors

Eggs have been found in Ontario nests from early April until early August, but the presence of 3 young in an Essex County nest on 29 August suggests a later egg date. Most nests with eggs were reported 10-29 May (Peck and James 1997). The Carolina Wren has a long egg-laying period that may extend from very late March into September even in northern, cool climates such as Vermont. This is due to its propensity for multiple brooding and replacement of lost clutches. One nest was almost completely built within 2 hours, but 4-7 days is more typical for nest completion. Eggs are laid at the rate of 1 a day. Although the female may start staying in the nest at night after she lays the first egg, full-time incubation does not start until laying of the last, or occasionally penultimate, egg. Incubation periods in Ontario were 14-15 days. Overall, incubation periods of 12-16 days have been reported (averages 14.8 and 15.8 days). Young fledge when they are 10-16 days old, but mostly at 12-14 days; the mean nestling period is 13.3 days (Bent 1948; Gill and Haggerty 2012; Haggerty and Morton 2020; Laskey 1948, 1950a; McGaha 1998; Nice and Thomas 1948; Peck and James 1997; Turcotte 1989).

Two broods are commonly raised in a season including in Ontario. Either a new or the old nest may be used for the second brood. In the southern part of the Carolina Wren's range, 3 broods are occasionally raised. Renesting may occur if a clutch is lost. The renesting interval after Alabama nests failed averaged 9.3 days compared with 11.0 days following successful nests. Females averaged 3.7 nesting attempts per breeding season. Clutches of 3-9 eggs have been reported in Ontario, with most containing 5 eggs. The normal clutch size is 3-5 eggs, with a mean of 4.3 in Alabama and a mode of 4 eggs. Further north in Tennessee, 5-egg clutches were most frequent. Of 255 nests throughout North America, mean clutch size was 4.8 (mode 5 eggs, range 3-7 eggs). There is 1 record of 8 eggs as well as the 9-egg clutch for Ontario. There is no significant decline in clutch size as the season progresses (Bent 1948; Haggerty and Morton 2020; Laskey 1948, 1960; Peck and James 1987, 1997; Sanborn 1932; Turcotte 1989).

The age at first breeding is 1 year. The mating system is monogamous and permanent pair bonds are maintained year-round. There are 2 records of possible polygyny occurring when 2 females nested on a single male's territory. The male assisted only at the nest of the primary female. Birds may establish pair bonds as early as July of their hatching year. Although pair bonds are

permanent for the lives of pair members, a deceased mate is quickly replaced. Divorce is rare and there are no reported cases of intraspecific nest parasitism or extra-pair fertilizations (Haggerty and Morton 2020; Haggerty et al. 2001; Laskey 1950a; Morton and Shalter 1977; Nice and Thomas 1948).

The Carolina Wren usually forages on the ground or close to it in leaf litter, around fallen trees and upturned roots, and in tangles of vegetation. It occasionally forages on vines, in squirrel dreys, and bark crevices. Occasionally it hitches up tree trunks and branches similar to a creeper or nuthatch, probing its bill into cracks. It obtains most food by gleaning but often turns over decaying vegetation with its bill to expose prey. In Louisiana, 83% of observations of foraging birds were 0.5-7.6 m from the ground (Haggerty and Morton 2020; Morton and Shalter 1977).

During incubation, the male feeds the female on the nest and she is given mostly caterpillars. Both adults feed the nestlings caterpillars, spiders, moths, crickets, grasshoppers, worms, and beetle larvae and adults. At 1 nest, young were initially fed very small spiders. After 7-10 days, nestlings were fed grasshoppers from which the legs had been removed. In the final stages of nesting, large grasshoppers complete with legs were the staple food items. An examination of 291 stomachs found that 94% of food consisted of animal matter and 6% was vegetation. Animal material included 22% caterpillars and a few moths, 19% bugs (leafhoppers and stink, soldier, leaf-footed, and chinch bugs), 14% beetles (weevils and ground, leaf, bean leaf, and flea beetles), 13% orthopterans (grasshoppers, crickets, and cockroaches), 11% spiders, 5% hymenopterans (ants, bees, and wasps), and 3% flies (crane flies). Miscellaneous animal material in the diet included millipedes, isopods, katydids, snails, and remains of lizards, frogs, and snakes. Vegetable matter eaten consisted of seeds of bayberry, sweet gum, poison ivy, sumac, smartweeds, and acorns. The proportion of plant food increases to 11% in winter and declines to 1% in summer. It has also been reported eating the fruit of mulberries (Beal et al. 1916; Chapman 1947; W.E. Davis 1991; Haggerty and Morton 2020; Holt 1918; Laskey 1948; Neudorf et al. 2013; Nice and Thomas 1948; Tinker 1909).

Brown-headed Cowbird parasitism of the Carolina Wren has yet to be reported in Ontario. Although the Carolina Wren is an uncommon host, it readily accepts cowbird eggs and young. Parasitism rates from various states range from 0% to 33.3%. Both cowbirds and wrens may be raised from parasitized nests. If there are 2 or more cowbirds in a nest, there is little likelihood of wrens fledging. The young wrens cannot compete for food and eventually become weakened and subsequently trampled or smothered to death by the young cowbirds (Grzybowski 1995; Haggerty and Morton 2020; Hahn and Hatfield 1995; Kilgo and Moorman 2003; Laskey 1948; Lowther 1991, 1997; Luther 1974; Messerly 1998).

Young of early nests may die of exposure during cold or wet weather. At a Tennessee nest, 1 of 3 9-day-old nestlings died when the temperature dropped to 16.7°C (Laskey 1948).

Habitat loss or degradation is not an issue for the Carolina Wren. Throughout its range, forest fragmentation and abandonment of marginal farmland has probably been beneficial (Haggerty and Morton 2020). In Illinois, Robinson and Robinson (1999) created 0.02-0.4-ha openings in contiguous forest. Numbers of wrens increased significantly in openings and they were significantly more abundant in recent cuts (1-5 years old) than in 10-15-year-old cuts. In South Carolina, Harrison and Kilgo (2004) studied the effects of small clear-cuts on Carolina Wrens. Plots were 11-13 ha; some

were completely cut but 0.2-ha and 0.61-ha patches were retained in other plots. In clear-cuts, wrens were absent the first year after cutting but increased the next year. Numbers were lower than prior to cutting, but not significantly. In the patch-retention areas, numbers of wrens declined significantly the first year, but were higher than pre-cutting the second year.

Jackson et al. (2011) monitored the reproductive success of Carolina Wrens breeding in forested floodplains of 2 mercury-contaminated rivers in Virginia. Nesting success was 34% lower on contaminated sites than on reference sites. Blood mercury concentration of the female was a strong predictor of nest success. A 10% reduction in nest success corresponded with 0.7 µg per gram mercury in the blood, 2.4 µg per gram mercury in body feathers, 3.0 µg per gram mercury in tail feathers, and 0.11 µg per gram mercury in eggs. These represented relatively low concentrations of mercury in the environment. Wrens exhibited high rates of nest abandonment and those nesting in floodplains adjacent to watercourses subject to mercury fish-consumption advisories may be adversely affected. Carolina Wrens accumulate mercury to higher concentrations than other songbirds due to their heavy reliance on spiders in their diet.

In pine-oak forests in North Carolina, the Carolina Wren responded positively to fire. It occurred more frequently immediately following fire regardless of its severity. Peak occupancy occurred in locations that had experienced high-severity fires 0-5 years previously (Rose and Simons 2016).

Price (2004) predicted that the range of the Carolina Wren might expand in southern Ontario if the average summer temperature increased by 2°C. In North Carolina, its abundance was correlated with temperature, suggesting that it would benefit from climate change (Lumpkin and Pearson 2013). Near Ann Arbor, Michigan, Job and Bednekoff (2011) demonstrated that the winter range limits for the Carolina Wren were more directly related to food supply and presence of bird feeders and were only indirectly related to temperature. Thus, it may not respond as predicted by some climate models.

Status

The Carolina Wren is a recent arrival to Ontario, particularly as a breeding species. The first record was from Mount Forest during the winter of 1890-91. In 1905, a fledgling was found at Point Pelee, which represented the first breeding record for Ontario and Canada (Baillie 1967; McIlwraith 1894). Baillie and Harrington (1937) considered it an uncommon and irregular resident in the south, north to Lambton County and east to Victoria and Northumberland counties. The first record in Elgin County was in 1930 where it is now a rare local resident (Lancaster et al. 2004). In the Kingston area, the first Carolina Wren was seen in 1923, but the next record was not until 1949. It has been observed every year since 1970 (Weir 2008). Only 39 pairs were estimated breeding in the province during the first atlas, which followed a period of severe winters (Austen et al. 1994; Richard in Cadman et al. 1987). In 1989, at least 100 birds were present at Point Pelee during the breeding season, but the population dropped to 25-30 in 1992 and 10 in 1993 (Austen et al. 1994). James (1991) considered it a rare permanent resident in the Carolinian Forest Region, nesting occasionally as far north as Simcoe County. Since the 1970s, its population and range have continued to expand. Numbers in Niagara Region began to increase in the late 1980s (Black and Roy 2010).

The second atlas demonstrated that the range of the Carolina Wren had expanded northward and eastward since the first atlas. It was documented throughout most of the Carolinian Forest Region and along the north shore of Lake Ontario and the St. Lawrence River, with records in the Ottawa area, near Lake Simcoe, and at the base of the Bruce Peninsula. There were 3 scattered records in the southern portion of the Canadian Shield. Its probability of observation increased significantly south of the Shield and notably in the Carolinian Forest Region. Densities were low with highest densities in Essex County and the Regional Municipality of Niagara (Read in Cadman et al. 2007).

The North American Carolina Wren population began to increase and expand northward in the late 19th and early 20th centuries. The typical pattern is that the range extends northward for several years, then contracts suddenly due to severe winter weather, then gradually recovers and usually surpasses its previous northern range. Cold weather with ice and snow decimates populations, but they often recover in a few years. The overall increase in range and population has been attributed to less severe winters, reforestation, abandonment of marginal farmland, and winter bird feeding (Bannon and Rail in Gauthier and Aubry 1996; Bent 1948; W.E. Davis 1991; Haggerty and Morton 2020; Overlease and Overlease 1987; Sutton 1930).

Breeding Bird Survey data indicate that the Carolina Wren increased in Ontario at annual rates of 4.55% 1970-2021 and 4.32% 2011-21. The long-term results were of medium reliability; the short-term results were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Some fledglings may disappear from the nesting area in 1-2 days, but most remain nearby for 22-37 days with stragglers persisting for 48-79 days (Haggerty and Morton 2020).

In Ohio, Vitz and Rodewald (2006) captured 4 adult and 47 juvenile Carolina Wrens in regenerating hardwood clear-cuts. Dense woody vegetation in clear-cuts may be important in providing cover and food for it. In Missouri, Porneluzi et al. (2014) netted birds during the postfledging period in an oak-pine-hickory forest 2-15 years after it was clear-cut. The Carolina Wren was among the more common species captured. Peak numbers occurred 2-4 years after cutting with a gradual decline thereafter.

WINTER

The Carolina Wren is a snow avoider. Important predictors of its presence are a short snow season and presence of frozen ground without snow (Keyser et al. 2022).

In Alabama, the Carolina Wren occurred most frequently in areas with dense ground cover in winter. Sites that had dense vegetation taller than 7.6 m that were used regularly during the breeding season were typically abandoned in winter (McClure et al. 2013a). In Missouri, the level of tree stocking had no effect on its abundance. It was equally abundant in savannahs, woodlands, and forests (Kendrick and Thompson 2013). In Arkansas, Kentucky, and Mississippi, it was equally abundant in row-crop fields with and without buffers of native grasses and forbs (Evans et al. 2015).

Severe winter weather is the most significant limiting factor for the Carolina Wren. Because it forages chiefly on the ground, prolonged periods of snow cover confine it to foraging under

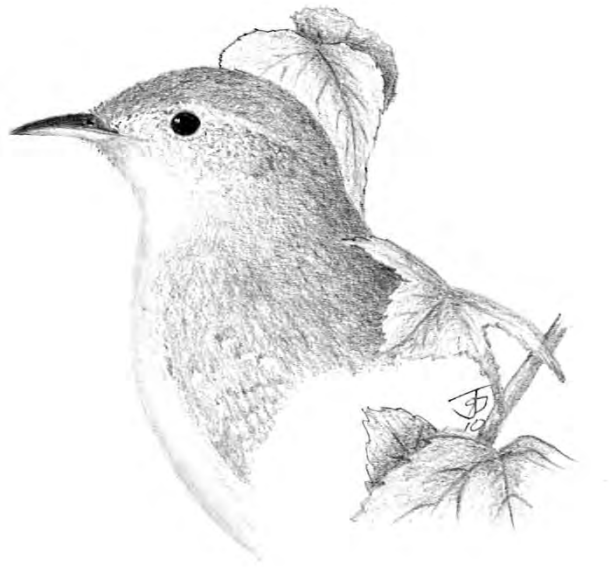
windfalls and other areas sheltered from snow. Over a 47-year period in the United States, the centroid of its distribution shifted northward during years with mild winters and few snow-cover days when snow depth exceeded 5 cm. It shifted southward dramatically in the late 1970s, early 1990s, and late 2000s during severe winters with extended snow-cover days. Northern populations experienced a 1.1% decrease for every day with 4 cm of snow cover. In southeastern Michigan, snow cover rather than temperature correlates with historical range expansions and fluctuations. Although snow cover may be more critical, it also appears vulnerable to cold weather, but there are cases of it being unaffected by long cold snaps. Christmas Bird Count (CBC) data suggest that it is absent where the average minimum January temperature is below −12°C, and regular sightings occur where the minimum January temperature is above −7°C (Bent 1948; W.E. Davis 1991; Haggerty and Morton 2020; Huang et al. 2016; Job and Bednekoff 2011; Morton and Shalter 1977; Root 1988).

Severe winter weather may be devastating to local or even continental populations. The first to succumb are those that were unsuccessful in establishing a territory because they are excluded from prime food resources. Winter mortality under poor conditions is commonly 80-90% and occasionally 100%. The Carolina Wren was documented on every Hamilton CBC from 1951-62, was absent 1963-69, and was present again 1970-75, apparently in response to weather conditions. After periods of absence, the next birds seen were invariably in autumn suggesting that these were hatch-year birds colonizing from the south. In a Tennessee area where it was common, no breeding birds were detected in 1940 after a severe January storm. A severe storm in Illinois appeared to result in 100% mortality in 1979. After a severe winter in the late 1970s in Ohio, numbers at 1 site dropped from 537 to 1. During the winter of 1935-36, temperatures in West Virginia ranged from −27°C to −34°C. Several birds were found dead and, although previously one of the most common permanent residents, the Carolina Wren practically disappeared. Following the 2 severe winters of 1976-77 and 1977-78, the population declined significantly in most of eastern North America. Due to the effects of winter conditions, populations oscillate, increasing during warm periods and decreasing abruptly after severe winters. An increase in Carolina Wrens observed at winter feeders has been reported in Ontario suggesting a response to warmer winters (Austen et al. 1994; Bent 1948; Curry 2006; Dunn and Tessaglia-Hymes 1999; Fitch 1958; Graber and Graber 1979; Haggerty and Morton 2020; Laskey 1948, 1950a; Morton and Shalter 1977; Overlease and Overlease 1987; Strain and Mumme 1988; Wilcox 2006).

The Carolina Wren is the only wren that regularly visits bird feeders. At the northern extent of its range, feeders may be essential for winter survival. The increase in popularity of bird feeding is probably a major contributor to its northward range expansion. Food is a greater limiting factor than temperature in the winter. It tends to be slightly more frequent at rural feeders than those in suburban and urban areas. Feeders with nearby shrubbery are more likely to attract it. Favourite feeder foods include bird puddings, hulled peanuts and peanut hearts, chopped walnuts and other nuts, suet, and peanut butter mixes. Infrequent choices include mixed seeds, millet, all types of sunflowers, safflower, cracked corn, milo, peanuts in the shell, pet food, fresh or dried fruit, baked goods, water, meat scraps and bone marrow, and popped corn. Away from feeders, the winter diet is similar to that of the breeding season, being predominantly insects and spiders (Bannon and Rail in Gauthier and Aubry 1996; Bent 1948; W.E. Davis 1991; Dunn and Tessaglia-Hymes 1999; Haggerty and Morton 2020; Job and Bednekoff 2011; Lancaster et al. 2004; Sutton 1930).

Northern House Wren

Troglodytes aedon

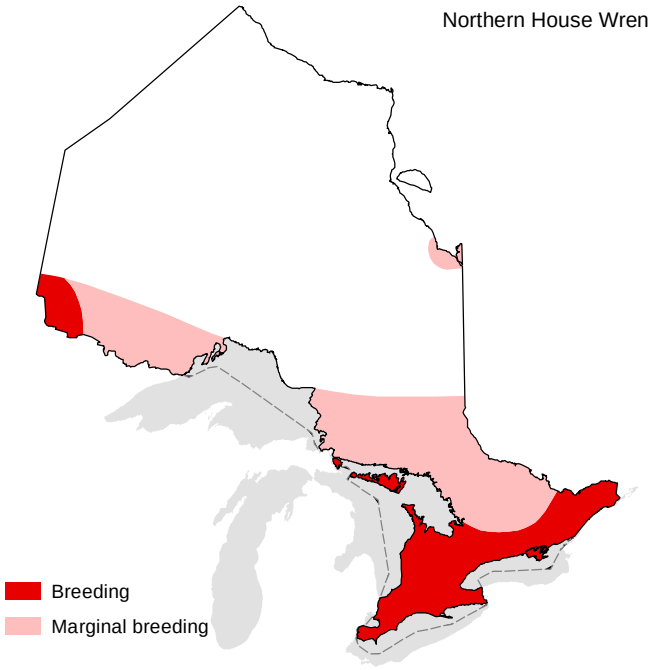


BREEDING SEASON

Habitat Requirements

In Ontario, the Northern House Wren nests in farmland, overgrown fields and pastures, orchards, fencerows, young plantations, and limestone savannahs (38.7% of records); woodlands, swamps, bogs, and beaver ponds (23.4%); rural and urban gardens, farmyards, cottage areas, and parkland (23.0%); river, lake, and pond shorelines and road and railway rights-of-way (14.1%); and treed sand dunes (0.8%). In woodland sites, the canopy was either open or nests were at the edge or in clearings. Deciduous and mixed woods were greatly preferred to coniferous woods. There appeared to be a slight preference for dry areas over wet areas (Peck and James 1987).

There are 2 consistent components of the Northern House Wren's habitat. It is strongly associated with the presence of shrubs and it prefers open habitats with some tree or shrub cover. Although shrubs are almost essential to the house wren, it avoids areas of very dense shrubbery. At Presqu'ile and Mer Bleue, nest boxes placed in sparse vegetation were selected over those in dense vegetation; nests in sparse vegetation were more successful (Belles-Isles and Picman 1986a). In Wyoming, Vermont, and Utah, it selected nest boxes in areas with smaller trees, fewer but larger shrubs, fewer saplings, and more herbaceous ground and understorey cover than areas containing unused boxes. Boxes in habitats with dense sapling or small shrub understories were avoided, but it frequently nested at sites with herbaceous cover and dispersed large shrubs. Nests in more open



areas were more successful, especially in areas with open canopies and surfaces and few decaying logs or dwarf shrubs (Finch 1989a; Parren 1991; Whitmore 1977). In Oregon, where the Bewick's and house wrens coexisted, the house wren was absent in riparian oak-ash forest with dense underbrush, but occurred where the denser shrubby understorey was replaced by grasses. It also nested in open pastures where a single tree provided a nest site and rose thickets provided foraging habitat (Kroodsma 1973). In California, occupancy rates of boxes were significantly correlated with riparian vegetation and negatively correlated with the percentage of grassland in the landscape. These broad-scale habitat features were also a good predictor of nest success (Milligan and Dickinson 2016). In Maryland suburbs, presence of the Northern House Wren was correlated with presence of shrubs as tall as 6 m, but decreased with increased tree volume at heights of 15.5-16.5 m (Thomas et al. 1977). In Manitoba, sites that were used were characterized as shrub pasture. The presence of a tree near the nest site was the most important variable; distance to the nearest tree was the only variable that differed between used and unused nest boxes. Average distance of nests from a tree was 12.1 m (Munro and Rounds 1985). Near Kingston, all occupied boxes were within 30 m of a forest; the mean distance was 13.9 m (Rendell and Robertson 1990). In Vermont, only 1 wren used a box more than 10 m from a perch taller than 3 m (Parren 1991). In Wisconsin upland forests, it is confined to shrubby woods and edges, especially if rock or wood piles are present (Mossman and Hoffman 1989). Taylor and Taylor (1979) considered it a species of small woodland openings and edges. In Wyoming, it used habitats where 50% of the ground was bare and shrub coverage was less than average. Areas with short shrubs were selected over those with tall, spreading shrubs (Finch 1989b, 1991a). In Iowa, it was positively associated with tree and shrub richness and size, vertical patchiness of vegetation, and snag density. It was positively associated with increasing diameter at breast height (DBH), but negatively associated with the number of snags smaller than 25 cm DBH (Stauffer and Best 1980). In California, it was equally abundant in oak savannahs with grass cover, oak savannahs with shrub cover, montane hardwoods, and oak woodlands (Wood et al. 2013). In Chicago, it was negatively associated with distance from edge in woodlots and the amount of urban cover (Schneider and Miller 2014).

The Northern House Wren is frequently considered a habitat generalist, but this is more a function of the fact that its preferred microhabitats occur within a wide range of areas. Knowledge of its true habitat preferences are confounded because a high proportion of studies have been conducted on populations breeding in nest boxes. In British Columbia, 79% of nests were reported from human-altered habitats and 12% from forest, but results were biased by a predominance of

nests studied at a single residence (Campbell et al. 1977). It may occur wherever there is shrub habitat with suitable nesting cavities. This may include urban and rural residential areas, hedgerows, shelterbelts, orchards, overgrown fields and pastures, shrubby rights-of-way, young burns and clear-cuts, shrub thickets and young forests, savannahs, and edges of woodlands. Aspen forests are important in the west, but seldom used in the east. Riparian and upland woodlands are inhabited, as are those fronting on lakes. In Ontario and Quebec, it is most abundant south of the Canadian Shield where extensive agriculture and urban development have fragmented the forest cover and provided its favoured thicket and shrub habitat. Several studies demonstrated that its abundance is correlated with the number of snags present (Back 1979; Beals 1960; Campbell et al. 1997; Evans and Conner 1979; Faanes and Andrew 1983; Flack 1976; Johnson 2024; Kirk et al. 1996; Kroodsma 1973; Lancaster et al. 2004; Leighton et al. 2002; McNicoll and Robert in Gauthier and Aubry 1996; Niemi and Pfannmuller 1979; Noon et al. 1979; Samson 1979; Temple et al. 1979).

In a Connecticut woodlot over a 59-year period, there was a progressive shift to larger trees, a sparser shrub layer, and a less diverse tree canopy. The Northern House Wren declined in the woodlot probably due to the decrease in coverage by shrubs (Buchanan et al. 2016).

The Northern House Wren is an early successional species that may move into previously unoccupied habitat after it is disturbed. Near Thunder Bay, it nested where a forest fire had occurred 5 years previously. By then, the understorey had developed to a height of 4 m and was dominated by poplar, willow, and alder with taller dead trees (Escott 2004). It commonly appears in burns or clear-cuts in early stages of succession. In California, it occurred in burned forests but was absent in adjacent unburned forests. In burned pitch pine stands in the northeast, densities were highest 1-12 years after fire. It was rare 20 years after fire (Bock and Lynch 1970; Capen 1979; Erskine 1977). It is a common inhabitant of old fields provided that suitable nest sites are available. In New Jersey, it occurred in the youngest (10 years) old-field habitats studied, and was also present in second-growth and climax forests that had been logged (Suthers 1988). In Wisconsin, it occurs in a wide range of pine and oak barren habitats (Mossman et al. 1991).

In North Dakota in open habitats, the Northern House Wren's probability of occurrence increased linearly with an increase in tree cover within 100 m to a maximum of 60%. In wooded landscapes, its probability of occurrence increased to about 50% tree cover and levelled out with increasing tree cover. It preferred landscapes that were 35-75% forested; no areas were present that had more than 75% forest cover (Cunningham and Johnson 2016, 2019).

The Northern House Wren is an obligate edge species. In large woodlands, it is confined to edges and openings such as margins of beaver ponds or areas affected by logging or fire. Densities in small, isolated woodlands may be 2-3 times greater than in unfragmented woodlands. It occurs more frequently in isolated, fragmented woodlands than expected and avoids large, contiguous forests. In Maryland, frequency of occurrence was 80% in 0.1-ha woodlands, 50% at 3 ha, 10% at 100 ha, and less than 0.5% in 3,200-ha woodlands. In the mid-Atlantic states, frequency of occurrence was 70% in a 0.3-ha woodlot, 50% in 3.2 ha, 15% in 100 ha, and 5% in 3,200 ha. Its abundance was negatively associated with forest area, the amount of forest within 2 km, and the number of trees at the point count location (Askins et al. 1987; Blake and Karr 1987; Brush 1994; Hobson and Bayne 2000; Lynch 1987; Johnson 2024; Robbins et al. 1989). In southern Ontario, its probability of

detection was negatively correlated with the amount of forest 100 m or more from edge and forest size, and positively correlated with the amount of forest cover within 2 km and regionally. None of these relationships were significant except for the amount of regional forest cover (Austen et al. 2001).

The female may begin roosting in the nest before or after laying begins, but always before it is finished. Both sexes roost in cavities at night, usually singly but occasionally together. Roost sites include old woodpecker holes, natural cavities in trees and posts, short burrows in banks, in the eaves of houses, between the tiles on a roof, in a gourd, and in the hollow end of a garden trellis. Fledglings roost together and occasionally with the female. They rarely return to the nest to roost, but other nest boxes may be used for roosting. Young frequently roost in more open situations such as in dense foliage or on the platform of an old American Robin, Gray Catbird, American Redstart, or Chipping Sparrow nest (Baillie and Hope 1947; Gross in Bent 1948; Johnson 2024; Skutch 1953).

Seventy-five percent of Ontario nests Ontario were in nest boxes; 12.8% were in cavities in trees, snags, and stumps; 7.1% were in holes or openings in fence posts, utility poles, and pipes; 2.7% were in holes and recesses in buildings, often under eaves; 0.9% were inside metal cans, tool boxes, kettles, and mail boxes; 0.5% were in old Barn Swallow nests; 0.2% were in old robin nests; 0.2% were in hanging fabric and paper bags; and less than 0.1% were in an old Baltimore Oriole nest, under sawdust in an icehouse, under a log pile, on the side of a flagpole float, in a broken light standard, in the head of a ceramic owl mounted on a post, in a metal can buried in the ground, and between 2 robin nests built on top of each other. Nest boxes constructed for Eastern Bluebirds, Tree Swallows, Purple Martins, and Black-capped Chickadees were used, often in the same season after the other species raised a brood. Of 180 nests in trees, 88.3% were in natural cavities and the remainder were in old woodpecker holes. Nests were in both dead (76.7%) and living (23.3%) trees; deciduous trees (85.3%) were preferred to conifers (14.7%). Tree species most frequently used for nesting were birch (19 nests), elm (13), white cedar (11), and apple (9). Three nests were on or near the ground. Excluding nests in bird boxes, nests in trees were 0.3-23 m from ground with most 1.2-3 m up; nests in buildings were 0.6-3.7 m from the ground, mostly 1.8-2.7 m (Peck and James 1987). One Algonquin Park nest was in an old Barn Swallow nest inside a building and another was in an old boot attached to a telephone pole (Tozer 2012).

A high proportion of nests reported elsewhere were in nest boxes. In addition to standard nest boxes, the Northern House Wren has nested in cardboard milk cartons, plastic gallon milk jugs, cigar boxes, gourds, bat boxes with slits on the top, and hanging coconut shells. Nest boxes that have been previously used are highly preferred over clean nests, possibly because previous use is indicative of success or good-quality habitat. Males remove old nests prior to constructing a new one and this may reduce ectoparasite loading. Unusual nest sites include old cow skulls, fishing creels, old boots, tin cans, inside old paper nests of wasps and hornets, in water pots, in teapots, in flowerpots, on shelves in sheds, in a soap dish, in a bag of feathers, in pump nozzles, in hats or pockets of scarecrows, in holes in iron pipe railings, in weathervanes, in holes in walls or buildings, in a coat hung up at a campsite, in tobacco boxes, and in mailboxes. One nest was on the rear axle of a car that was used daily. The birds went with the car when it was driven and the nest was successful. There are several reports of it using old nests of other species. It nests fairly frequently in Baltimore Oriole and robin nests, and less frequently in other species' nests. Robin nests tend to be

used when there are 2 adjoining nests available. One nest was in a Cliff Swallow nest on the bank of a river; the nest was without a neck and 4 other swallow nests appeared to have been used. The house wren has also nested in old Barn Swallow and Eastern Phoebe nests, 1 nest was in an old Belted Kingfisher nest in a sand bank, 1 was in a Bank Swallow burrow, and another was deep in the interstices of an Osprey nest. Most studies report no preference for orientation of the cavity entrance for either nest boxes or natural nests. In Alberta, 68% of nests were oriented east to south, and the orientation of successful nests was significantly different from failed nests. Successful nests were oriented in an east-southeast direction (Benton 1950; Black 1983; Brush 1994; Common 1948; Dales 1926; Finch 1989a; Fletcher 1944; Gillespie 1946; Grauman and Kuyt 1999; Gross in Bent 1948; Gutzwiller and Anderson 1986a; Johnson 1996, 2024; Kaluthota and Rendall 2017; Kennedy and White 1992; Lancaster et al. 2004; Leighton et al. 2002; Mills 1981; Pacejka and Thompson 1996; Pribl and Picman 1997; Skutch 1953; Thompson and Neill 1991). In Ohio it nested in polyvinyl chloride tubes 27.5 cm long with a 9.5-cm inside diameter. These were hung horizontally, both ends were capped, and an entrance hole of 5.1 cm diameter was drilled in 1 end (Tyson et al. 2011).

In natural cavities and cavities made by primary excavators, the Northern House Wren typically uses cavities closer to the ground and with smaller entrances than other cavity nesters. No preference appears to be shown for cavity entrance orientation, or snags versus live trees. In Arkansas, it appeared to prefer aspens; 83% of nests were in aspens which were only 12% of the available trees. In Alberta, all 91 nests in natural cavities were in trembling aspen, which was the most abundant tree species. In Iowa, snags that were soft or intermediate in hardness were selected; hard snags were used less than their availability. In Colorado, non-knothole cavities were used more frequently than cavities created by knotholes. It nests mostly in small, dead limbs and frequently uses old Downy Woodpecker nests. Optimum DBH of nest trees has been estimated at 20 cm, but trees as small as 15 cm DBH are used, and limbs as small as 7.5 cm in diameter may be used for nesting. Height of natural nests ranges from 0.9 to 50 m, with most 1.8-5.4 m from the ground. In Arkansas, nests averaged 9.0 m from the ground. In Montana burns, it nested in trees with 90% bark cover that averaged 12 m tall with an average DBH of 30 cm. In Alberta, natural nest cavities were often reused within breeding seasons and in subsequent years (Campbell et al. 1997; Evans and Conner 1975; Flack 1976; Gross in Bent 1948; Gutzwiller and Anderson 1986b; Hutto and Gallo 2006; Johnson 2024; Kaluthota and Rendall 2017; Li and Martin 1991; Munro and Rounds 1985; Sedgwick and Knopf 1980; Skutch 1953; Stauffer and Best 1980, 1982).

The Northern House Wren is a vigorous defender of its territory. The male builds 2-3 nests within the territory, rarely as many as 7. Only 1 nest is subsequently finished by the female, but the dummy nests assist in establishing the territory. It is notorious for destruction of other nests. Holes are pecked in eggs, and the eggs are often thrown out of the nest onto the ground. Nestlings may also be pecked and ejected from the nests and there is circumstantial evidence of house wrens killing other adult wrens in the nesting cavity. Nests of all bird species within the territory may be attacked and those as far as 100 m from an active house wren nest may be destroyed. Territorial intrusions by other house wrens, mostly males, are common. In some cases, these are attempts at extra-pair copulations. Floater males often intrude and take away surplus nest sites and attempt to take over active nests. Replacement males that pair with females with eggs or nestlings frequently kill the first brood (Belles-Isles and Picman 1986b, 1987; Brush 1994; Dales 1926; Finch 1990; Horn et al. 1996;

Johnson 2024; Kendeigh 1941; Kennedy and White 1996; Kermott et al. 1990, 1991; McNicoll and Robert in Gauthier and Aubry 1996; Parren 1991; Pribl and Picman 1991; Quinn and Holroyd 1989; Rendell and Robertson 1990). Nests are typically a minimum of 30-35 m apart; closer nests usually have a visual obstruction between them. Early arriving males have a large territory that shrinks as more birds arrive. Late-arriving males must squeeze in between established males to claim a territory. Late-arriving birds are almost always juveniles. In Oregon, the mean size of 14 territories was 0.9 ha (range 0.4-1.8 ha). These birds were nesting in natural cavities rather than boxes. In Ohio, 178 territories of birds nesting in boxes averaged 0.4 ha (range 0.03-1.44 ha); most territories were 0.2-0.5 ha. Territory size decreased with increasing density of birds (Johnson 2024; Kendeigh 1941; Kroodsma 1973; Muller et al. 1997).

Natal philopatry is low, with most information from Ohio. Of 7,375 nestlings, 2.1% returned to breed. It was estimated that 11.5% of surviving birds returned. In another study, 2 of 356 banded chicks (0.6%) returned to breed the following year. Also in Ohio, 71.5% of returning nestlings first bred when nesting was initiated in the spring. The remainder first nested when other birds were initiating their second broods. Many nestlings skipped 1 or less commonly 2 years before returning to breed. In Illinois, return rates of nestlings was significantly less than for adults, and significantly more male nestlings (3.6%, range 1.9-11.0% per year) returned than females (2.0%, range 0.6-3.7% per year). In Ohio, 62.9% of returning nestlings were male and 37.1% were female. Significantly more chicks (3.9%) from early nests returned than those from late nests (1.1%). There was no significant difference in the distances yearling males (607.5 m, range 120-1,707 m) and females (674.0 m, range 124-1,728 m) nested from their natal box. The median distance moved by early-season yearlings (661 m) was significantly greater than for late-season yearlings (493.5 m). At another Ohio site, yearlings nested as far as 3.0-3.3 km from their natal nest (Drilling and Thompson 1988; Kendeigh 1941; Kendeigh and Baldwin 1937; Payne 1990; Robinson and Rotenberry 1991).

Drilling and Thompson (1988) studied adult Northern House Wren site fidelity in Illinois. Significantly more male (38.1%) than female (23.3%) adults returned to breed the following year. A total of 36.6% of adult males returned to breed for at least 2 years compared with 20.6% of females. Many females returned 3-4 years to breed, and a few 5-6 times. Ten females and 7 males were not recaptured in the year between their first and second captures. Adult females moved significantly further (134.0 m, range 0-1,634 m) between successive nests than males (67.0 m, range 0-684 m). Females that were unsuccessful at their previous nesting moved significantly further (215.0 m, range 0-1,368 m) than those that were successful (134.0 m, range 0-1,634 m), but there was no difference in distances moved by previously successful (62 m) and unsuccessful (85.0 m) males. The outcome of the previous year's nesting attempts did not affect return rates, but returning females produced more offspring than non-returning females. The return rate of males was not influenced by breeding success or number of young raised. Previously unsuccessful females tended to be more successful if they moved 2 territories or further from their previous nest, but distance moved by males did not affect success. In Ohio, 631 of 1,831 adults (34.5%) returned to breed in a subsequent year. Most settled in a territory that overlapped their previous territory (58%) or was adjacent to the previous territory (12%). The percentage of females returning did not differ significantly from that of males, although there was a greater tendency for females to wander. Of returning males, 31% nested in the same box compared with 26% for females. An additional 53% of males and 44% of females

nested within 300 m of their former nest box. Maximum distance that a returning male nested from his previous nest was 1.8-2.1 km compared with 2.7-3.0 km for females (Kendeigh 1941; Kendeigh and Baldwin 1937). In Wyoming, return rates of females were 29% for birds raising 1 brood, 38% for birds raising 2 broods, 29% for monogamous females, and 38% for primary females in a polygynous relationship. There were no significant differences among these return rates (Czapka and Johnson 2000). In Ohio, the return rate of adult females was 10% (Robinson and Rotenberry 1991). In New Jersey, 5 of 127 adults (3.9%) returned the following year and there was 1 multiple return (Suthers 1988).

Limiting Factors

Eggs have been reported in Ontario nests from the first week of April until 1 September, with most present in the last 3 weeks of June (Peck and James 1987, 1997). Females begin choosing mates within a few days after their arrival. The male begins building nests in empty cavities as soon as he arrives and claims a territory within hours of arrival. The female begins completing the nest as soon as pairing occurs. In New Jersey, nests initiated before 14 June took 13.9-15.0 days to build compared with 10.0-12.0 days for later nests. In Wyoming, timing of nest construction varied annually depending on flooding severity because wrens waited until flood waters receded to build their nests. The mean length of time required to build a nest was 5.0-13.3 days. Late in the breeding season, the female may initiate egg laying before she completes the nest lining. One egg is laid per day, but there was a 2-day interval between the third and fourth eggs at 1 Ontario nest and a 3-day interval between the fourth and fifth eggs at another. In some clutches, eggs are incubated slightly beginning with laying of the first egg. Initiation of daytime incubation may be delayed until the penultimate or final egg in other clutches. The incubation period was 10-19 days in Ontario, mostly 12-14 days. The short Ontario incubation periods indicate clutches where incubation occurred before the clutch was complete. In the longest incubation periods, there was a delay in incubation of 6-10 days after the clutch was completed. In British Columbia, incubation periods of 14-15 days have been reported; elsewhere incubation periods of 12-13 days are typical. The incubation period shortens as the breeding season progresses. In Illinois, the incubation period for clutches completed by mid-June averaged 12.7 days compared with 12.2 days for later clutches. Depending upon when incubation is initiated, hatching may be synchronous over a 24-hour period or asynchronous over 2-4 days. Nestling periods of 12-20 days have been reported, with 17-18 days most typical; young usually fledge earlier than this only if the nest is disturbed (Baldwin 1921; Brackbill 1960a; Campbell et al. 1997; Dunn 1976; Finch 1991b; Gross in Bent 1948; Harper et al. 1994; Johnson 2024; Kendeigh 1941; Kennedy and White 1992; Peck and James 1987; Quinn and Holroyd 1992; Skutch 1953).

The Northern House Wren commonly raises 2 broods a year, depending upon latitude and when the first clutch was initiated. There are reports of 3 broods per year from the south, but references to third broods may be renesting attempts. At lower latitudes, almost all females that begin breeding in May or early June attempt a second brood. At higher latitudes only the females that bred the earliest raise a second brood. Second broods are common in Ontario. In Ohio, 89% of males involved in second broods retained the same territory. Territories were changed only due to pressure from other males or to accommodate new mates. At the end of the first nesting period, 23% of males left the study area and 24% of males present for the second nesting were new to the site; 41% of females disappeared and 27% of females present for the second nesting were new. Of

the new birds, 95% of males and 92% of females were yearlings. In Illinois, 50-60 days elapsed between laying of the first egg of the season and production of the second clutch. In Wyoming, there was an average of 36-60 days between the laying of the last egg of the first clutch and the laying of the first egg of the second clutch. In Ohio, females that laid clutches of 6 or 7 eggs were more likely to lay a second clutch than those that had smaller or larger first clutches. Renesting is common if a clutch is lost; 3 renestings occurred at 1 Ontario nest. Clutches of 2-9 eggs have been reported in Ontario, with 6 and 7 eggs most frequent. In eastern Ontario, house wrens regularly laid 4-7 eggs (mean 6.1). Ontario clutch sizes are typical. Usually 4-7 or 8 eggs are laid; larger and smaller clutches are rare. Clutch size increases northward and decreases as the season progresses. Mean clutch sizes of 6.2-6.5 eggs have been reported. Clutches laid before mid- to late June usually contain 6-8 eggs; later clutches have 4-6 eggs. In Ohio, first clutches averaged 6.3-6.5 eggs compared with 5.2-5.7 eggs for second clutches. Most females laid 5 or 6 eggs in their second clutch regardless of the size of their first clutch (Campbell et al. 1997; Finch 1991b; Gross in Bent 1948; Kendeigh 1941; Kennedy and White 1991; Johnson 2024; Palmer-Ball 1992; Parren 1991; Peck and James 1987; Picman and Belles-Isles 1988b; Robinson and Rotenberry 1991; Thompson and Neill 1991; Whittingham et al. 2002; Young 1994).

Both sexes are capable of breeding when they are 1 year old. Yearlings nest later in the season than adults, typically initiating nests when adults are starting their second broods. It is uncertain if yearlings are late migrants or unpaired floaters until they initiate nesting. In Ohio, 12-18% of Northern House Wrens did not breed in their first year (23.4% of males and 6.7% of females). Less than 5% of experienced breeders do not breed in a given year. In most populations, there appears to be a surplus of unmated males and females; lost mates are typically replaced within 3 or 4 days (Drilling and Thompson 1988; Gross in Bent 1948; Johnson 2024; Kendeigh 1941; Kendeigh and Baldwin 1937; Kermott et al. 1990, 1991).

The mating system is predominantly monogamous, but considerable numbers of males are polygynous. Females select mates and appear to reject those that do not have more than 1 potential nest site in their territory. Polygyny is enhanced by provision of surplus nest boxes in a territory. In Wyoming, 53.3% of males were polygynous when nest boxes were provided compared with 9.6% that had only natural cavities within their territory. Eighty-three percent of males with boxes and 47% of males with natural cavities consistently attempted to attract a second mate. In Illinois, 24.2% of males were bigamous and one (0.2%) was trigamous; 2.8% of males had 2 bigamous matings in a season and one had 3 bigamous matings. In Alberta, 21.7% of males were polygynous and 35.7% of females were mated to a polygynous male. At another Alberta site, 18 males nested polygynously and 6 of them did so while the first nest was active. The others were sequentially polygynous within the breeding season, changing mates for the second brood. In Ohio, only 6% of matings were polygynous, but 2 populations nesting in nest boxes in New York had polygyny rates of 13-40% (average 20%). In a Wyoming population where only natural cavities were present, 9.6% of males attracted a second mate; 15-35% of males were polygynous in subsequent years when each male was provided 2 nest boxes. Polygyny is usually asynchronous with the secondary female initiating egg laying after the primary female. Secondary females tend to lay smaller clutches because they nest later. Mate sharing does not appear to affect the reproductive output of the primary female's first clutch, but these birds are much less likely to attempt a second clutch and may have lower

overall reproductive output than females mated to monogamous males. If a primary female suffers nest loss, she may renest with the same male and become the secondary female in the relationship. Polygynous males rarely retain both mates for a second brood, but produce 4 broods in a season when they do. In Wyoming, 94% of monogamous and primary females fledged at least 1 young compared with 69% of secondary females. Both sexes solicit extra-pair copulations, but the rate of extra-pair copulations is diminished by the territoriality of males. In Illinois, 8.4% of nestlings were unrelated to their putative father. The proportion of extra-pair nestlings was significantly higher in nests defended by polygynous males (10.2%) than monogamous males (7.4%). The incidence of extra-pair nestlings increased as the breeding season progressed. The frequency of broods containing extra-pair nestlings was greater for secondary broods of polygynists (42.9%) than for primary broods of polygynists (17.2%), or for monogamists (26.0%). The pair bond is very temporary and frequently lasts for only a single brood. Although pairs may occasionally stay together to raise 2 broods, usually a different mate is selected for the second nesting. A different mate may also be selected when renesting. In Illinois, 45.3% of birds with 3 nests in a year had a different mate for each nest. For monogamous pairs, 55.4% switched mates for the second nest and 44.6% remained paired. About half of males that care for their first young lose their territory and consequently their mate; over 90% of non-caring males retain their territory. In Ohio, 13% of males remated with their mate of a previous year compared with 22% of females. One pair was mated in 3 years, but only for 1 nesting during each of these years. Based on returns, 58% of pairs that had the opportunity to remate in subsequent years did so. In all cases when birds remated in a subsequent year, they returned to an area that overlapped the territory they held the previous year (Baldwin 1921; Bart 1990; Czapka and Johnson 2000; Drilling and Thompson 1991; Gross in Bent 1948; Johnson 2024; Johnson and Kermott 1991; Kaluthota and Rendall 2017; Kendeigh 1941; Llambías et al. 2012; Quinn and Holroyd 1992; Soukup and Thompson 1997). Picman and Belles-Isles (1988b) observed 5 probable cases of intraspecific parasitism in 23 nests at Presqu'ile and Mer Bleue. In 3 cases, 2 eggs were laid in the nest in a single day and in the other 2 cases an egg was laid after the original clutch was completed.

In Manitoba, most food was obtained by gleaning (82.5% of observations), 12.5% by hovering, and 4.7% by other techniques. There was a large variation in foraging behaviour at different nest sites, with birds using foraging substrates similar to their availability. Ground foraging occurred least, with dead and live limbs preferred for foraging. Most foraging occurred in the subcanopy, in saplings and shrubs, and in herbaceous ground cover. Peach-leaved willow was selected for foraging; green ash was used less than its availability. Manitoba maple and sandbar willow were important species for foraging (Guinan and Sealy 1989). In southern California, 26% of foraging activities occurred on leaf litter, 49% in shrubs, and 26% in trees (Johnson 2024).

The male may feed the female while she is incubating, but this behaviour may be rare in some populations. In the first third of the nestling stage, the female spends much time brooding, so feeding by the male is essential to prevent starvation of the young. Juveniles from the first brood may help to feed nestlings in the second brood. Nestlings are fed small invertebrates including spiders, hairless caterpillars, grasshoppers, cockroaches, moths, mosquitoes, grubs, flies, butterflies, horse flies, beetles, monarch butterflies, underwing moths, harvestmen, soldier bugs, owlet moths, leafhoppers, crickets, and ants. Of 40 gizzards removed from 15-day-old nestlings, 100% contained

adult or larval beetles, 70% had leafhoppers, 62% had crickets or grasshoppers, 50% had flies, 43% had spiders, 40% had caterpillars, 23% had earwigs, and 45% contained fragments of land snails. Young are also fed significant amounts of grit. A video of 755 trips to Illinois nests revealed that nestlings were fed 29.5% grasshoppers and crickets, 22.5% caterpillars, 13.2% spiders and harvestmen, 5.3% bugs, and 3.8% flies, bees, and wasps. In New York, adults captured spiders, beetles, adult lepidopterans, spiders, and harvestmen in proportion to their availability. Orthopterans and caterpillars were captured more than expected and flying insects were selected less than expected. Slugs were readily available but fed to nestlings only in a drought year. Adults eat invertebrates almost exclusively and have a diet similar to the young. Fairly immobile prey such as spiders, beetles, bugs, and various types of larvae are overrepresented in the diet compared with their availability. More mobile invertebrates such as small flies, leafhoppers, and springtails are underrepresented. In Manitoba, midges were present in 84.2% and 82.0% of stomachs over 2 years and accounted for 51.9% and 29.5% of food items. Beetles and flies other than midges were taken early in the season. Other adult insects, mostly butterflies, moths, and hymenopterans, were consumed in late July and early August. Spiders and beetles were taken consistently. Wrens appeared to select for beetles in addition to midges and bugs. No prey items were represented in stomachs in proportion to their availability. Most prey was 3-9 mm in length, but occasionally larger and smaller invertebrates were eaten. Other items infrequently consumed included mites, book lice, large mayflies, and mosquitoes. Another study examined stomachs from a wide geographic area and found the diet to be comprised of 29.3% bugs (stink and ebony bugs and leafhoppers); 17.6% grasshoppers, crickets, and locusts; 13.9% moths and caterpillars; 13.8% beetles; and 8% ants. Small numbers of millipedes, ticks, lice, aphids, snails, and small crustaceans were eaten. The food of 68 birds from the southeastern states was examined and animal food was eaten exclusively: 29.3% bugs (predominantly stink bugs, but also ebony bugs and leafhoppers), 17.6% orthopterans, 13.9% lepidopterans (including many adult moths), 13.8% beetles (weevils and ground, lady, and leaf beetles), 8.2% ants, 3.3% bees and wasps, 10.5% spiders, 2.8% millipedes, and trace amounts of snails and isopods. Another study examined 52 stomachs from the United States and determined that the diet consisted of 98% animal matter and 2% vegetation. The vegetation included bits of grass and similar matter and was probably ingested incidentally. Half the food consisted of grasshoppers and beetles and the rest was caterpillars, bugs, and spiders. In a Utah population, nestlings were occasionally fed small fish and fish appeared to be a regular but rare component of the diet (Beal 1897a; Beal et al. 1916; Common 1948; Gross in Bent 1948; Guinan and Sealy 1987; Johnson 2024; Johnson et al. 1992; Mayoh and Zach 1986; Pearse et al. 2004; Skutch 1953; Williams and Pennock 1995).

Cowbird parasitism of the Northern House Wren is rare. In Ontario, 5 of 1,214 nests (0.4%) were parasitized. Parasitism has not been reported elsewhere in Canada and there are currently only about 5 other records of parasitism. Both cowbird and wren young may fledge from parasitized nests. The house wren appears to be a suitable host, but it may reduce the incidence of parasitism by selecting small cavity entrances. Cowbirds cannot access cavities with an entrance diameter smaller than 38 mm (Campbell et al. 1997; Gross in Bent 1948; Hamerstrom 1947; Hodges 1949a; Johnson 2024; Lowther 1985, 1991; Peck and James 1997; Pribl and Picman 1997).

In Iowa, a Prothonotary Warbler parasitized a house wren nest. The nest initially contained 3 wren eggs and 1 warbler egg. One wren egg disappeared and the other 2 did not hatch. The wren successfully fledged the warbler (Dodson et al. 2024).

Although presence of suitable nesting cavities may be a limiting factor in some localized areas, habitat loss is not a major factor for the Northern House Wren. There may be some limited competition for cavities from European Starlings and House Sparrows, but this wren prefers cavities with smaller entrance diameters so this is not a significant limiting factor. Deer mice and white-footed mice may be more significant competitors for nesting cavities than other bird species. The house wren benefits from forest clearing and habitat fragmentation, and increased its range significantly once forest clearing began. The more recent abandonment of marginal agricultural land has provided additional breeding habitat, at least temporarily. Provision of nest boxes has resulted in large increases in populations (Johnson 2024; Kendeigh 1941; McNicoll and Robert in Gauthier and Aubry 1996).

Extreme weather may affect abundance of the Northern House Wren. Population declines often occur after unusually cold winters. In California, it declined significantly during a 5-year drought and recovered dramatically at the end of the drought. Prolonged hot temperatures may depress populations or reduce reproductive success. If weather is unfavourable when first clutches are usually initiated, some birds may not breed. Reproductive effort declines when the average night temperature for May, June, and July drops below 17°C or when the average night temperature in May or June is less than 14°C. In Ohio, mean daily temperatures above 26.7°C appeared unfavourable. Excessive rain during the breeding season may reduce nesting success (Johnson 2024; Kendeigh and Baldwin 1937; Verner and Purcell 1999).

In the Carolinian Forest Region of Ontario, abundance of the Northern House Wren was negatively correlated with basal area. It was most abundant in heavily cut forests (diameter-limit cuts) followed by woodlots harvested by single-tree selection and by unharvested stands (Holmes et al. 2004). In Montana, it was more abundant in burns where logs had not been salvaged than where postfire logging occurred (Hutto and Gallo 2006). Kronland and Restani (2011) reported similar results in the same state, although differences in abundance in the control and logged areas were not significant. In Oregon, it responded positively to fire and increased with increasing severity of the burn (Stephens et al. 2015).

Doherty and Grubb (1998) examined breeding success of the Northern House Wren under high-voltage lines (69kV and 765 kV) in Ohio. There was no effect due to electromagnetic fields on any measure of reproductive success. At a nuclear research establishment in southeastern Manitoba, it avoided adverse effects of radiation by selecting boxes that were not exposed to high radiation. Birds abandoned some boxes with high exposure rates before laying eggs. Radiation did not affect the number of fledglings produced or clutch size, hatching success, incubation time, and nestling time. At higher breeding densities, some birds may use high-exposure boxes where breeding success or growth of nestlings may become reduced due to radiation (Zach and Mayoh 1982).

No significant difference in reproductive success has been identified in Northern House Wrens nesting in natural cavities and nest boxes. Mortality rates were lower in boxes and birds using boxes laid larger clutches, hatched more eggs, and fledged more young than those using natural cavities.

Although the differences were not significant at individual study areas, they may be at a population level (Johnson and Kermott 1994; Purcell et al. 1977). Nest boxes have contributed significantly to the House Wren population by providing nest sites where none previously existed.

In Washington, DC and Baltimore, Maryland there was no difference in clutch size of suburban and rural birds, but suburban nestlings weighed less and had smaller body size than rural birds prior to fledging. It appeared as though the average quality of prey for nestlings may be lower at suburban sites. Suburban birds fledged more young than rural birds due to higher rates of predation on rural nests (Newhouse et al. 2008).

The Northern House Wren was vulnerable to the West Nile virus. It experienced a several-year decline following the spread of this disease in the 2000s, but appeared to have recovered by 2005 (Johnson 2024; Kilpatrick et al. 2007).

Elliott et al. (1994) studied reproductive success and accumulation of organochlorines in Northern House Wrens breeding in British Columbia orchards. Wrens nesting in orchards had 106 times more DDT, 5.5 times more DDE, and 15 times more DDD in their eggs than those nesting in other habitats. There was no difference in nesting success between orchard-nesting birds and birds nesting in other habitats. The organochlorine burdens were acquired locally in orchards rather than on the wintering grounds. Beginning mostly in the 2000s, house wren eggs and tissues have been monitored as indicators of bioaccumulation of toxins such as PCBs, polychlorinated dibenzofurans, polychlorinated dibenzo-p-dioxins, cholinesterase inhibitors, and heavy metals (Johnson 2024).

Nestlings may be subjected to parasitism by blowfly larvae, but the effects of this are fairly minor. Parasitism may slightly delay development of the young which could potentially increase nestling or fledgling mortality. Parasitism did not appear to affect nestling survival if it occurred after young were 6 days old. Infestations occurring very early in a nestling's life may be fatal, but infestations at this age occurred in only 12% of Wyoming nests. Parasitized nestlings showed normal haemocrit levels but had significantly reduced (less than 25%) concentrations of haemoglobin in their bloodstreams. This may have a profound effect on survivorship of fledglings because anaemic birds have a reduced ability to sustain flight (Eastman et al. 1989; L.S. Johnson et al. 1991; O'Brien et al. 2001).

In North Carolina, abundance of the Northern House Wren was significantly correlated with the number of houses and other buildings within 200 m (Lumpkin and Pearson 2013). In subdivisions in Rhode Island, abundance declined with increasing amounts of retained forest (Johnson 2024).

At noisy urban sites, Northern House Wrens sang songs with a narrower frequency range and faster rate than in quieter rural areas. It modified its trill structure to reduce sound masking and improve signal transmission. Wren songs had similar minimum frequencies at both sites, but frequency was increased as noise levels increased (Redondo et al. 2013). Urban house wrens inhabiting noisier territories had smaller song repertoires. Those in the noisiest locations tended to include more high-frequency elements in their songs. Not all males modified their songs to reduce masking effects of noise (Juárez et al. 2020).

DesGranges and Morneau (2010) considered the Northern House Wren sensitive to climate change because its presence was correlated with the mean number of annual degree-days equal

to or greater than 10°C in May, June, and July. Price (2004) predicted that the breeding range of the house wren would contract northward in southern Ontario if the average summer temperature increased by 2°C.

Status

The Northern House Wren is probably much more common now than prior to European settlement and subsequent forest clearing. It was not known to occur in Ohio in the 1830s but moved in quickly after the settlers arrived (Mayfield 1988). A similar pattern probably occurred in Ontario, where it was common by the turn of the 20th century and continues to be common (Lancaster et al. 2004; Mills 1981; Weir 2008). Baillie and Harrington (1937) considered it a common breeding species from the southern border north to at least Lake Abitibi and west to Lake of the Woods, but present more sparingly in the north. Mills (1981) noted that it was not as common in Muskoka and Parry Sound districts as it was historically, but that populations were recovering from a low in the 1960s. The decline may have been due to forest maturation. During the first atlas, it was ubiquitous south of the Canadian Shield, with density estimates of more than 1,000 pairs in some squares. Previously common in Algonquin Park (MacLulich 1938), it disappeared there due to in-growing of forest openings and removal of dwellings. It occurred sporadically in the Canadian Shield during the first atlas (Gould in Cadman et al. 1987). James (1991) considered it common north to Georgian Bay and Ottawa, locally rare and occasional to Sioux Lookout and Timmins, and a vagrant north to James Bay.

The second atlas demonstrated that there had been no change in the breeding range of the Northern House Wren since the first atlas. It was found in virtually every square south of the Canadian Shield and had a scattered distribution in the southern Shield and the Boreal Forest Region. There was no change in its probability of observation province-wide, but there was a significant increase in the Great Lakes–St. Lawrence Forest Region in the Shield. It was most abundant south of the Shield, particularly from Huron to Haldimand counties and in a band along the edge of the Shield from Georgian Bay to Brockville. Lower densities occurred in the intensive agricultural areas in the southwest and in the dense urban areas of the Greater Toronto Area (Brewer in Cadman et al. 2007).

Breeding Bird Survey data for 1970-2021 indicate that the population increased at annual rates of 0.587% in Canada and 1.22% in Ontario. For 2011-21, the annual rates of increase were 1.6% in Canada and 1.52% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Some young become independent approximately 10 days after fledging whereas some may still be receiving food from their parents 2 months later; independence usually occurs 12-13 days after fledging (Johnson 2024). One adult led its 5 fledglings back to the nest for 2 consecutive nights. Temperatures were below freezing (–2°C and –3°C) those nights. The first day after fledging, young remained within 7-12 m of the nest, but wandered 40-104 m from it the following day (Scholer 2015). Typically fledglings do not return to the nest because they are particularly vulnerable to predators within the nest and nests are often infested with ectoparasites.

MIGRATION

Northern House Wrens that breed in Ontario migrate through the southeastern United States and winter as far north as Maryland. One banded at Long Point was recovered in Texas; one banded in

Pennsylvania was recovered in the Dunnville Marshes (Brewer et al. 2018). It is unknown if individuals migrate singly or in flocks (Johnson 2024).

The Northern House Wren is a nocturnal migrant that arrives in the province near the end of April, with migration continuing until mid-May or even June. Occasionally birds arrive as early as the end of March. Males arrive on the breeding grounds a few days before females; in Ohio, females arrived about 9 days after males. Older, experienced birds tend to arrive before yearlings, although some first-time breeders also arrive early. Some first-time breeders do not appear on territories until mid- to late June. Autumn migration occurs predominantly in September with most birds gone by the end of September or early October, with occasional stragglers to mid-October. There are a few records from late December or very early January (Black and Roy 2010; Curry 2006; James 1991; LaForest 1993; Lancaster et al. 2004; Weir 2008).

During migration, the Northern House Wren occurs primarily in edge and shrubby habitats. It prefers woodland edges, gullies, thickets, ravines, open forest stands, hedgerows, raspberry patches, shrubby roadsides and power-line rights-of-way, and thickets around ponds, orchards, gardens, and abandoned buildings (Campbell et al. 1997; Fitch 1958). During spring migration in Minnesota and Wisconsin, it was significantly more abundant in floodplain forests than in upland forests (Kirsch et al. 2013).

The Northern House Wren shows considerable site fidelity during migration and some birds probably follow the same route every year. Taylor et al. (1983) examined 2,218 recoveries of house wrens and found that 97% of them were at or near the place of banding. There were 207 cases (9.3%) of the same bird repeating at the same site at least 1 year after being banded; 80.1% repeated once after the first recovery, 13.0% repeated twice, 6.3% repeated 3 times, and one repeated 4 times. Somershoe et al. (2009) also demonstrated house wren site fidelity during migration in Florida.

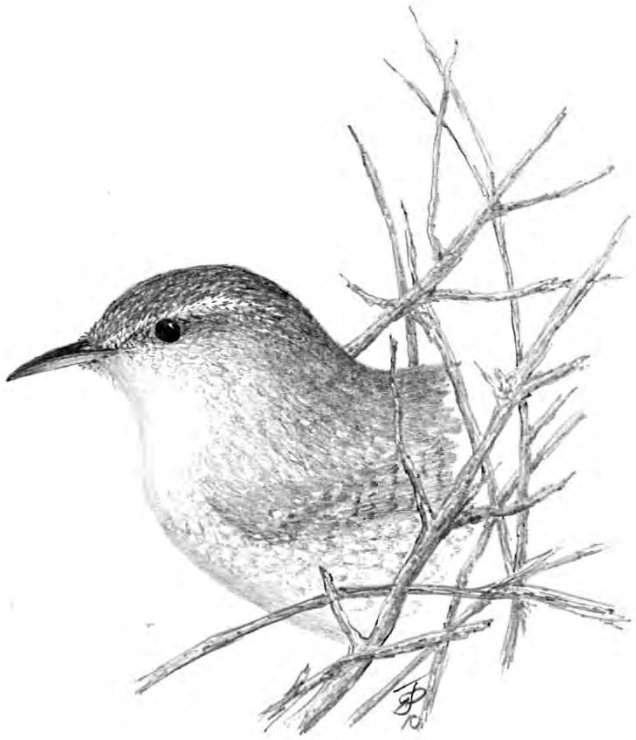
During migration, the Northern House Wren is vulnerable to being killed due to collisions with tall structures. It frequently collides with television towers, lighted buildings, and lighthouses (Gross in Bent 1948; Johnson 2024; Taylor et al. 1983).

In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season during 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming during the second period. Spring arrival dates of the Northern House Wren were significantly earlier during the second period, but there were no significant differences in autumn departure dates or length of the breeding season.

The Northern House Wren is uncommon during migration in Ontario (James 1991).

Winter Wren

Troglodytes hiemalis



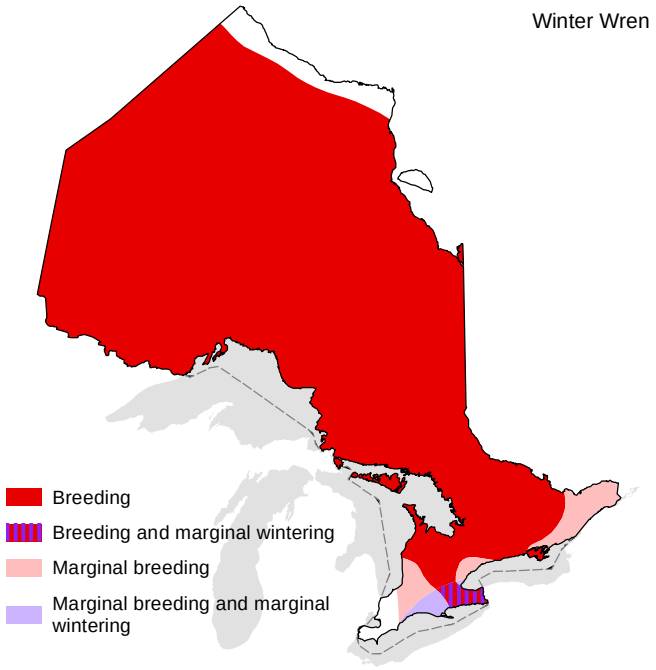
BREEDING SEASON

Habitat Requirements

In Ontario, the Winter Wren breeds in deciduous, mixed, and coniferous forests. It nests predominantly in swamps or near bodies of water. Two nests were in bogs treed with conifers and one was in a mixed forest near buildings (Peck and James 1987).

The Winter Wren was common in a black spruce swamp south of Moosonee and was likely to be found anywhere in the Hudson Bay Lowland where there was substantial forest (Wilson and McRae 1993).

In the Boreal Forest Region, the Winter Wren was associated with older coniferous mixed-wood forest with lower edge ratios and more intact forest cover. Rempel et al. (2007) predicted its habitat would be maintained under natural conditions as well as timber harvesting that adhered to the forest management guidelines for key species. It occurred in older, closed, coniferous forests in a mature forest matrix (Rempel 2007). Near Pickle Lake, it occurred in small numbers in black spruce forests at widely scattered areas (James 1980). In northwestern Ontario, it was most abundant in



coniferous forest, was present in mixed shrub communities, and absent in other habitat types (McLaren and McLaren 1981). Near Hearst, it nested in clear-cuts 5-24 years old and in uncut upland mixed stands (Welsh and Fillman 1980). Near White River, it was more abundant in mature forests than in clear-cuts 3-25 years old, but not significantly (Venier and Pearce 2005).

In white pine stands in the Canadian Shield in the Great Lakes–St. Lawrence Forest Region, abundance of the Winter Wren was significantly correlated with presence of medium and large pine trees. It was more common in old-growth than mature stands, but not significantly (Kirk et al. 2012). In Quetico Park, it nested in all stages of succession following forest fire with no significant differences in abundance from early successional to old-growth forest (Apfelbaum and Haney 1985). It was rare in jack pine and jack pine mixed stands near Gogama. Forest type was not as important as local conditions. It was associated with damp depressions in the sandy soils that were mostly too dry to support suitable habitat for it (James and Peck 1995a). In Algonquin Park, it nested in black spruce and black spruce–white cedar wetlands and in upland hemlock forests and was absent in other forest types (Martin 1960). In Muskoka and Parry Sound districts, it nested in dense, moist forests of many types (Mills 1981).

In Durham Region in the Great Lakes–St. Lawrence Forest Region south of the Shield, the Winter Wren nested in wet habitats including a black spruce bog, a riparian forest of white cedar–balsam fir–spruce, and 2 flooded woodlands with considerable hurricane damage and downed timber. Speirs and Orenstein (1975) considered it a mid-succession species associated with white cedar. At Presqu'ile, nesting occurred in coniferous forests and wet hemlock–grey alder forests (LaForest 1993).

In the Carolinian Forest Region near Hamilton, McIlwraith (1894) reported the Winter Wren nesting in cedar swamps made impenetrable by fallen timber. It is still present in these swamps as well as other extensive swamps in the Hamilton region (Curry 2006). In Elgin County it breeds in deeply shaded ravines that support hemlock (Lancaster et al. 2004). Baillie and Harrington (1937) stated that the Winter Wren bred in Ontario in deep woods and swamps.

Many studies concluded that the Winter Wren is an obligate old-growth forest species. In Alberta, it was associated with conifers in aspen stands and was significantly more abundant in old-growth stands than in mature and young stands (Schieck et al. 1995). In Saskatchewan, it occurred only in forests that were 140 years old or older (Cumming and Diamond 2002). Hejl et al. (2020) stated that the Winter Wren was unique among wrens in its association with old-growth forests.

Old-growth structure (snags, downed logs, and large trees) are used for nesting, foraging, and roosting. Nonetheless, it nests in a wide range of habitat including treeless islands, cliff faces, clear-cuts, and logged forests, although habitat suitability is lower in these habitats. In Quebec, it nested in young and mature black spruce forests, but not in clear-cuts or burns. It was equally abundant in forests with sapling growth 5-11 m tall and in those that were 120 and 200 years old (Imbeau et al. 1999). In Pennsylvania, it had a positive affinity for old-growth forest. It was present in 90.0% of old-growth forests, in 7.7% of forests statewide, and in 14.7% of forests in the Appalachian Plateau (Haney 1999). In the Yukon, it is regularly encountered only in dense old-growth riparian white spruce forests with a complex understorey, abundant leaf litter, and large fallen trees (Sinclair et al. 2003). In southern agricultural Quebec, it nests mostly in mature isolated woodlots with some conifer growth, or in peatlands. Further north, it nests mostly in coniferous and mixed forests, but also in mature dense deciduous and hemlock stands (Gagnon and Robert in Gauthier and Aubry 1996).

Despite the Winter Wren's apparent affinity for old-growth forest in certain areas, it nests in much younger stands and even clear-cuts. It is strongly associated with dense shrubbery, upturned root wads, and old logs. These preferences result in it inhabiting a wide range of forest ages from recent clear-cuts to old-growth forest. It may occur in clear-cuts or blowdowns where there is residual slash or upturned roots for cover, but is absent in burns where there is limited retained undergrowth. Near Hearst, it nested in clear-cuts 5-24 years old (Welsh and Fillman 1980). In New York, it nested near or within hemlock blowdown in a forest, but disappeared after the blowdown was cleaned up. In Alberta, retention of trees in clear-cuts allowed it to remain in the open areas. Its abundance increased with increasing basal area of trees left starting 3 years after cutting. In central Quebec, its density was 1.5 times higher in birch stands than black spruce–moss stands and more than twice as high as in old burns and shoreline ecotones in coniferous forests. In British Columbia, it occurred in mixed forests with a dense understorey, deep ground litter, and numerous fallen trees in various stages of decomposition. In subalpine areas of New Hampshire, it demonstrated a specialty for fallen logs. In New England, its presence was affected both by size class of timber and forest type. It occurred only in sawtimber-sized forests, the largest size-class of trees, and in stands dominated by red maple and hemlock. In the Boreal Forest Region, the Winter Wren was in a guild that was primarily associated with conifers and it occurred in rold stands. In subalpine areas of New Hampshire and Maine, its abundance was positively correlated with the percent ground cover and the total foliage volume of deciduous trees larger than 10 cm diameter at breast height (DBH). It was negatively correlated with canopy closure, the number of woody stems per ha, the number of snags larger than 10 cm DBH and taller than 5 m, and the total foliage volume of coniferous trees larger than 10 cm DBH (Burris and Haney 2005; Campbell et al. 1997; DeGraaf and Chadwick 1987; DeGraaf et al. 1998; Hejl et al. 2020; Gagnon and Robert in Gauthier and Aubry 1996; Holmes and Robinson 1988; Kirk et al. 1996; Sabo 1980; Sinclair et al. 2003; Tittler et al. 2001; Yunick 1990; Zarnowitz and Manuwal 1985).

The Winter Wren is frequently associated with water or with wet to damp habitats. In southern Quebec, it is often found near streams or lakes or in poorly drained or swampy forests (Gagnon and Robert in Gauthier and Aubry 1996). Streams were an important component of territories in

subalpine areas of New Hampshire (Sabo 1980). Hejl et al. (2020) stated that it frequently nests and forages near water, especially streams, but also bogs, swamps, and lakes. It is more restricted to riparian areas in the drier parts of its range, but water appears to be important to it throughout. Territories are preferentially established along watercourses or other sources of water, resulting in a patchy distribution.

In many areas, the Winter Wren is strongly associated with coniferous trees. Coniferous forest was most frequently inhabited throughout British Columbia (Campbell et al. 1997). In New Jersey, Benzinger (1994) considered it a facultative hemlock species. He estimated that 70% of the New Jersey population nested in hemlock growth and 30% in hardwoods containing pines. The most frequently occupied areas included ravines, stream valleys, and slopes, most of which supported hemlock. It was restricted to heavily wooded sites suggesting that microclimate might be a factor. Hemlock cover may result in lower air temperatures and higher humidity. Hejl et al. (2020) concluded that highest nesting densities occurred in coniferous forests. In an extensive forest near Richmond, Ontario, the Winter Wren was common in mixed swamps and coniferous forest. Over a 4-year period, it occurred in only 1 deciduous stand where there was extensive American yew in the understorey (personal observation).

Although the Winter Wren is strongly associated with coniferous stands, it occurs in a variety of forest types. In addition to mixed forests, cedar and spruce swamps, and upland and lowland fir communities, it has nested in many other forest types. These include sugar maple–beech–yellow birch hardwoods, dry boreal forests rich in nutrients, northern hardwoods, lowland hardwoods, and aspen-birch stands (Back 1979; Crawford and Titterington 1979; Dawson 1979; Holmes and Robinson 1988; Kirk et al. 1996; Noon et al. 1979; Samson 1979; Temple et al. 1979). Forest type may not adequately describe the microhabitats within the forest that it is selecting. Habitat features higher than 3 m may be relatively unimportant because it forages and nests close to the ground (Benzinger 1994).

The Winter Wren is often considered a forest-interior species. In southern Ontario, its probability of detection was positively correlated with the amount of forest cover 100 m or more from edge, forest size, and the amount of regional forest cover, but it was negatively correlated with the amount of forest within 2 km. These relationships were not significant (Austen et al. 2001). In a forest near Richmond, Ontario, it was significantly more abundant 180 m from edge than at 120, 60, or 0 m (Gore & Storrie Limited 1992). Lindell et al. (2007) summarized studies that determined its abundance in relation to forest edge. One study found that there was no relationship between its distribution and edge; 2 showed an avoidance of edge. In Newfoundland balsam fir stands, it was equally abundant in riparian edges, nonriparian edges, and forest interior. It was also equally abundant in 20-50-m wide riparian buffer strips retained between clear-cuts and water bodies and watercourses (Whitaker and Montevecchi 1997, 1999). In eastern Quebec forests, there was no difference in its density in riparian and nonriparian balsam fir–white cedar stands (LaRue et al. 1995).

Hejl et al. (2020) stated that Winter Wren abundance was higher in forests larger than 20 ha and in more continuous habitats surrounded by late successional forest than in smaller habitats and areas surrounded by edge, particularly clear-cuts. Size of clear-cuts may be important because it will nest near forest edge in small clear-cuts but may not nest in large clear-cuts or in the interior of

clear-cuts (Hejl et al. 2020). In Wisconsin, it was not present in linear tracts less than 100 m wide (Hejl et al. 2020). In Michigan, its abundance was positively correlated with patch size (Crozier and Niemi 2003). Drolet et al. (1999) studied its occurrence in 100-ha landscapes where forest cover ranged from a few remnant hectares to over 90 ha. They found no significant correlation between Winter Wren abundance and the amount of coniferous forest, mixed forest, mixed regeneration, clear-cuts, or windthrow within 100-ha squares, or with presence of budworm outbreaks.

In Ontario, there are some components of the Winter Wren's habitat that are consistent throughout its range, but other habitat requirements may vary from areas south of the Canadian Shield to in the Shield. Throughout Ontario, it is strongly associated with large, fallen logs and tangled undergrowth. South of the Shield, it is restricted to forested habitat where it appears to be area sensitive, seldom occurring in forests smaller than 20-30 ha. Exceptions occur, and it nests in wooded ravines with hemlock cover. In the south, it is most often found in mature and old-growth coniferous and mixed swamps containing white cedar, balsam fir, and spruce. These areas provide the cooler microhabitat that it appears to prefer as well as downed timber, upturned root wads, and the dense undergrowth that it requires. Deep, wooded ravines also provide these microhabitats. It may also nest in wet forests with dense shrub growth and windfalls, and these may have limited canopy closure due to high wind damage. South of the Shield, it is found mostly in forest interior, probably because cool moist habitats, fallen logs, and upturned roots seldom occur in forest-edge habitats. In the Shield, it appears to be less exacting in its habitat requirements. Complex understorey structure in the form of fallen logs, root masses, and shrubs is still necessary. Its presence is often strongly associated with water and it may occur at forest edges along beaver ponds, rivers, and lakes. While associated mostly with conifers in the south, understorey characteristics and presence of water appear more important in the Shield. Forest maturity is also not as important in the Shield, and it may nest in all successional stages of forest provided that the understorey structure is suitable and there is water nearby.

Early in the breeding season, the male occasionally roosts in his own dummy nest and also in hollow logs while the female roosts in the nest that is ultimately used for nesting. Both members of the pair roost alone at this time. Once the young fledge, the brood roosts together, and the female may lead the young to the roost for about 2 weeks. Some nests may be used for brooding but not for nesting (Hejl et al. 2020).

All Ontario nests were well hidden and shaded. Most were in fallen tree roots and in holes in tree stumps and fallen logs. Single nests were found under live birch roots growing under a building, under a bank of a ditch, in moss on a rock, and on a rock ledge. Nests were 0.08-2 m from the ground, but mostly 0.3-1.1 m up. One nest was in an old phoebe nest on a ledge (Peck and James 1987, 1997). In Algonquin Park, 1 nest was in a woodshed between a beam and the roof of the building. One nest was on a cottage above a window between the rafters of an overhanging roof. Later the same year, another nest was found at the same cottage in a sand-sifting box hanging on the outside wall of a shed. One of these nests was 2.1 m from the ground (Tozer 1996).

Throughout North America, the Winter Wren is a secondary cavity nester that nests primarily in natural cavities or old woodpecker holes, occasionally in cavities that it excavates in creek banks, and rarely in or on human-made structures or in a free-hanging nest constructed in a tree (Hejl et al.

2020; Zarnowitz and Manuwal 1985). In British Columbia, 52% of nests were in living or dead coniferous or deciduous trees and 24% were in banks and cliffs. Most were in a cavity: 33% in natural cavities and woodpecker holes, 26% among roots of overturned trees, and 26% under an overhang in a soil bank or cliff or an overhang of a building (Campbell et al. 1997). Bent (1948) reported most nests in cavities in the soil of upturned roots, but also some in rotten stumps, under roots of standing trees, in woodpecker holes, in rolls of bark of large trees, in logs, suspended from tree limbs, and in soil banks. Evans and Conner (1979) reported that the optimum size of snag for nesting was 20 cm DBH and that cavity entrances should be a minimum of 3 cm. It occasionally nests in nest boxes and other artificial features. Nests have been in and on buildings, in hanging flower planters, in old stoves left outside, in an air vent in a suburban house, in shrubs, on a bridge, in an abandoned automobile, and in a pair of snowshoes (Bent 1948; Campbell et al. 1997; Gagnon and Robert in Gauthier and Aubry 1996; Yunick 1990).

The territory size of the Winter Wren varies depending upon habitat type, food availability, density of breeding pairs, and whether the male is monogamous or polygynous. North of Lake Nipigon, 3 territories were 0.49-1.13 ha (average 0.89 ha; Kendeigh 1947). Average territory size in Algonquin Park was 0.49 ha (range 0.06-1.17 ha). The average depth of territories was 4.3 m (Martin 1960). Average territory size was 0.9 ha in a mature hemlock stand near Mirabel, Quebec (Gagnon and Robert in Gauthier and Aubry 1996). In subalpine areas of New Hampshire, territories averaged 1.6 ha (Sabo 1980). In Maine red spruce forest, Morse (1977) reported a territory size of 3.64 ha. In British Columbia, the average size of territories was 0.68-1.46 ha over 3 years (Hejl et al. 2020). Territory densities may be low and territory sizes larger when physical barriers and unsuitable habitat preclude the presence of neighbours. Territory size is affected by habitat structure and composition that determine the number of nest sites and singing posts and availability of food. When density of breeding birds is low, the most favourable habitats are occupied. Less favourable sites are occupied only when the population is high (Hejl et al. 2020). Where Winter Wrens are resident, the male defends the territory year-round, but the size of the territory may shrink after the breeding season. Females occupy a home range of 0.2-1.4 ha during the breeding season. These home ranges are usually non-overlapping, although limited overlapping may occur. Ranges of females mated to the same male do not overlap (Hejl et al. 2020). Near Quebec City, territories were not clumped with no evidence of coloniality (Bourque and Desrochers 2006).

The rate of natal philopatry is unknown (Hejl et al. 2020). Limited data suggest that adult site fidelity is high. In British Columbia, 16 of 44 nests (36.4%) were reused the following year, and 5 were used by the same male (Hejl et al. 2020).

Limiting Factors

Eggs have been found in Ontario nests from late May to mid-July, mostly during the first 3 weeks of June (Peck and James 1987, 1997). The length of time required to complete a nest is unknown. The interval between the beginning of nest building and the initiation of egg laying is 3-22 days. Eggs are laid at the rate of 1 a day, although a day is occasionally skipped. Incubation often starts with the laying of the last egg, but may start as early as when the first egg is laid. It has been suggested that incubation starts with the last egg in clutches laid in April and May and with the first egg in later clutches. The incubation period is 14-16.5 days. The young leave the nest when they are 15.5-19

days old, typically 16-17 days. The family group remains within the male's territory for 6-36 days after the young from first brood fledge and then the family unit dissolves (Bent 1948; Campbell et al. 1997; Hejl et al. 2020).

The lengthy egg-laying period suggests that 2 broods may be raised in Ontario (Hejl et al. 2020; Peck and James 1997). Renesting almost always occurs after failure of the first nest; 2 attempts at renesting may be made. There is a strong correlation between the number of nests completed and the number of breeding attempts a male makes each season (Hejl et al. 2020). Clutches of 4-6 eggs have been reported in Ontario, with 5-6 eggs most frequent (Peck and James 1997). Clutches of 1-9 eggs have been reported with most containing 5-6 eggs, or occasionally 7 eggs. Clutch size increases with latitude (Bent 1948; Campbell et al. 1997; Hejl et al. 2020).

The age at first breeding has not been documented. Both sexes presumably breed in their first year and every year thereafter similar to other North American wrens. Some adult males remain unmated during at least part of the breeding season (Hejl et al. 2020). The mating system is predominantly monogamous, but bigamy occurs and trigamy is rare. Polygyny appears to be more prevalent where food or nest sites are abundant but unevenly distributed. There appears to be no difference in nesting success between monogamous and polygynous males (Hejl et al. 2020).

The Winter Wren's foraging techniques have been considered similar to those of the Black-capped Chickadee, except that the wren almost never forages above heights of 3 m. In Algonquin Park, the Winter Wren had the lowest territory of any bird species, where it was not observed over 2.4 m from the ground. Average foraging heights in other regions were 0.7 m in subalpine communities and 1.7 m in northern hardwoods. Within this vertical range, it may forage on all available substrates including the ground, logs, root masses, shrubs, and trees (Hejl et al. 2020; Holmes and Robinson 1988; Martin 1960; Sabo 1980). The foraging substrate that is used most frequently varies depending upon the habitat and availability of food. In northern hardwoods, it foraged most frequently in the shrub layer on bark and leaves, followed by on the ground and around the bases of living trees, in herbaceous or fern cover, and in the air. In subalpine communities, it foraged most on the forest floor (81.5%) and seldom on coniferous (6.3%) and deciduous (4.5%) tree foliage (Hejl et al. 2020; Holmes and Robinson 1988; Sabo 1980). It occasionally forages underwater along ditches and stream banks by immersing the upper half of its body to capture aquatic invertebrates or small fish (Bent 1948; Heck 1994). Hawking and aerial foraging are rare foraging techniques (Holmes and Robinson 1988). Occasionally it forages on tree trunks in a fashion similar to that of the Brown Creeper (Hejl et al. 2002). In New Hampshire, foraging techniques were 24.9% probing, 61.3% gleaning, 2.5% jumping to hover, 6.8% hovering, and 4.5% hawking. Slightly more than 50% of foraging manoeuvers were directed towards prey on bark: 50% of these were on tree trunks and exposed roots; 41% on dead logs and branches laying on the ground; and 9% on the bark of twigs or branches near the ground. It was primarily a gleaner in all substrates, but it also probed bark extensively on fallen dead wood and less frequently in the ground litter. While searching for food, it also hopped into knotholes and cracks between upturned roots. It mechanically searched low substrates for prey by hopping slowly and examining crevices. It also probed clusters of dead leaves suspended in shrubs (Holmes and Robinson 1988). In subalpine New Hampshire communities, foraging strategies were 63.3% fallen log manoeuvers, 14.3% gleaning

from the litter, 11.5% pecking at the litter, 5.2% gleaning from leaves, 2.8% pecking at twigs, 1.4% gleaning from tree trunks, 1.0% hawking from leaves, and 0.3% gleaning from twigs (Sabo 1980).

Both adults feed the nestlings; the male rarely brings food to the female as she incubates (Hejl et al. 2020). Bent (1948) reported that nestlings were fed a variety of moths, including spruce budworm moths and geometer moths; crane flies; cutworms; caterpillars; a variety of small insects; and spiders.

The adult Winter Wren's diet is similar to that of nestlings; it feeds predominantly on invertebrates. It is an opportunistic or weakly selective forager, and the quantity of available food is a factor in its habitat selection and dispersion. Insects and spiders are staples in the diet. The major invertebrate groups consumed include beetles, bugs, caterpillars, ants, fleas, mites and ticks, pseudoscorpions, millipedes, spiders, and harvestmen. In a sample of 122 British Columbia stomachs, 66% contained beetles, 51% spiders, 30% moth and butterfly caterpillars, 23% mites and ticks, 10% millipedes, 10% harvestmen, and 2% snails. The abundance of soft-bodied invertebrates was probably underestimated. Other food items included centipedes, springtails, bristletails, lacewings, and unidentified seeds. Consumption of certain foods varied seasonally: millipedes occurred in 2%, 28%, and 50% of stomachs during the breeding season, autumn, and winter, respectively, compared with 5%, 4% and 17% for springtails and 3%, 52%, and 0% for seeds during the same periods (Hejl et al. 2020). Bent (1948) reported the diet to consist almost exclusively of invertebrates: beetles, bugs, spiders, caterpillars, and ants and other small hymenopterans. Forest insects consumed included beetles (weevils and long-horned and leaf beetles), leafhoppers, aphids, lacewings, sawflies, and caterpillars. Grasshoppers, crickets, crane flies, millipedes, and snails were minor components of the diet; dragonflies, harvestmen, mites, pseudoscorpions, and isopods were rarely eaten. In New Hampshire, Holmes and Robinson (1988) observed adults taking spiders, harvestmen, and a variety of insects. In New York, one captured 3 small trout fingerlings by dashing through several metres of 1-cm-deep water to grab the fish (Heck 1994). It has been observed eating red cedar berries in October. Near Manitouwadge, there was no correlation between the abundance of the Winter Wren and spruce budworm (Venier et al. 2009). In New Brunswick, Morris et al. (1958) found an inverse relationship, with the Winter Wren decreasing with increasing budworm abundance. Mitchell (1952) examined the contents of 9 stomachs during a spruce budworm outbreak in Maine. Over 2 years, the diet consisted of 3% and 11% budworm larvae and pupae by volume.

The Winter Wren has not been documented being parasitized by the Brown-headed Cowbird (Hejl et al. 2020).

Forest fragmentation and logging are the greatest limiting factors to the Winter Wren. In Ontario south of the Canadian Shield, activities that reduce forest sizes below 30 ha are likely to result in the loss of breeding Winter Wrens. Even larger forest remnants may become unsuitable habitat if they become drier or less complex in structure. In Maine, it was more abundant distant from a highway even when habitat was taken into account. Ferris (1979) concluded that the highway was having a negative effect on the Winter Wren. It was not determined if the aversion to the road was due to a response to predators, noise, edge, or other factors. In the Canadian Shield of Ontario, it was equally abundant in early successional and mid-successional clear-cuts and burns in the same seral stages.

It was significantly less abundant in early successional and mid-successional stands than in mature stands (Zimmerling et al. 2017). Hejl et al. (2020) stated that it was one of few species that was clearly harmed by forest fragmentation in the west. There is concern for it in certain areas due to declines in snags, downed trees, large trees, and old-growth forest. Hejl et al. (2020) predicted that a combination of forest fragmentation and simplification of forest structure through even-aged management would probably result in its decline. It may be somewhat more resilient to forest-management practices in the east, where it occasionally nests among residual trees and slash in clear-cuts. Vanderwel et al. (2007, 2009) summarized studies that examined the effects of partial timber harvesting in the Boreal Forest Region, with particular reference to Ontario. There was no change in its abundance when 30%, 50%, or 70% of trees were removed. It experienced a 25-75% decrease in abundance when about 85% of trees were removed. In Algonquin Park, group-selection and single-tree harvesting of tolerant hardwoods had no significant effect on the Winter Wren (Jobes et al. 2004; Tozer et al. 2010). In New York, Webb et al. (1977) studied the response of Winter Wrens when 25%, 50%, 75%, or 100% of merchantable trees were removed in diameter-limit forest management. A declining trend in wrens was observed with increasing logging intensity, but the trend was not significant. It appeared to be negatively affected only when logging approached being a clear-cut. In Minnesota, tree removal in residual riparian buffer strips did not negatively affect it. It responded positively when trees were cut-to-length on site rather than being removed whole. The cut-to-length harvest resulted in greater amounts of slash being left within the forest (Hanowski et al. 2002, 2005). In Maine, the Winter Wren was associated with all seral stages resulting from clear-cuts of spruce-fir forests. Highest density occurred in the first 2 years after cutting when the habitat was characterized by dense slash and abundant open ground. Numbers remained high 3-12 years after clear-cutting as the habitat evolved through dense raspberries and regenerating hardwoods less than 2 m tall to hardwood regeneration taller than 2 m with a well-developed coniferous regeneration stratum. Density declined by approximately 50% as the habitat changed to hardwood regeneration taller than 4.5 m with trees with a DBH of 10-15 cm (Titterington et al. 1979). In Vermont, the territory of a Winter Wren included mostly a clear-cut area but also adjacent hardwood forest (Lent and Capen 1995).

In Alberta, the Winter Wren was equally abundant near noisy compressor stations and quiet well pads. It appeared to be unaffected by chronic noise (Bayne et al. 2008). It exhibited no response to energy sector disturbances. There was no difference in its abundance at seismic lines, pipelines, well pads, or forest interior adjacent to these features (Bayne et al. 2016).

Price (2004) concluded that the Winter Wren might disappear as a breeding bird from southern Ontario if the average summer temperature increased by 2°C.

Status

The Winter Wren was probably more abundant south of the Shield prior to European settlement than it is at present. McIlwraith (1894) stated that it was predominantly a migrant in the Hamilton area, although a few remained to breed in large swamps in Flamborough Township, where it still nests (Curry 2006). Baillie and Harrington (1937) concluded that it bred in small numbers from Middlesex and Leeds counties north to Moose Factory and west to Manitoba. In Muskoka and Parry Sound districts, it is the most common breeding wren (Mills 1981), but it is much less common than

the Northern House Wren south of the Shield (Richard in Cadman et al. 1987). James (1991) reported that the Winter Wren was a common resident throughout the province south to Rondeau Park, but becoming rare in the northern Hudson Bay Lowland and south of Georgian Bay and the Shield.

The second atlas demonstrated that the range of the Winter Wren had not changed significantly since the first atlas, although it was found in many more squares on Manitoulin Island and in a band south of the Canadian Shield. Its probability of observation increased significantly province-wide and in every region except the Carolinian Forest Region, where the trend was positive but not significant. It was most abundant in the Shield, particularly in the Boreal Forest Region in Thunder Bay and Cochrane districts. South of the Shield, it was considerably less abundant and absent from intensive agricultural areas in the southwest (Brewer in Cadman et al. 2007).

There are insufficient Breeding Bird Survey data to determine population trends of the Winter Wren (A.C. Smith et al. 2023).

MIGRATION

In North America, different populations of Winter Wrens have different migratory strategies. Some are completely migratory whereas others are partially migratory or resident (Hejl et al. 2020). It appears as though most of Ontario's population is migratory. Although some birds overwinter in the extreme south, it is likely that most of these have migrated from further north. Most areas where it is observed in winter are not suitable breeding habitat, or are areas where it is not known to breed. There are a few locations where it breeds and also occurs in winter. These birds may be maintaining their territory year-round.

Average spring arrival is in late March to early or mid-April in the south, but not until mid- to late April in the southern Shield. The peak of migration in the south is in the last half of April. Autumn migrants may arrive in the south in the last third of August, but the peak of migration is from mid-September until mid-October. In the south, migrants may continue to move southward through December in response to adverse weather conditions. Most of the population is gone by late October or early November (Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

During migration, the Winter Wren prefers dense tangles of shrubs and undergrowth, as well as brush piles. It is not confined to habitat that it uses during the breeding season and may occur in city parks and gardens, rural residential lots, thickets at edges of wetlands, cool gullies along watercourses, power-line rights-of-way, logging slash, riparian areas, and a variety of woodland types with brushy areas (Campbell et al. 1997; Hejl et al. 2020; McIlwraith 1894).

In British Columbia where the Winter Wren is resident, females leave their breeding territory after the breeding season, but males remain in the general area. Autumn territory size of males in British Columbia ranged from 0.42 to 1.31 ha (Hejl et al. 2020). It is unknown if males maintain autumn territories in Ontario.

During the nonbreeding season, the Winter Wren may roost nocturnally during periods of low temperatures or cold, rainy weather. Those that remain near the breeding grounds may roost in

their own or Carolina Wren dummy nests. Birds may also huddle close together on a branch to preserve heat (Hejl et al. 2020).

During the day, the Winter Wren may occasionally be observed in mixed flocks with other species. Migration is predominantly nocturnal, and it is commonly killed by striking towers and other illuminated tall structures at night (Hejl et al. 2020; Taylor et al. 1983).

The Winter Wren is common during migration (James 1991).

WINTER

Christmas Bird Count data indicate that the Winter Wren winters only in areas that receive over 81 cm of precipitation annually (Root 1988). It was most often found during winter in Elgin County in woodlands where there was a coniferous component and where streams stay open all winter (Lancaster et al. 2004). Throughout its range, it is often found in riparian areas during winter (Hejl et al. 2020). In winter, it may use a variety of habitats, including any type of woodland and occasionally around houses and gardens in villages and towns (Bent 1948; Hejl et al. 2020).

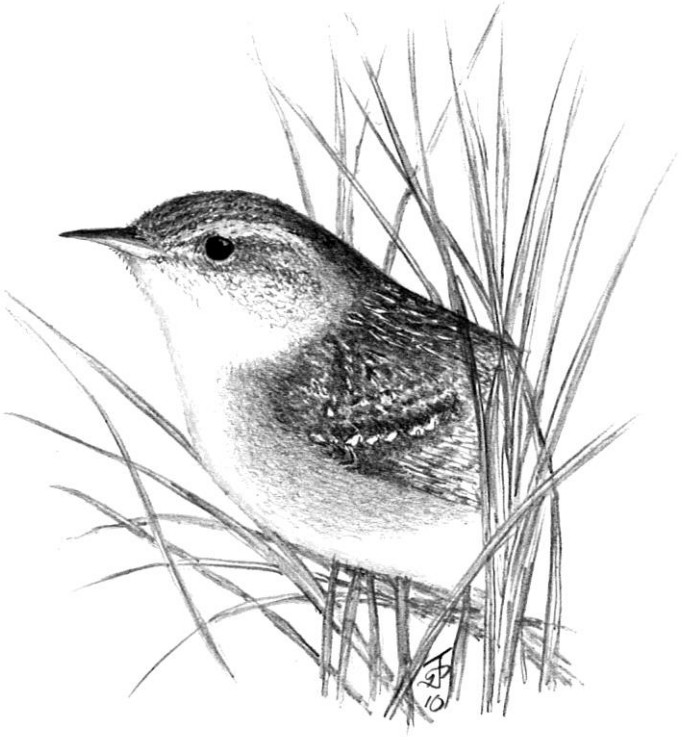
Roosts are an important winter habitat component. Winter Wrens may roost in nest boxes, in woodpecker holes, nests that were not used for breeding, mammal burrows, abandoned or open outbuildings, and crevices in occupied houses. There is 1 record of 4 or 5 roosting together on a pine limb under an accumulation of needles. Males, females, and hatch-year birds roost together communally (Bent 1948; Campbell et al. 1997; Hejl et al. 2020).

The greatest limiting factor in winter is severe weather. During exceptionally cold and snowy weather, many Winter Wrens die. Marked declines in breeding populations often occur after severe winters. Severe winters in the southeastern states several years between 1966 and 1978 resulted in significant population declines (Bent 1948; Hejl et al. 2020).

The Winter Wren is rare in winter, occurring primarily along the northern shore of Lake Erie, but also north to Hamilton and occasionally to Presqu'ile Park and Kingston. One early March record from Muskoka suggests overwintering (Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Weir 2008). It is possible that it is more common during winter than it was historically. McIlwraith (1894) knew of no winter records for the Hamilton area or the province. It occasionally overwinters in the Hamilton area now (Curry 2006). In Elgin County, it was not known to occur in winter in 1891 but by 1954 a few remained in winter (Lancaster et al. 2004).

Sedge Wren

Cistothorus stellaris

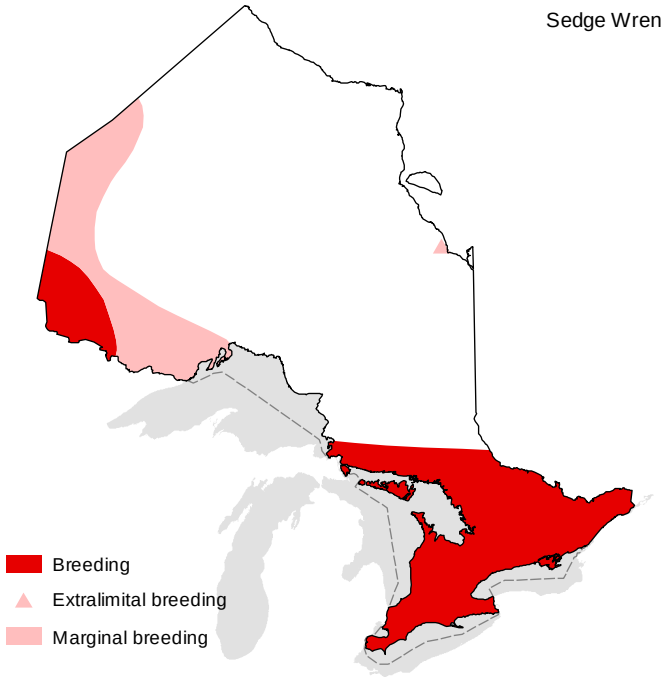


BREEDING SEASON

Habitat Requirements

In Ontario, the Sedge Wren nests in sedges or cattail meadows and marshes (48.6% of nests); in cultivated and uncultivated tallgrass fields and pastures (42.9%), including 2 nests in strawberry patches; in bogs (5.7%); and in an old, overgrown, wet gravel pit (2.9%). Wet habitats were slightly preferred (54.3%) to upland habitats, but nests were rarely over water. Most habitats used for nesting were open, although scattered trees and shrubs were occasionally present (Peck and James 1987). Breeding has occurred in Ontario in marshes (especially those dominated by sedges), bogs, fens, old fields with tall rank growths of grass, wet meadows, and hayfields (LaForest 1993; Lancaster et al. 2004; MacLulich 1938; McIlwraith 1894; Sandilands 1984; Weir 2008).

Typical Sedge Wren habitat consists of damp or wet areas dominated by sedges or grasses, often in the interface between wetlands containing standing water and upland meadows. Nesting habitat is often bounded by cattail marsh on 1 side, which may be occupied by the Marsh Wren, and dry habitats. There is usually very little and often no water where it nests, although it may occasionally nest where water is as deep as 50 cm. The territory is usually dominated by graminoids early in the season, but goldenrods, asters, blue vervain, and other herbaceous species may be



prevalent later in the season. Most territories support 2 or 3 small trees or shrubs such as willows, meadowsweet, chokecherry, and hawthorns that are used as singing perches by the male. Occasionally shrubs may be fairly dense, particularly at edges of bogs and fens and more upland borders of marshes, but it tends to avoid cropland and areas of extensive woody vegetation. Height of vegetation may be important. It may wait to initiate nesting until vegetation is 1-2 m tall and it seldom nests in vegetation shorter than 0.5 m. It selects dense vegetation. Higher breeding densities occur in denser cover of similar vegetation types. In tallgrass prairie, it prefers tall dense vegetation, usually with a well-developed litter area. In the Boreal Forest Region, the Sedge Wren nests predominantly in fens. In other regions, it nests in wet prairie-sedge meadows; lake-edge marshes; restored prairies of big bluestem, switch grass, and Indian grass; fields of smooth brome and reed canary grass; cultivated rice fields; cordgrass sloughs; sedge meadows; beaver meadows; natural tallgrass prairies; stands of river bulrush in semipermanent ponds and lakes; common reed stands; dry depressions or sloughs in upland fields that contain water only after storms; damp hayfields and old fields; drier margins of marshes; lightly grazed pastures; and fields managed for waterfowl production. It selects soils and vegetation that are highly vulnerable to drying or flooding caused by annual and seasonal variation in rainfall so that habitat suitability may constantly be changing. It nests in tall, dense growths of sedges (especially fens in the Shield) and usually avoids short, sparse, or open vegetation, flooded areas, and wetlands dominated by cattails. In Minnesota, average characteristics of territories were 303 sedge stems, 16 forb stems, and 50 shrub stems per m^2 and a predominant vegetation height of 1.1 m. Higher densities occurred in areas of medium shrub densities (11-32 stems per 25 m^2) than in areas with more or less shrub growth. In Wisconsin, its density was positively correlated with cover of woody vegetation, maximum vegetation height, vegetation density, cover of herbaceous vegetation, and cover of residual vegetation. North Dakota populations were lower during a drought than during a wet period. Its abundance was positively associated with the number of ponds present. Where it was present in North Dakota, litter depth was greater, maximum vegetation height was taller, and there was more sweet clover than where it was absent. Areas where it was absent had more shrubs taller than 1 m and more coverage by aspen within 100 m and 500 m than areas where it was present. Increased woodland coverage negatively affected it as did the presence of tall shrubs. Occurrence dropped from 40% in areas with no woodland cover within 500 m to 0% at about 30% woodland coverage (Askins et al. 2007; Bedell 1996; Bent 1948; Burns 1982; Clausen 1989; Crawford 1977a; Dancey 1995a, 1995b; Dechant et al. 2002e; Erskine 1977; Fragnier and Robert in Gauthier and Aubry

1996; Grant et al. 2004; Greenlaw 1989; Hartley 1994; Herkert et al. 2020a; Jalava 1993; Johnson and Igl 2001; Leighton et al. 2002; Lingle and Bedell 1989; Meanley 1952; Meeks 1996; Mousley 1934b; Niemuth et al. 2008; Picman and Picman 1980; Walkinshaw 1935).

Panci et al. (2017) conducted point counts in coastal wetlands of all the Great Lakes to determine landscape-scale preferences of the Sedge Wren. It was 2.5 times more likely to occur west of longitude 84°W at sites with less than 11 km of roads within 1,000 m. It was negatively affected by road density within 1,000 m. Its occurrence was 4.1 times more likely at points with less than 9% woody wetland within 2,000 m. In Ontario, it occurred almost exclusively along the shoreline of Lake Superior in the Sault Ste. Marie and Thunder Bay areas. It preferred landscapes that were 0-12% forested in North Dakota (Cunningham and Johnson 2019).

Tozer et al. (2024) identified the habitat preferences of the Sedge Wren in coastal Great Lakes marshes. It was positively correlated with wetland cover, negatively affected by water levels, and negatively correlated with the amount of urban and agricultural land within the watershed. Robert et al. (2009) studied its habitat use in southern Quebec fens. Occupied areas had higher lateral visibility (or lower vertical cover) and lower shrub cover than random areas including lower density of shrubs taller than 1.5 m (61.1 compared with 357.5 per ha), fewer shrub stands along transects (0.8 compared with 3.8), and greater distance to the nearest shrub (7.0 m compared with 4.4 m). Mean lateral visibility was less than 25% below 1 m and did not differ between occupied and unoccupied sites. Visibility was consistently greater at stations occupied by wrens for higher height classes. There were no differences between occupied and unoccupied sites for water depth, plant species richness, diversity, vegetation height, evenness, and structural heterogeneity. The primary factor affecting its distribution appeared to be shrub density, with a mean density of 93 shrubs per ha at occupied sites compared with 409 at unoccupied sites. Most shrubs were alders with minimal cover by willows and meadowsweet. Lake sedge dominated the herbaceous layer, with subdominants of water sedge, purple loosestrife, marsh fern, and Canada bluegrass. These species covered 85.5% of the non-woody layer and their relative cover did not differ significantly between occupied and unoccupied sites. Cover of cattails, big bur-reed, and spotted jewelweed varied between occupied and unoccupied sites, but coverage by these species was low.

Some studies suggested that the Sedge Wren may be area sensitive; others concluded that it is not. Johnson and Igl (2001) studied relationships between its density and patch size in Montana, South and North Dakota, and Minnesota. At 1 site, patch size was significantly correlated with density; at 3 other sites there were no statistically significant correlations although trends were positive. They concluded that it was area sensitive based on increasing density with increasing patch size, but noted that Herkert (1994a) found no effect of patch size in Illinois. In Michigan Great Lakes coastal wet meadows, its presence was positively correlated with meadow size, but not significantly (Riffell et al. 2001). Another Michigan study found that its abundance was negatively correlated with wetland size (Crozier and Niemi 2003). In Iowa, it was negatively associated with the area of wetland within a 3-km radius and with the total area of wetland that was inhabited, but positively associated with the area of wet meadow within the wetland (Fairbairn and Dinsmore 2001a, 2001b). In Michigan, Walkinshaw (1935) reported as many as 40 males singing in an area of approximately 4 ha, but could only find 1 pair in smaller habitat patches. In Quebec, Mousley (1934b) reported a pair

nesting in a 0.27-ha patch. It appears as though the Sedge Wren is not particularly area sensitive because it has been documented nesting in some very small, isolated habitat patches and correlations between increasing density with increasing patch size are weak. In a review paper, Ribic et al. (2009) concluded that the Sedge Wren was area sensitive.

The population of Sedge Wrens studied by Robert et al. (2009) in southern Quebec was a long-term population in a region where there are large tracts of wetlands, including fens. Most other Sedge Wren sites in that province have been in small, wet meadows surrounded by forests or agricultural land uses. Populations in these habitats are small and site tenacity is low. This suggests that the amount of wetland in a landscape may be an important factor in determining both population size and frequency of occupation of habitat. Although it may or may not be area sensitive, larger patches are probably more likely to consistently support populations. Thogmartin et al. (2006) used Breeding Bird Survey (BBS) data in grassland-dominated landscapes to determine its broad-scale habitat preferences. It was positively associated with the amount of grassland, wetland, and mucky soils, and negatively associated with the mean January temperature, percent forest cover, and presence of the species on adjacent counts. They concluded that it was not sensitive to grassland area, but was more abundant in landscapes where the number and size of wetland patches were high.

Ontario nests were in upright clumps of both dead and living stalks of sedges, grasses, herbaceous species, and cattails. Two were at the base of a small tree, one was on the ground at the base of a clump of sedges, and one was fastened to grass stems and meadowsweet branches. Elevated nests were 0.1-0.9 m from ground, with most 0.2-0.5 m up. Dummy nests were frequently present and one was as close as 3 m to the nest that was used (Peck and James 1987).

Most nests are in dense, thick mats of sedges or grasses or occasionally herbaceous species. They may be placed near the ground or water at the base of a shrub. Although some nests are on the ground, most are a short distance above it, ranging from 0.05 to 1 m above the substrate with most 0.5 m or less in height. In addition to the nest that is ultimately used for nesting, the male builds several complete nests that may potentially be used for roosting, decoys for predators, and attracting additional females to the territory. In Minnesota, males built an average of 9 nests in their territory; 9% were incomplete. In Michigan, nests that were used averaged 30 cm from the ground. False nests tended to be higher and not as well concealed. The following year, the substrate in the same area was much drier and active nests averaged 50 cm from the ground (Bent 1948; Burns 1982; Herkert et al. 2020a; Meanley 1952; Mousley 1934b; Walkinshaw 1935).

The Sedge Wren is territorial and territories are non-overlapping. Territories are used for courtship, nesting, and most of the foraging. Twelve territories in Minnesota averaged 0.178 ha (range 0.05-0.36 ha). The maximum seasonal territory size of an individual bird was 0.226 ha (average 0.128 ha). As the season progressed, males tended to stop defending some portions of their territory and drifted to new areas (Burns 1982).

The Sedge Wren is often considered colonial because numerous pairs may be present in a small area. This is primarily a function of its small territory size and the fact that some males may be polygynous, resulting in very high local nesting densities. There appears to be no evidence that it is

a truly colonial species from a behavioural perspective. It does not concentrate nesting in a small portion of a larger patch of suitable habitat, the nesting area does not function as an information source for finding rich food resources, and communal defence of nests has not been observed.

No information is available on natal philopatry. The Sedge Wren is one of the most nomadic North American birds. Birds may suddenly appear or disappear within a breeding season. Habitat suitability may change within an area due to differences in precipitation rates and other factors such as natural succession, with wrens being quick to colonize or abandon a site. Even where there is no apparent change in habitat, birds may be abundant 1 year and absent the next. In many areas in the east, it is very erratic with few sites supporting wrens on a regular basis. Those that do are usually fens or sedge-grass meadow marshes. Of 91 sites occupied since 1959 in Quebec, only 12% were occupied more than 4 years and there was only 1 site that was consistently occupied since 1970. Breeding wrens were present at 1 site in Illinois for 14 consecutive years, although it was unknown if any of the same birds were involved. The entire population is very mobile, with breeding concentrated in widely separated portions of its range during different times within its breeding season. The first period of nesting is in late May and June and occurs primarily in the north in Ontario, Quebec, Saskatchewan, North Dakota, Wisconsin, and North Dakota. The second nesting period extends from July until September. Breeding then is much more widespread with birds expanding into southern (Nebraska, Kansas, and Missouri) and northeastern (Vermont and Massachusetts) portions of the breeding range. Although it has yet to be confirmed, there is strong circumstantial evidence that Sedge Wrens may raise multiple broods in widely separated areas of its range within the same year. The general exodus from early northern breeding sites corresponds closely to its arrival in the south where it may not appear until July or August, and breeding may continue until September or even early October. In the south, arrival dates on the breeding grounds are often unpredictable and vary with precipitation. Birds typically arrive in Nebraska in July or August, but during a very wet year arrival was in May. Birds in other areas have been observed arriving in a flooded area in May, abandoning it and returning in July to breed throughout August. It appears as though it has adapted these erratic movements over a long period of time. Each male improvises a suite of songs, and no 2 wrens have identical songs. The wide range in songs allows males to have functional songs anywhere (Bedell 1996; Burns 1982; Dancey 1995b; Fragnier and Robert in Gauthier and Aubry 1996; Herkert et al. 2020a; Kroodsma et al. 1999; Meeks 1996; Robert et al. 2009; Weir 2008).

Limiting Factors

Eggs have been found in Ontario nests from early June until the third week of July, with most present in the last half of June (Peck and James 1997). Curry (2006) reported that the Sedge Wren occasionally did not arrive at some sites near Hamilton until late July or August. It is possible that these are late-nesting birds. Throughout its range, it is inconsistent in the timing of nesting; timing at a given site may vary year to year. There may be eggs or young in nests from early May until mid-September at some sites. Nesting may be mostly in June and July at some areas and primarily July and August in others (Bedell 1996; Burns 1982; Herkert et al. 2020a; Koenig and Stahl 2007; Kroodsma et al. 1999; Lingle and Bedell 1989; Meanley 1952). Secondary females of polygynous males may not

begin laying until late in the season when primary females are initiating their second clutch (Burns 1982).

The male begins building nests about 2 weeks after arrival on the breeding ground. Approximately 7-8 days are required to build a nest exterior. The female selects a nest and adds the lining to complete it. One egg is laid per day. Incubation begins before the clutch is complete, with eggs hatching over a 2-3 day period. The incubation period at 1 Ontario nest was 12 days, but the average incubation period is approximately 14 days (range 12-16 days). In Iowa, the mean incubation period of 21 nests was 13.8 days (range 13-16 days). The average nestling period of 67 young at this site was 13.6 days (range 11-16 days). In Quebec, young left the nest when they were 13-14 days old, but could not fly (Burns 1982; Crawford 1977a; Herkert et al. 2020a; Mousley 1934b; Peck and James 1997; Walkinshaw 1935).

Some females raise 2 broods in a season; others raise a single brood. Primary females of polygynous males may raise 2 broods; secondary females raise one. Females of monogamous males typically raise a single brood. Egg dates for Ontario suggest that only 1 brood is raised in a season. Some Ontario populations become established late in summer and it is possible that these birds are nesting and raising their second brood of the year. It is unknown if birds that become established in areas in July and August are breeding for the first time or have raised another brood somewhere else (Burns 1982; Crawford 1977a; Herkert et al. 2020a; Jalava 1993; Walkinshaw 1935). Clutches of 4-8 eggs have been reported in Ontario, mostly 5-7 eggs (Peck and James 1997). Clutches of 2-8 eggs have been reported, with 7 eggs the most frequent clutch size. In Minnesota, all first clutches of primary females mated with a polygynous male and all females mated to a monogamous male contained 7 eggs. Later clutches were more variable, with 4-7 eggs, and significantly smaller (5.7 compared with 7.0 eggs). Polygynous males produced an average of 8.6 young annually compared with 5.9 by monogamous males. In Iowa, secondary females laid significantly smaller clutches (mean 5.2 eggs, range 5-6) than primary (mean 7.6 eggs, range 7-8) and monogamous females (mean 7.1 eggs, range 5-8). Secondary females raised fewer young than primary females and those mated to a monogamous male, but differences were not significant. Polygynous males produced an average of 5.6 young annually compared with 3.0 for monogamous males (Bent 1948; Burns 1982; Crawford 1977a; Herkert et al. 2020a; Walkinshaw 1935).

The age of first breeding is unknown, but is probably 1 year. It is unknown if adults breed every year (Herkert et al. 2020a). The Sedge Wren is in a guild of species that nests in wetland and grassland habitats and there is a high incidence of polygyny in this group. All females breed, but not all males hold a territory (Greenlaw 1989). Polygyny may be common, with rates of 9% and 30-50% of polygynous males being reported. There have been no reported cases of a male being mated to more than 2 females. In Iowa, some males maintained territories in June and July and remained mateless but it was unknown if they attracted females later in the breeding season. In most cases, double-brooded females mate with the same male for both clutches, but occasionally they mate with a different male for the second brood. Females appear to choose territories and hence partners based on the degree of protection that the vegetation offers from predation. Males defending territories with dense vegetation are more likely to be polygynous (Burns 1982; Crawford 1977a).

Foraging occurs mainly at ground level where the Sedge Wren searches for insects in moist soil and at bases of grasses and sedges. Young are fed moths, spiders, mosquitoes, flies, grasshoppers, and bugs, with spiders often dominating the diet. Although few data are available, it is likely that the adult diet is comprised predominantly of insects and spiders. The only diet information is from the wintering grounds. Stomachs of 34 wintering birds in Florida contained only spiders and insects, including ants, bugs, weevils, lady beetles, moths, caterpillars, locusts, crickets, and grasshoppers. In Alabama, the winter diet consisted of weevils, ants, bugs, grasshoppers, and spiders (Burns 1982; Herkert et al. 2020a; Mousley 1934b; Walkinshaw 1935).

There are no records of nests containing Brown-headed Cowbird eggs or young, but a Sedge Wren was observed feeding a large cowbird fledgling in North Dakota. The entrance diameter to the nest is usually too small (1.5-2.5 cm) to accommodate a cowbird (Herkert et al. 2020a).

Habitat loss and degradation appear to be the greatest limiting factors to the Sedge Wren. The damp to wet sedge and grass meadows that it prefers for breeding are highly vulnerable to being converted to residential areas or to being drained and farmed. These habitats are also frequently grazed. Grazing and trampling by livestock reduces vegetation structure and density and makes it less suitable for nesting. These types of meadows may be cut for hay, and it occasionally nests in hayfields. Mowing may destroy active nests and makes the habitat unsuitable for nesting. In Iowa, it nested in low density in alfalfa fields, but established territories mostly along grassed waterways. After mowing occurred, it abandoned the fields. Although disturbance of certain habitats may be detrimental, lack of disturbance may be detrimental in others. Its response to burning varies depending upon the initial density of the vegetation and the intensity of the fire. Various studies have reported positive, negative, or no response to fire. Meadows that become overgrown with shrubs and trees initially result in decreased abundance of breeding wrens and ultimate abandonment of the site if succession continues. In Minnesota, its density declined with all measures of woody vegetation: number of shrubs within 50 m, number of trees within 100 m, and the proportion of tree cover within 100 and 1,000 m. Density also declined slightly with the proportion of grass within 1,000 m. It was predicted that its density would increase 4-fold if tree-related variables were reduced from the 90th to the 10th percentile. Attempts to increase grass cover quality by increasing litter depth, grass height, and grass extent were predicted to lead to marginal increases in the Sedge Wren. Woody vegetation may attract a new guild of predators. Fine-scale habitat features are of primary importance as birds settle on territories but habitat is initially selected at a landscape scale of 1,000 m. The negative correlation with grass cover within 1,000 m was because grass and tree cover were correlated. Wrens may avoid larger grasslands when they contain trees or are close to wooded areas (Dechant et al. 2002e; Fragnier and Robert in Gauthier and Aubry 1996; Frawley and Best 1991; Herkert et al. 2020a; Jalava 1993; Lingle and Bedell 1989; Thompson et al. 2014).

In the United States, the Sedge Wren uses fields planted to switch grass for nesting and during migration. Fields planted to mixed grass–prairie forbs are also of benefit to it. Intensification of agrofuel production that maximizes biomass, homogenizes vegetation structure, and results in the cultivation of small fields is likely to reduce species richness and abundance of grassland birds (Robertson et al. 2012).

Weather may affect the Sedge Wren. Unusually dry or wet weather may make habitat unsuitable for nesting. In the core of its range, low populations appear to be associated with drought. Excessively dry weather is probably the most important weather factor, but populations fluctuate along Lake Erie with lake water levels, increasing with decreasing levels, although numbers are always low. Severe winter weather on the wintering grounds may result in mortality. Populations may have declined significantly after the severe southern winter of 1940 (Dancey 1995b; Herkert et al. 2020a; Jalava 1993).

Picman and Picman (1980) demonstrated that Sedge Wrens pecked and destroyed eggs in other nests. Intraspecific nest destruction may be an important source of loss.

Status

The Sedge Wren has probably never been common in Ontario. McIlwraith (1894) concluded that it was a western species that was irregular in its distribution. At this time, it had not been recorded near Hamilton or Ottawa, or anywhere in northern Ontario, but was common in New York and abundant in western Manitoba. He presumed that it was a probable breeder in southern Ontario despite the lack of records. Curry (2006) reported it was observed almost every year in the 1930s and 1940s in the Hamilton area and concluded that McIlwraith had simply overlooked the species. It seems more likely that the Sedge Wren arrived in the province after McIlwraith's 1894 publication. It had not been reported in Elgin County by 1891 (Lancaster et al. 2004) and the first record for the Kingston area was in 1922 (Weir 2008). Herkert et al. (2020a) stated that the Sedge Wren population appeared to have expanded eastward and northward following the arrival of European settlers and forest clearing. Baillie and Harrington (1937) considered it fairly common but irregular, breeding from the southern border north to Kenora District, southern Sudbury District, and the Ottawa area. The earliest nest record was from the Lake of the Woods area in 1920, where it was locally common. During the first atlas, the Sedge Wren bred in the Great Lakes–St. Lawrence Forest Region in scattered localities south of the Canadian Shield and sparingly in the Shield. There were also a few records in the Boreal Forest Region, primarily in the northwest (Gould in Cadman et al. 1987). James (1991) considered the Sedge Wren a rare to locally uncommon breeder north to Kenora, Sault Ste. Marie, and Sudbury; occasional and rare in the west north to Sandy Lake; and a vagrant in the James Bay area. Jalava (1993) stated that it was rare to uncommon in southern and central Ontario, but relatively abundant in the Lake of the Woods area. Except for the Lake of the Woods area, Ontario is peripheral to the main breeding range, which encompasses Minnesota, Wisconsin, northcentral Michigan, and southern and central Michigan (Bedell 1996; Jalava 1993). In most other areas, it tends to be rare, local, and erratic in occurrence; much apparently suitable breeding habitat is unused.

The second atlas revealed that there had been no overall change in the distribution of the Sedge Wren since the first atlas. It occurred predominantly in the Great Lakes–St. Lawrence Forest Region both in and south of the Shield, with minor concentrations along the Niagara Escarpment, from Kingston to Ottawa, and in the Rainy River and Kenora areas. It was scattered in distribution and generally uncommon and particularly scarce in the intensive agricultural areas of the southwest. In the Carolinian Forest Region, its probability of observation was only 4%, with concentrations in the Windsor and Hamilton areas. Scattered records occurred in the Boreal Forest Region and Hudson Bay Lowland north to Attawapiskat and the Berens River area. There was no change in its probability

of observation since the first atlas province-wide or in any region. From 2001 to 2004, it was detected on only 4 of over 2,000 point counts in the Rainy River area, but 316 point counts conducted in 2005 resulted in 43 counts with one or more wrens detected. This was an exceptionally wet year and the high numbers were probably due to immigration from areas such as Manitoba, Wisconsin, and Minnesota (Brewer in Cadman et al. 2007). In Great Lakes coastal wetlands, the Sedge Wren decreased at a nonsignificant rate of 3.2% per year 2011-21 (Tozer et al. 2024).

The overall population and range of the Sedge Wren probably increased with European settlement and removal of the forest cover in the east. Prior to that, it was probably confined to prairies, fens, and meadow marshes. Loss of these types of habitats occurred due to agriculture and urbanization with subsequent decreases in amounts of natural habitat. Long-term (1970-2021) population trends determined from BBS data included annual decreases of 0.37% in Canada and 1.42% in Ontario. The short-term (2011-21) trends were annual decreases of 0.253% in Canada and 2.63% in Ontario. The long-term trend for Canada was highly reliable; the other estimates were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

After leaving the nest, young move around under dense vegetation similar to mice and they stay together with the adults until migration time (Herkert et al. 2020a).

MIGRATION

Average arrival in Ontario is mid-May, with earliest arrivals in very late April. Most spring migrants leave nonbreeding areas in the south before the end of May (Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). There may be widespread movements of Sedge Wrens during the breeding season between the early (May and June) and late (July to September) nesting periods, mostly in southerly and easterly directions. In the northern portion of its range, there may be a gradual exodus that begins in early August with most birds gone by the end of September (Herkert et al. 2020a). Most have left the province by mid-October (James 1991), although it has been observed well into November (Curry 2006; Weir 2008).

During migration, the Sedge Wren is typically found in habitat similar to that used during the breeding season. It may also occur in mesic grasslands, saltwater marshes, and alfalfa, clover, and rye fields (Herkert et al. 2020a). In Kansas, it was usually associated with rushes or tall grasses in riparian areas. Fitch (1958) also observed it at a small pond surrounded by a 5-m-wide rim of smartweed.

The Sedge Wren is a nocturnal migrant. It frequently strikes television towers and buildings during autumn migration (Taylor et al. 1983), although there is only a single record of mortality at the Lennox generating station near Kingston (Weir 2008).

The Sedge Wren is a rare migrant in Ontario (James 1991).

Marsh Wren

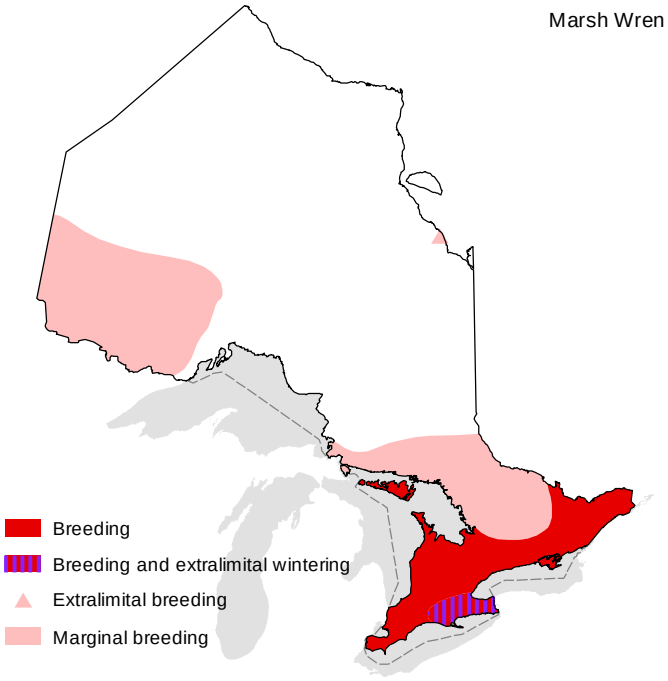
Cistothorus palustris

BREEDING SEASON

Habitat Requirements

In Ontario, the Marsh Wren nests predominantly in shallow freshwater marshes and marshy borders of lakes, rivers, and ponds. Most nests (52.2%) were in large and small cattail stands; 21.2% in unspecified marsh habitat; 9.6% in horsetail marshes; 8.8% in bulrushes, other sedges, and cattail-sedge marshes; 5.7% in grass (often reedgrass and common reed) and cattail–common reed marshes; 2.3% in bur-reed and cattail–bur-reed marshes; and 0.3% in cattail-leatherleaf. Single nests were found in a willow swale, a wet pasture, and meadowsweet bordering a marsh (Peck and James 1987).

In southern saltwater marshes, the Marsh Wren nests predominantly in cordgrass. In freshwater marshes, it nests mostly in cattail and mixed cattail-bulrush marshes, and less frequently in pure bulrushes or seldom in sedge, sweetflag, horsetail, or grass (common reed, reedgrass, wild rice) marshes. Although it tends to avoid areas of extensive shrub cover, it has nested in steeplebush, mangroves, alders, elderberries, sweet gale, buttonbush, and willows. Robust emergents such as



cattails and bulrushes are necessary to support the bulky nests. A high proportion of nests in grasses and sedges other than bulrushes fail due to collapse of the supporting vegetation. Cattails are highly preferred for nesting and, in New York and Minnesota, narrow-leaved cattail was preferred over broad-leaved cattail. Bulrush species that are used tend to be more robust species such as river bulrush, soft-stemmed bulrush, and hard-stemmed bulrush. In Wisconsin, it nested in 98% of deepwater cattail stands, 100% of shallow-water cattail stands, 72% of dry cattail stands, 88% of river bulrush stands, and 0% of sedge stands (Bent 1948; Campbell et al. 1997; Gutzwiller and Anderson 1987; Kale 1965; Kroodsma and Verner 2020; Manci and Rusch 1988; Verner 1965a; Verner and Engelsen 1970; Welter 1935; Wheeler 1931). Gutzwiller and Anderson (1987) prepared a habitat suitability index (HSI) model for the Marsh Wren. For type of emergent nesting habitat, cattails, cordgrasses, and bulrushes scored 1.0 (optimal habitat) on their model; reedgrass, reed canary grass, and sedges scored 0.5; buttonbush scored 0.1; and other emergents that are occasionally used scored 0 (unsuitable habitat). Erskine (1977) reported that it occurred only in the southern portion of the Boreal Forest Region where it nests predominantly in fens. Along the St. Lawrence River in Quebec, it prefers large marshes dominated by cattails and ponds with abundant emergent vegetation (Tanguay and Robert in Gauthier and Aubry 1996). In British Columbia, ideal habitat included a mix of cattails, shrubs, and grasses, but wet ditches with emergent vegetation also provided nesting habitat. Fifty-one percent of nests were in stands of cattails, 23% were in steeplebush, 8% were in sedges, and 6% were in willows (Campbell et al. 1997). Greenlaw (1989) considered the Marsh Wren to be 1 of only 6 North American passerines associated predominantly with marshes.

Presence of standing water is an important habitat feature. At Horicon Marsh in Wisconsin, the Marsh Wren nested in dry cattail stands, but at densities that were only 29.1% and 31.3% of those in shallow-water and deepwater cattail stands, respectively (Manci and Rusch 1988). It preferred stands of emergent vegetation from a few cm deep to 1 m in Quebec (Tanguay and Robert in Gauthier et al. 1996). Verner and Engelsen (1970) concluded that cattails were preferred only if they were in standing water. In North Dakota, water depth was more important than amount of water coverage of the marsh, and areas of dead cattails were avoided for nesting (Linz et al. 1996). Gutzwiller and Anderson (1987) ascribed a score of 0 for areas with no water on their HSI model; 0.5 for 10 cm of water; and 1.0 for 15-40 cm of water. Marshes that dry out in mid-to late summer may be used successfully but permanent water through the nesting season is required to supply a dependable

food source and provide protection from predators (Gutzwiller and Anderson 1987; Kroodsma and Verner 2020).

Density of emergent vegetation is another important habitat factor. The Marsh Wren selects the densest areas for nesting because numerous plant stems are required to support the nest. Gutzwiller and Anderson (1987) evaluated percent canopy of emergents in their HSI models. Their curve sloped from a score of 0 to 0.1 for 0-50% canopy coverage, from 0.1 to 1.0 for 50-80% canopy coverage, and remained at 1.0 for 80-100% coverage.

In coastal wetlands of the Great Lakes, the Marsh Wren occurred predominantly south of latitude 45°N where there was less than 42% developed area within 500 m. Models predicted its occurrence in areas with less than 13% emergent herbaceous wetland and less than 1% cropland, and also where there was more than 13% emergent herbaceous wetland and less than 26% woody wetlands. All these preferences were at the 500-m scale. It was predicted to be in low abundance if the percent coverage by cattails was less than 14% and in high abundance if cattail coverage exceeded 14% (Panci et al. 2017). Also in Great Lakes coastal marshes, it was positively associated with wetland cover but unaffected by water levels and amounts of urban and agricultural land within the watershed (Tozer et al. 2024). In Minnesota, the Marsh Wren was positively associated with agricultural cover at a scale of 4,000 ha. Its frequency of occupation was 10% at 10% agricultural cover and increased to 50% at 80-100% agricultural cover. It had a somewhat positive association with developed land at the same scale. Its frequency of occupation was 60% at 0% developed land, dropped to about 40% at 10-15% developed land and increased steadily to almost 100% at 35% developed land. Individual wetlands or small wetland complexes are probably sufficient to support it. Its positive association with agriculture may be explained by its common use of weedy agricultural drains. It may also nest in cattail and common reed marshes near urban and rural development (Saunders et al. 2019).

The Marsh Wren does not require large wetlands for nesting. In Connecticut, it occurred only in marshes 4 ha or larger but its density did not increase with increasing wetland area (Benoit and Askins 2002). Bent (1948) stated that isolated marshes smaller than 0.4 ha were avoided. Gutzwiller and Anderson (1987) considered 0.4 ha to be the minimum patch size that could be considered habitat, although nests were found in California in 0.04-ha patches of lakeside emergents that were at least 60 m from the nearest other patch. In Iowa, Brown and Dinsmore (1986) thought that the Marsh Wren was possibly area sensitive but acknowledged that their results were not conclusive. It was present in 25% of marshes smaller than 1 ha, 83% of marshes 1-4.9 ha, 100% of marshes 5-10.9 and 11-20 ha, and in 83% of marshes larger than 20 ha. In Iowa, it was not associated with marsh size and its density decreased with increasing marsh size. Fairbairn and Dinsmore (2001a, 2001b) concluded that this may have been because smaller marshes tended to support a higher proportion of vegetative cover than larger ones. Its presence was not associated with any landscape-level parameters. In the Prairie Pothole Region of the United States, its abundance was positively correlated with the amount of wetland habitat at the 10-km^2 and 100-km^2 scales, but not at the 1,000-km^2 scale. More important factors included the amount of precipitation and spring temperature the previous year (Forcey et al. 2014).

In Ontario, there was no difference in the abundance of Marsh Wrens at the edge (2.4 individuals) and in the interior (2.3 individuals) of marshes (Tozer et al. 2006). Birds raising a second brood tend to move into more open areas and nest in deeper water nearer the edge of emergents (Welter 1935). The portions of a marsh that are inhabited by Marsh Wrens may be influenced by the presence of blackbirds. Where Red-winged Blackbirds, Yellow-headed Blackbirds, and Marsh Wrens nest together, Red-winged Blackbirds tend to nest above shallow water or dry areas on the wetland margins, Yellow-headed Blackbirds nest in scattered emergents bordering open water, and Marsh Wrens nest in the denser vegetation between the 2 blackbird species. Where only Yellow-headed Blackbirds are present, wrens are confined to the margins of wetlands. Where only Red-winged Blackbirds are present, Marsh Wrens may nest within their territories but select areas of denser vegetation for nesting than the blackbirds (Gutzwiller and Anderson 1987; Leonard and Picman 1986; Linz et al. 1996; Picman 1980a).

During the nesting season, males usually roost nocturnally in emergent aquatic vegetation but may also roost in incomplete nests that they had built (Kroodsma and Verner 2020).

Most Ontario nests were over water, but a few were over damp ground and 14 ranged from beside open water to as far as 91 m from it. Most were in cattails, with lesser numbers in bulrushes, grasses, sedges, horsetails, bur-reeds, loosestrife, willow shrubs, and meadowsweet. The supporting vegetation was usually dead, but occasionally a mix of dead and living, or living. Water depths below nests ranged from 5 to 91 cm and heights above ground or water were 0.2-1.5 m, with most 0.5-0.9 m up. One active nest had an active Least Bittern nest on top of it (Peck and James 1987).

Elsewhere, most nests are in emergent wetland vegetation over water, but nests have been found more than 150 m from water. Cattails are highly preferred for nest attachment but bulrushes are often important later in the season as water levels decline. In Lake Erie marshes in Ohio, nests were mostly in areas where a single plant species was present. These included barnyard grass, rice cutgrass, reed canary grass, river bulrush, soft-stemmed bulrush, big bur-reed, and narrow-leaved cattail. No nests were found in common reed. Vegetation around nests averaged 89.4-98.9 cm in height. Nest height above the substrate tends to increase with the season as emergent vegetation grows taller. Early nests tend to be 15-60 cm above water; later nests may be as high as 2 m above water if in cattails, but are still low if in sedges and most other emergents. In British Columbia, nests were reported from almost at water level to 2.4 m above water, with most 0.6-0.9 m up. In Washington, nest height was directly proportional to the height of the supporting vegetation and increased with time. Nonbreeding nests tended to be higher than nests used for breeding, and mean nest height varied by study area. Mean heights of nonbreeding nests at 3 locations were 95.0 cm (range 58-196 cm), 80.0 cm (range 33-152 cm), and 90.4 cm (range 33-185 cm). Heights of breeding nests at the same locations were 92.7 cm (range 51-196 cm), 76.2 cm (range 36-178 cm), and 84.6 (range 30-140 cm). Nests are occasionally built on top of each other and in 1 case, 2 pairs of stacked nests were bound together into a 4-nest apartment. The number of dummy nests a male builds within his territory may range from 1 to 50. The functions of nonbreeding nests are uncertain but they may be used for displaying and courtship, roosting at night by adults, shelters for fledglings, winter shelters for resident birds, or as decoys to reduce predation on active nests. At Seeley's Bay, the number of dummy nests in a territory had no influence on males' success at attracting a female

or on predation rates (Bent 1948; Campbell et al. 1997; Kale 1965; Kroodsma and Verner 2020; Lazaran et al. 2013; Metz 1991; Verner 1965a; Verner and Engelsen 1970; Welter 1935; Wheeler 1931).

Male Marsh Wrens vigorously defend territories, although territories may be very small. Territorial boundaries or even entire territories may be changed once females arrive. Territorial disputes are most frequent prior to nest construction and drop off sharply thereafter but continue through nesting. Active defence of a territory ceases after the second brood is raised unless a third attempt is made. All the territory is used and almost all activities occur within the territory, although adults may occasionally forage off their territories in undefended areas. Territory boundaries are often defined by unsuitable breeding habitat or changes in vegetation such as small drainage channels, open water, or dry land so that territories are often defended only on 2 sides. Breeding females have subterritories within the male's territory and do not tolerate other females. Females mated to an individual polygynous male nest as far as possible from each other and defend their nesting area from the other. The smallest territories reported were in Georgia saltwater marshes where areas defended by males were as small as 28 m^2. Some of the smallest territories were held by males that failed to attract a mate. In this population, mean territory sizes ranged from 60 to 155.8 m^2 at different areas and in different years. The overall average used portion of territories was 82 m^2. Territories of paired males ranged from 40 to 242 m^2. Territory sizes are smallest for bachelor males and increase for monogamist and bigamist pairs. Bigamist males typically have larger territories than monogamist males. In some locations, bigamists' territories are twice as large as those of monogamists. In other areas territory size differences are not significant. In Washington, the average size of bachelor territories in 4 wetlands was 192-1,189 m^2 (range 168-2,601 m^2); territories of monogamous males averaged 472-1,826 m^2 (range 240-3,180 m^2), territories of bigamous males averaged 341-3,236 m^2 (range 240-3,600 m^2), and a single trigamous male had a territory size of 240 m^2. Territory sizes in more northern and freshwater habitats appear to be larger than those in Georgia. Overall, mated males may defend territories ranging from 60 m^2 to more than 10,000 m^2. In New York and Minnesota, male territories were 1,200-1,400 m^2 in cattails and almost 2,800 m^2 in grasses. In Washington, mean territory sizes at different locations were 418, 483, 1,254, 1,366, and 1,690 m^2 (overall range 167-3,595 m^2). In Manitoba, mean size of 4 territories was 231 m^2 when Yellow-headed Blackbirds were present and 586 m^2 10 days after the blackbirds were removed. Territories in freshwater marshes are smallest in mixed cattails and bulrushes, cattails, and bulrushes and larger in less optimal vegetation communities (Gutzwiller and Anderson 1987; Kale 1965; Kroodsma and Verner 2020; Leonard and Picman 1986; Verner 1964, 1965a; Verner and Engelsen 1970; Welter 1935).

The Marsh Wren is frequently considered colonial or semi-colonial, but there appears to be limited or no evidence for this in freshwater marshes. McIlwraith (1894) stated that the large numbers of nests gives the impression that the birds breed in colonies, but that this had not been noticed to be the case. It vigorously defends its territory against neighbours and there has been no documentation of birds cooperatively defending against predators or in finding food. In freshwater marshes, there is no evidence of birds clumping together and breeding in 1 area of suitable habitat and leaving other suitable habitat unoccupied. In wetlands in Washington and Manitoba, all marsh habitat was occupied by territorial wrens (Leonard and Picman 1987; Verner 1965a). In a marsh at

Seeley's Bay, territories were separated by more than 30 m (Metz 1991). Kale (1965) provided the only evidence for colonial nesting in saltwater cordgrass marshes in Georgia. The proximity of other wrens appeared to be an important criterion in selecting nesting territories. Birds tended to aggregate into breeding colonies with some areas of suitable habitat occupied and used intensively by groups of wrens. Adjacent suitable habitat was not occupied or was deserted early in the season. Areas that were occupied by a high density of wrens 1 year were often unoccupied in subsequent years even if no habitat changes occurred.

Natal philopatry appears to be low, especially in migratory populations. In Manitoba, 1 of 540 (0.18%) nestlings returned to breed the following year. It was a male that held 2 territories the year it returned. The first was about 140 m from his natal territory and the second was within 40 m (Leonard and Picman 1987). In Saskatchewan, 2 of 165 nestlings and fledglings (1.2%) returned the following year and nested within 100 m of their natal territory (Kroodsma and Verner 2020). In Washington, 0 of 34 young returned (Verner 1965a). In another Washington area, 10 yearling males dispersed an average of 1,951 m from their natal territory (range 180-4,090 m). None were found between 4.1 km and 160 km from their natal territory (Kroodsma and Verner 1991). This may have been a resident population.

Adult site fidelity is variable, with eastern birds being more faithful to their previous breeding areas than those on the prairie or further west. On Long Island, 12 of 28 adult males (43%) and 12 of 33 adult females (36%) returned in successive years. In Washington, 12 of 13 returning males (92%) had territories on the same lake in successive years. Five occupied the same territory and 2 moved to an adjacent territory the second year. The mean dispersal distance was 0.4 km (range 0-3.4 km). At 1 site at Delta Marsh in Manitoba, 2 of 19 males (10.5%) returned the second year and 2 of 28 (7.1%) returned the third year; at a second site, return rates of males were 2 of 22 (9.1%) and 0%. With 1 exception, all returning males settled either on or within 100 m of their previous territory. At Seattle, 2 of 3 breeding marshes were destroyed. Of 13 adult males, 10 adult females, and 61 young banded in the destroyed marsh, only 1 returned to the remaining marsh which was about 400 m distant. In the remaining marsh, 2 of 5 adult males (40%), 3 of 9 adult females (33%), and 0 of 34 young returned to breed the following year. One Saskatchewan bird moved approximately 80 km between successive breeding seasons. In most populations, males retain the same territory to raise a second brood, although the territory boundaries may be adjusted somewhat. New York and Minnesota birds may defend a new territory in a more open area to raise a second brood (Gutzwiller and Anderson 1987; Kale 1965; Kroodsma and Verner 2020; Leonard and Picman 1987; Verner 1965a; Welter 1935).

Limiting Factors

Eggs have been found in Ontario nests from the second week of May until mid-August, with most present in the first 3 weeks of June (Peck and James 1987). Males typically start nest construction the day after they arrive. Males take an average of 2 days to complete a dummy nest; some nests are built in a day, others take 3 days to complete. Females begin nest construction 6-15 days after their arrival and take 5-8 days to complete a nest. If a clutch is lost, females may complete the construction of a male nest for the second nesting attempt. In Georgia, the timing of initiation of nest building varied by as much as 2-3 weeks over several years, but the temperature was fairly consistent at 15°C

when nesting began. The female may begin egg laying the day after she completes the nest or not until a week later. One egg is laid a day; rarely females may lay 2 eggs on consecutive days and then delay laying for several days before completing the clutch. In some populations there may be 3 peaks of egg laying: first nesting attempts, which is the highest peak; the second peak consists of second brood attempts, first nesting attempts of yearlings, and renestings; and the third peak is the smallest and includes second brood attempts and replacement nests. Incubation is frequently initiated before the clutch is complete, although usually not before the third egg is laid. There is an interval of 1.5-2.5 days between hatching of the first and last eggs and in many nests young of 2 or 3 age classes are evident. The incubation period of Ontario nests was 13-15 days. Elsewhere, incubation periods of 12-16.5 days have been reported, with most eggs hatching in 13 days. Incubation periods may decrease as the season progresses. In Washington, incubation periods were about 16 days in April, 14-15 days in mid-season, and 13 days in July. The normal nestling period is 12-13 days but may be as long as 15-16 days. If a nest is disturbed, young may leave the nest at age 10-11 days before they can fly (Bent 1948; Kale 1965; Kroodsma and Verner 2020; Lazaran et al. 2013; Peck and James 1987; Verner 1965a; Welter 1935).

Most older Marsh Wrens raise 2 broods per year. Yearlings initiate breeding late in the season and probably raise only a single brood. Ontario egg dates strongly suggest that 2 broods are raised annually and perhaps even 3, although this is unlikely. The Marsh Wren breeds in more northerly areas in May to mid-July. In more southerly areas, such as Kansas and Missouri, it first appears in late July and August to breed. These birds apparently come from the north and may travel a minimum of 300 km. It appears as though it raises 2 broods in disparate geographic locations. Renesting usually occurs if a nest is lost, but not always. The tendency to renest appears to be an individual preference. In the same population, some females made 6 nesting attempts before they were successful; others did not renest at all. Renesting tends to occur 5-6 days after clutch loss, but 3 of 14 New York females (21%) started laying a replacement clutch within 36 hours. The number of second broods raised annually varies considerably. In Georgia, 35% of females raised 2 broods 1 year compared with 15% the second year and 0% the third and fourth year. Only 1 female attempted to raise a third brood during a 4-year study and it was unsuccessful. In Washington, 2 females attempted to raise 3 broods, but the breeding season was not long enough for them to be successful. A new nest is built for second broods and replacement nests, even if the same territory is used. Second clutches are initiated 1 week to 1 month after fledging of the first brood. The longer period of a month occurred in Georgia populations, but northern birds would not be able to delay this long due to the shortness of the season. Clutches of 2-9 eggs have been reported in Ontario, mostly 5 or 6 eggs. All 17 clutches at Seeley's Bay contained 6 eggs. Clutch size is larger and more variable in the north. Overall, clutches of 3-10 eggs have been documented, not including the Ontario 2-egg clutches, with 4-6 eggs the most frequent clutch sizes. Clutch size declines with the season (Bent 1948; Campbell et al. 1997; Kale 1965; Kroodsma and Verner 2020; Peck and James 1987; Metz 1991; Robbins 2015; Verner 1965a; Welter 1935; Wheeler 1931).

The age at first breeding is 1 year and adults attempt to breed every year thereafter. First-year males attempt to breed, but may be less successful in attracting a mate. In Washington, some females mated with males that already had a mate despite the presence of unmated males. Females

probably select males with superior territories, even if they are already mated. Females are monogamous, but many males are bigamous and a few are trigamous. Marsh-breeding birds tend to have a high rate of polygyny, although this tendency is not as high for the Marsh Wren as for many other species. After a male is successful in attracting a mate, he shifts to another part of his territory, usually 1-2 days before laying or shortly thereafter, and starts building a new courting centre where he advertises for additional mates. Not all birds are successful in acquiring additional mates and their success rate appears to be a function of the quality of their territory. Polygyny may be less frequent in eastern populations, with only 5% of Georgia males being bigamous. Western birds learn more songs than eastern ones and the vocal exchange between neighbours is more complex in western populations. Consequently, western birds are more apt to be polygynous. The rate of polygyny is variable and has been reported as 12.5-50% of males in Washington, 25-33% in New York and Minnesota, and 41-54% in Manitoba. In Georgia, no males remained bigamous for the second brood. In Washington, some males were bigamous throughout the season whereas others were not, suggesting that some females may have switched mates. Trigamy is rare with 1 case reported from Washington and 7 from Manitoba. In Washington, females mated to the same male nested at distant ends of the male's territory so that they did not encounter each other. In Georgia, females mated to the same male nested within 4-5 m of each other. Females defend a small territory around the nest, excluding other females and males, possibly due to their egg-pecking tendencies. Most pair bonds are retained through a single breeding season. In New York, most females stayed with the same male all season including those that had repeated nest failures. In Washington, 13 of 16 females (81%) remained with the same male for successive breeding attempts; the others switched mates (Greenlaw 1989; Kale 1965; Kroodsma and Verner 2020; Leonard and Picman 1997; Verner 1964, 1965a; Verner and Engelsen 1970; Welter 1935).

Almost all foraging occurs in marsh habitat, and this defines the diet to a large extent. In Washington, adults often foraged in dense shrub patches adjoining territories and fledglings were led into these thickets to feed. Most food is collected near or at the surface of water or occasionally slightly below the water's surface. When foraging near water or the ground, the Marsh Wren perches on adjacent emergent vegetation. It does not appear to land on the ground even when no water is present. Invertebrates are regularly gleaned from vegetation. Occasionally, it sallies into the air to capture larger flying insects such as dragonflies (Gutzwiller and Anderson 1987; Kale 1965; Kroodsma and Verner 2020; Verner 1965b; Welter 1935).

Young are initially fed small arthropods and the size of prey presented to them increases as they age. Insects and spiders are the predominant foods. Nestlings and fledglings are fed relatively large food items such as grasshoppers, dragonflies, sawflies and other hymenopterans, beetles (ground, predaceous diving, and long-horned beetles), horse flies, moth adults and larvae, and large spiders. Food items in nestling stomachs may be as long as 30 mm and as heavy as 70 mg. Adults eat much smaller food, with most items shorter than 10 mm and weighing less than 5 mg, but a few items are larger than 15 mm and 12 mg. Important adult foods include bugs (aphids, leafhoppers, treehoppers, scale insects, and assassin, damsel, and stink bugs), which may comprise as much as 29% of the diet; 17% larvae, pupae, and adult lepidopterans; 16% beetles; 8% ants and wasps; 11% flies, grasshoppers, dragonflies, and miscellaneous insects; and 5% spiders. Mites may be locally

important in the diet. Many of the insects consumed are aquatic species such as odonates and flies such as crane flies, mosquitoes, and midges. Beetles, aquatic flies, and spiders dominate the diet, and ants and parasitic wasps may be important foods. The Marsh Wren may consume snails and other molluscs. Often spiders are the most frequently consumed prey; in 1 area they were present in 78% of stomachs and constituted 15% of the volume of food. There is a single observation of a Marsh Wren drinking the contents of a Red-winged Blackbird egg. There is also 1 record of a Marsh Wren plucking a 24-28-mm-long fish from the water and swallowing it head first. It does not appear to be selective when feeding and consumes the prey that is most abundant and accessible. Although it eats spiders and insects almost exclusively, 2% of material in 53 stomachs of California birds consisted of vegetation, which was comprised of a few sedge seeds and 1 amaranth seed. In Washington during a dry year, wrens nesting in cattails ate mostly plant material but ate mostly aquatic insects when there was ample standing water (Ayers and Armacost 2010; Bent 1948; Gutzwiller and Anderson 1987; Kale 1965; Kroodsma and Verner 2020; Verner 1965a, 1965b; Verner and Engelsen 1970; Welter 1935).

The only instance of Brown-headed Cowbird parasitism of the Marsh Wren was reported in British Columbia. Of more than 1,200 nests that Picman (1986) examined, he found one that contained 2 broken wren eggs and a cold, undamaged cowbird egg.

Habitat quality is important in determining the breeding success of males. A male's pairing success is positively correlated with the percentage of the territory that is covered by cattails. The percent cattail coverage in territories was 83.2% for bachelors, 85.1% for monogamous males, and 87.8% for bigamous males. In Manitoba, pairing success was positively associated with cattail density, cattail height (28.9 cm in preferred habitat compared with 12.1 cm in unused habitat), and water depth (132.1 cm compared with 91.9 cm). In Washington, the amount of bulrushes within a territory was negatively correlated with male pairing success. The amount of dead emergent vegetation within a territory negatively affects pairing success. In some areas, pairing success appears to be correlated with the number of male nests built in the territory; in other areas it is not. Quality of vegetation appears to be the most important factor. Unmated females move among territories and assess habitat quality before selecting a mate. Territories tend to support the same number of breeding females each year even if different males are defending them. Therefore, polygyny is associated more with high-quality territories than with individual males. In territories with more cattail cover, denser vegetation, and deeper water, a higher proportion of nests were successful and the total number of young fledged per male was significantly higher (Gutzwiller and Anderson 1987; Kale 1965; Kroodsma and Verner 2020; Leonard and Picman 1987; Linz et al. 1996; Manci and Rusch 1988; Verner and Engelsen 1970).

Habitat loss and degradation may affect populations. Historical wetland destruction and drainage undoubtedly reduced the amount of habitat available for Marsh Wrens. Wetland losses are much less frequent in the province now and in some areas there may be gains in wetland habitat due to active wetland restoration projects. Low water levels in marshes due to drainage, diversion of surface runoff, or drought may make habitat less suitable or unsuitable. At Last Mountain Lake in Saskatchewan, 140 singing males were counted in 1988. The marshes were dry the following year and only 3 males were on territory (Kroodsma and Verner 2020). At Horicon Marsh in Wisconsin,

density of birds varied annually in shallow-water cattail stands and declined when water levels were lower (Manci and Rusch 1988).

Many marshes are becoming invaded by common reed which eliminates many native emergent plant species. The Marsh Wren rarely nests in common reed, so presence of this species may decrease habitat quality. In Ohio Lake Erie marshes, aerial spraying was undertaken to control common reed. Although the Marsh Wren did not nest in this species, density of males decreased 4-fold and active nest density decreased 10-fold. The most significant change in nesting behaviour was in the timing of egg laying. Females delayed egg laying an additional 36 days, waiting for regeneration of native plants from the seedbed. Lazaran et al. (2013) concluded that aerial spraying of common reed may have as much of a negative impact on the Marsh Wren as the presence of the plant itself. In Ontario, most common reed control is now done manually.

There appears to be direct interspecific competition between the Marsh Wren and the Red-winged and Yellow-headed blackbirds. In certain areas, Red-winged Blackbirds may occupy and defend all suitable nesting habitat and wrens nest within their territories. The nests of the 2 species are segregated, with the highest degree of segregation occurring where the density and height of cattails varies most. Nest segregation is less pronounced, but still occurs, in homogenous, dense stands of cattails. Blackbirds of both species frequently approach Marsh Wren nests and may land on the nest and be aggressive to the wrens. Yellow-headed Blackbirds may remove wren eggs and nestlings. Blackbirds force wrens to sing from lower perches on cattails. Wrens have smaller territories where they overlap blackbird territories. Through these activities, blackbirds may depress the mating success of wrens and reduce their nesting success. In turn, Marsh Wrens peck the eggs and nestlings of both blackbird species. Blackbird nesting success increases significantly with distance from wren nests. Both blackbirds and the Marsh Wren eat dragonflies and damselflies; damselflies are a staple of the Red-winged Blackbird's diet. There may be direct competition between the species and food may be limited in many areas (Leonard and Picman 1986; Picman 1977a, 1980a, 1980b, 1982; Verner 1975).

Marsh Wrens attack other nests of their own species. When Picman (1977b) removed incubating females in British Columbia, many Marsh Wrens attempted to break their eggs. One bigamous male pecked eggs in both his females' nests. An additional 12 males were trapped that were either trespassing neighbours or nonbreeding floaters. Ten females of unknown origin also attacked the eggs. In 1 case, the second female of a bigamous male attacked the nest of the primary female. Twenty-one juveniles of unknown origin also attacked the eggs. No nests were destroyed when incubating females were present, but there were many attacks when females were removed.

In Minnesota, mosquito control with Bti and methoprene had no negative effects on the Marsh Wren (Hanowski et al. 1997).

Cold winters and springs with above-average precipitation may affect survival, timing of nest initiation, and reproductive success. Grant and Kirby-Smith (1992) reported mortality in a North Carolina marsh as a result of a heavy December snowfall that coincided with 4 days of subfreezing temperatures. Numbers of wrens declined to 0. No birds were present the entire winter but numbers recovered the following year. In cold springs, nest initiation may be delayed 1-2 weeks or more. Late

springs result in a shortage of food and a delay in the growth of emergents. Later initiation of nesting results in smaller mean clutch sizes and a longer average time to complete 1 cycle and start a second brood (Kroodsma and Verner 2020; Manci and Rusch 1988; Verner 1965a). Although spring rains may affect reproductive success, drought may have adverse effects. In North Dakota, its abundance was significantly correlated with the number of ponds present, which was dependent upon the amount of precipitation received (Niemuth et al. 2008). In the Prairie Pothole Region of Canada, its abundance was positively correlated with spring temperature but not with amount of annual precipitation, although it was positively correlated with the amount of precipitation in the previous year (Forcey et al. 2007, 2014).

Status

The Marsh Wren has always been a common to locally common breeder in southern Ontario south of the Canadian Shield, and probably also in the Lake of the Woods area. Historically, it was probably more common in the south than at present due to loss of marsh habitat. McIlwraith (1894) considered it a common summer resident found in suitable habitat throughout the province and stated that it bred in all the inlets around Hamilton Harbour. Curry (2006) considered it an uncommon but widespread breeder in the Hamilton area and noted that the marshes that McIlwraith referred to no longer existed. Baillie and Harrington (1937) reported that it was a common breeder in cattail marshes in southern Ontario north to Simcoe, Peterborough, and Renfrew counties and also at Lake of the Woods. Where marsh habitat is common, the Marsh Wren may be one of the more abundant species. It was one of the most common marsh birds in the Kingston area (Weir 2008). Tozer et al. (2006) studied marsh birds at Long Point, Matchedash Bay, and in the Peterborough area. The Marsh Wren was the third most abundant bird behind the Red-winged Blackbird and Swamp Sparrow. Mills (1981) reported that both marshes and Marsh Wrens were rare in Muskoka and Parry Sound districts. In Elgin County, where marshes are rare, it was very unevenly distributed in 1891, with 2-3 pairs nesting near St. Thomas. In 1954, the St. Thomas reservoir was the only breeding area. It is still a rare breeder in Elgin with most records from sewage lagoons (Lancaster et al. 2004). McCracken (in Cadman et al. 1987) considered the Marsh Wren locally common in southern Ontario with estimates of more than 100 pairs per square in large marshes on Lake St. Clair, Lake Erie, in Georgian Bay, at Luther Marsh, and in the Kawartha region. The southern Ontario population and the population near Lake of the Woods appear to be discrete and occupied by 2 different subspecies. During the first atlas, a nest was found north of Moosonee 600 km north of its previously known range. James (1991) considered the Marsh Wren locally common south of the Canadian Shield, uncommon and sparsely distributed in the southern Shield, rare in the Lake of the Woods to Lac Seul area, and occasional near Thunder Bay.

The second atlas revealed that there had been no significant change in the distribution of the Marsh Wren, although it was observed in more areas in northwestern Ontario than during the first atlas. Its probability of observation did not change province-wide, but increased significantly in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region. It was well distributed south of the Shield but with large gaps in distribution due to lack of suitable marsh habitat. Highest concentrations occurred at Lake St. Clair, in the Point Pelee and Rondeau areas, and in the Prince

Edward County to Kingston area. There was a broad band of occurrence along the southern edge of the Shield, but densities in this area were only moderate (Tozer in Cadman et al. 2007).

Tozer (2013) summarized population trends of the Marsh Wren as determined by the Great Lakes Marsh Monitoring Program from 1995 to 2012. During this period, it declined significantly at a rate of 1.1% per year. These data include monitoring routes and stations that are within the American portion of the Great Lakes basin, but exclude Ontario stations and routes that do not drain into the Great Lakes. In Great Lakes coastal wetlands, it increased at an annual rate of 11.3% 2011-21 (Tozer et al. 2024). Breeding Bird Survey data for 1970-2021 indicate that it increased at an annual rate of 1.71% in Canada and 1.69% in Ontario. The annual rates of increase 2011-21 were 3.05% in Canada and 1.99% in Ontario. The Canadian trends were of medium reliability; the long-term Ontario trend was highly reliable and the short-term trend was of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young can capture some food on their own 10 days after fledging, but are cared for by the adults for at least 2 weeks after fledging. One bird was fed by an adult 27 days after fledging; another young was independent and far from the nest 23 days after fledging (Kroodsma and Verner 2020).

Fledglings initially remain in family groups that wander about and frequently leave the nesting territory. Initially, young stay in dense emergents but prefer more open areas near water later in the summer. For the first week after fledging, young remain in the vicinity of the nest but may wander a distance of 1-2 territories. As they become more independent, the young move further away and flocks of juveniles form, often comprised of 25-30 birds. Individual juveniles within flocks have been found further than 0.6 km from the nest about a month after fledging (Kale 1965; Kroodsma and Verner 2020; Verner 1965a; Welter 1935).

Fledglings tend to return to the breeding nest several nights after fledging and may later roost in courting nests or among vegetation. The brood appears to be led away from the roosting nest in the morning by the adults and back to it in the evening, travelling greater distances as the young age (Kroodsma and Verner 2020; Verner 1965a; Welter 1935). In Florida, Chicalo et al. (2019) reported that there were no fledglings or fewer fledglings than expected in some of the natal nests. On 8 occasions (17.8%) involving 6 broods, at least 1 fledgling was found in a dummy nest within the territory. Individuals from 2 of the 6 broods were found in dummy nests only after they had been disturbed in their natal nest. In 2 territories, an entire brood of 4 fledglings was located in a nearby dummy nest. Fledglings in dummy nests were 14-15 days old. Occupied dummy nests were within 5 m of the natal nest.

MIGRATION

Eastern populations are migratory and winter on the Atlantic and Gulf coasts with the extent of migration depending on the severity of winter. Older males are the most sedentary and young birds are the most migratory. Some western and southern populations may be resident. In Ontario, spring migrants arrive in numbers in mid-May, but early migrants arrive in mid- to late April. Females arrive 7-10 days after the males. In early June, there may be another wave of arriving males and more males and females arrive in mid-June. These may be young from the previous year (Black and Roy 2010;

Curry 2006; Kroodsma and Verner 2020; LaForest 1993; Leonard and Picman 1987; Weir 2008; Welter 1935).

Autumn departure starts in August but birds continue to move south from the breeding areas into October. Adults migrate as soon as they complete the post-nuptial moult. There are 2 waves of autumn migrants. The first includes adults and some young of the first brood. The second wave is predominantly juveniles from the second brood. After early September, most remaining birds are young from second broods. In southern Ontario, most birds are gone by mid-October, with rare stragglers in early November or even later (Black and Roy 2010; Curry 2006; Kroodsma and Verner 2020; LaForest 1993; Weir 2008; Welter 1935).

During migration, the Marsh Wren is typically found in wetlands with emergent vegetation and also in dense shrub cover around the perimeter of freshwater marshes. Occasionally it occurs in drier habitats distant from marshes. It has occurred in dry weed patches, damp pastures dominated by sedges, wet alfalfa fields, weedy agricultural drainage ditches, and any habitat with wet soils and dense, low vegetation. Drier habitats atypical of breeding habitat are more likely to be used during autumn migration (Bent 1948; Campbell et al. 1997; Kroodsma and Verner 2020).

Migration occurs at night. Significant numbers may be killed at tall buildings and communication towers. From 1975 to 1977, 7 were killed at the Lennox generating station chimneys near Kingston. Most kills due to strikes occur during autumn migration; high numbers of mortalities have been documented in Tennessee and Florida (Kroodsma and Verner 2020; Taylor et al. 1983; Weir 2008; Welter 1935). Taylor et al. (1983) found large number of dead House, Sedge, and Marsh wrens at a tower in mid-October and suggested that the 3 species of wrens were migrating together.

The Marsh Wren is an uncommon migrant in Ontario (James 1991).

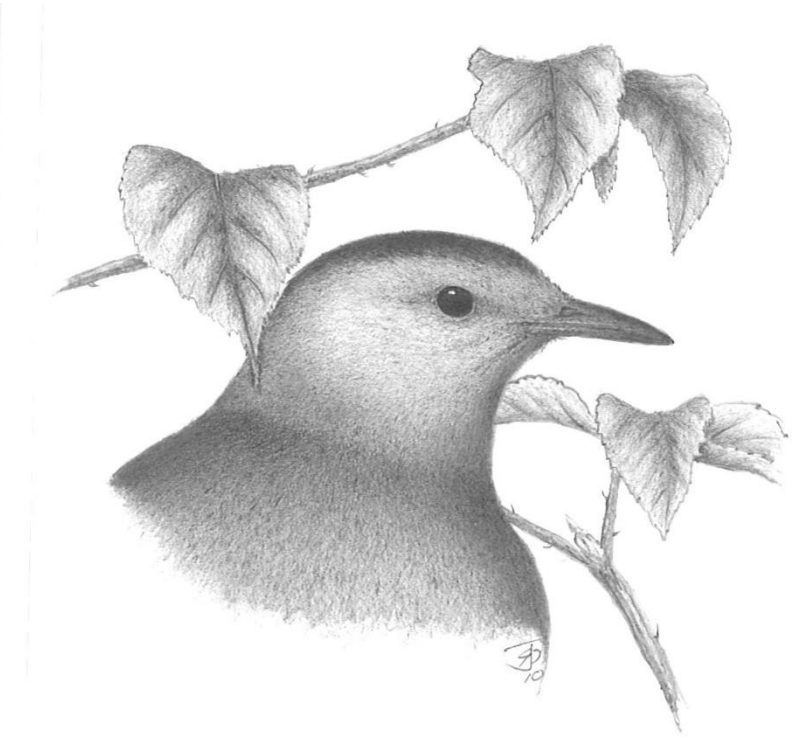
WINTER

The Marsh Wren is a rare and irregular winter resident in Ontario. Ontario is well north of the normal winter range of this species and winter records should be considered extralimital. In the south, there are numerous records from December or early January, but most of these birds probably move further south as winter progresses or perish. In the Hamilton area, there are at least 5 winter records of birds persisting until the end of February in 1 case and into April to the normal spring arrival time in the other cases (Curry 2006; James 1991; LaForest 1993).

Christmas Bird Count data indicate that the Marsh Wren population increased 0.075% annually 1970-2021 and 3.45% annually 2009-21 (National Audubon Society 2022).

Gray Catbird

Dumetella carolinensis

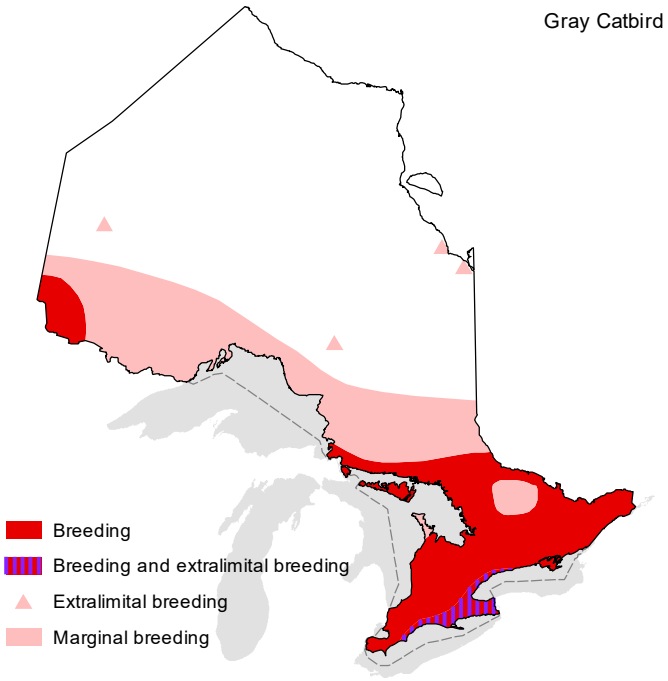


BREEDING SEASON

Habitat Requirements

In Ontario, the Gray Catbird has nested in shrubby overgrown fields and pastures (40.8% of nests); in deciduous woodlands (7.7%); in coniferous woodlands (7.3%); in mixed woodlands (5.9%); in unspecified woodlands (4.9%); in urban and rural gardens, cottage areas, fairgrounds, and farmyards (12.5%); in river floodplains (9.1%); in orchards and farm fencerows (4.5%); in wetlands, including willow swales, alder thickets, bogs, beaver meadows, and marshes (9.1%); and on road and railway rights-of-way (1.7%). Woodlands used for nesting were usually open. Many nests were at edges of woodlots or along roads, paths, and shorelines; some were in clearings. One nest was in a single tree in 0.6 m of water in a small lake (Peck and James 1987).

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, James (1979a) did not find the catbird in any pure jack pine stands near Parry Sound, but it occurred in open pine stands mixed with deciduous species. In Muskoka and Parry Sound districts, it preferred shrubby, moist areas (Mills 1981) and in Algonquin Park, it occasionally occurred in shrubbery along streams (MacLulich 1938). In Algonquin Park, it is often associated with water, nesting in dense vegetation bordering clearings, roads, marshes, lakes, rivers, and creeks (Tozer 2012).



In Durham Region in the Great Lakes–St. Lawrence Forest Region south of the Shield, it nested in a very young pine plantation dominated by willow shrubs, in a meadow of apple trees and hawthorns, and in deciduous and mixed upland and wetland stands that were highly disturbed with open canopies and a dense shrub-sapling layer. Speirs and Orenstein (1975) considered it an early succession species that also persisted in openings and around fringes of later-succession forests.

In the Carolinian Forest Region at Rondeau, Nickell (1965) found most nests in open shrub and grassland areas, none in areas dominated by red cedar, and only 2 in white pine stands, where it nested in greenbrier.

Throughout its range, the Gray Catbird is strongly associated with shrub or sapling growth, and its abundance increases linearly with shrub abundance. It is positively associated with invasive, nonnative shrubs such as honeysuckle. Closed-canopy forests are avoided as are large, open areas. It is most abundant in shrubby areas adjacent to forests, including utility corridors cut through forests; in old fields dominated by shrubs; in fencerows; in shrubs around ponds, marshes, lakes, and streams; and in shrubby areas in urban areas. In Illinois, it reached its greatest abundance in hedgerows and urban areas. Many of the shrubby areas inhabited are in a dense tangle of grape or Virginia creeper vines. Although it often inhabits moist areas associated with bodies of water, watercourses, and thickets dominated by alder, willow, or dogwood, it also nests in dry forest edges and cultural thickets. Forests are usually not used for nesting but it is opportunistic and will nest in shrubby areas within forests created by fallen trees. Small gaps in forest cover are readily used, but large gaps tend to be avoided although it nests in 1-24-ha clear-cuts in New York. It inhabits clear-cuts about 5 years after cutting once shrub and sapling growth becomes established. It is usually much more abundant in cut-blocks than uncut forests. Other habitats that it may use include orchards, hedges, cemeteries, parks, residential yards, very young coniferous plantations that are still dominated by deciduous shrubs, marshes, abandoned farmland and home sites, edges and gaps of a wide variety of upland and lowland forest types (but rarely in coniferous forests and more mature plantations), pine and oak barrens dominated by shrubs and saplings, shrubby gullies, and thickets of wild rose, juneberries, or raspberries. It is absent in bogs unless they are fringed by other suitable habitat (Back 1979; Bielefeldt and Rosenfield 1994; Brewer 1955; Campbell et al. 1997; Capen 1979; Corbat et al. 1988; Dessecker and Yahner 1987; Faanes and Andrew 1983; Finch 1989b, 1991a; Graber and Graber 1963; Graber et al. 1970; Gross in Bent 1948; Keller et al. 2003; Leighton et al. 2002; Mossman 1989; Mossman and Hoffman 1989; Mossman et al. 1991; Nickell 1965; Niemi and

Pfannmuller 1979; Noon et al. 1979; Robbins et al. 1979; Samson 1979; R.J. Smith et al. 2020; Suthers 1988; Taylor and Taylor 1979; Temple et al. 1979; Vincent and Bombardier in Gauthier and Aubry 1996; Yahner et al. 2002). Preferred habitat in urban areas of Massachusetts included a deciduous shrub layer 1.8-4.6 m tall and a deciduous overstorey at 3.4-10.7 m. Presence of dense woody vegetation was important (Thomas et al. 1977). In a Connecticut woodlot over a 59-year period, there was a progressive shift to larger trees, a sparser shrub layer, and a less diverse tree canopy. The Gray Catbird declined in the woodlot, probably as a result of the decrease in shrub coverage (Buchanan et al. 2016).

In North Dakota in open landscapes, the catbird's probability of occurrence increased as tree cover within 100 m increased to 40% then levelled off. In wooded landscapes, its probability of observation remained stable at about 10%, similar to the more wooded areas in open landscapes (Cunningham and Johnson 2016). It preferred areas where there was 52-75% tree cover in North Dakota and 23-58% tree cover in New York (Cunningham and Johnson 2019). In North Carolina, it was negatively correlated with the amount of tree canopy at the 200-m scale. As tree canopy increases, shrub coverage declines. It was positively associated with elevation at the 200-m scale, suggesting it was capable of occupying small forest gaps in high-elevation landscapes. At the 1,000-m scale, it preferred more heterogeneous landscapes which consisted of mosaics of forest patches, lawns, and pastures with interspersed roads and other structures. It was not correlated with the amount of exurban development (Gilbert and Ferguson 2019).

The catbird is an early successional species. In Pennsylvania clear-cuts, it was absent in 1-year-old stands and occurred only in 5-year-old and mature stands. Five-year-old stands were selected and these stands had high densities of woody stems (Corbat et al. 1988). In North Dakota, it was less common in aspen stands having 15-23 cm diameter at breast height (DBH) trees (Grant and Berkey 1999). In New Jersey, it occurred in old fields that were 10, 20, and 40 years old. Suthers (1988) considered it an obligate edge species that occurred in shrubs. Densities were lowest in the 40-year-old field where a single pair was present. The edges of the field had become forested, the centre was densely covered with saplings 2-26 cm DBH, and fruit was rare. In Wisconsin, it reached its greatest abundance in pioneer stands where shrubs were most abundant (Bond 1957). In South Dakota green ash woodlands, it was most abundant in late seral stages of forest. More mature stands had a higher density of chokecherry, greater green ash DBH and basal area, and a higher percentage of canopy closure with less patchy overhead cover (Rumble and Gobeille 1989). It is likely that the catbird was keying in on the abundant chokecherry in the understorey.

Some studies determined that the Gray Catbird prefers wet habitats; others found the opposite. In the mid-Atlantic states, abundance of the catbird was correlated with increasing moisture but it was most common in xeric stands in Wisconsin (Bond 1957; Graber et al. 1970; Robbins et al. 1989). In Wyoming, it was a habitat specialist associated with high foliage density at mid-canopy or shrub height. The structure of the lower woody vegetation strata appeared to be more important than the moisture regime (Finch 1991a). In Rhode Island, it was one of the most frequently detected species at small seasonal pools. It was more abundant at urban seasonal pools suggesting that it may be exploiting these resources in the absence of competition from species intolerant of urban habitat. Pools provide high densities of flying insects and the higher density of shrubs around pools may

provide food and shelter (McKinney and Paton 2009). Nickell (1965) found that the catbird frequently nested on the periphery of wetlands occupied by Red-winged Blackbirds. The blackbirds kept catbirds out of their territories, but catbirds were able to use the shrubby outer fringe. Dominant shrubs in these areas were Carolina rose, buttonbush, sandbar willow, swamp birch, highbush blueberry, winterberry, nannyberry, and meadowsweet.

Some studies identified microhabitat requirements of the catbird. In the mid-Atlantic states, its abundance was positively correlated with the number of trees larger than 38 cm DBH and negatively correlated with the number of trees within a 0.04-ha circle, percent canopy cover, and canopy height (Robbins et al. 1979). In Maryland, its abundance was negatively correlated with shrub species diversity and abundance of pines (Lynch 1987). In Iowa, it was positively correlated with sapling richness, sapling and tree size, vertical patchiness of vegetation, vertical stratification of vegetation, and snag size. It was negatively correlated with sapling and tree density, slope, and the number of deciduous trees and vines (Stauffer and Best 1980).

The catbird is associated with fragmented patches and small forested areas. All but 1 study determined that it is not area sensitive and that it decreases in abundance as forest size increases. In southern Ontario, its probability of detection was negatively correlated with the amount of forest 100 m or further from edge, woodlot size, the amount of forest cover within 2 km, and the amount of regional forest cover. The latter 2 relationships were significant (Austen et al. 2001). In Pennsylvania, it occurred most frequently in fragmented landscapes during the breeding season (Keller and Yahner 2007). Keller et al. (1993) reported that its abundance declined significantly as the width of riparian forests increased. Probability of occurrence was 39% in 50-m wide forests and declined to 1% in 800-m wide forests. In the mid-Atlantic states, its abundance was negatively correlated with the percentage of forest within 2 km and forest area. Its probability of observation was 72% in 0.3-ha woodlots, 50% in 10-ha woodlands, 35% in 100-ha woodlands, and 20% in 1,000-ha woodlands (Robbins et al. 1989). In Maryland, its abundance was negatively associated with forest size. Probabilities of observation were 80% in 0.1-ha woodlots, 50% in 10-ha woodlands, 35% in 100-ha woodlands, and 18% in 3,200-ha woodlands (Lynch 1987). In North Dakota aspen stands, probability of occurrence was 65% in 1-ha stands, 45% in 10-ha woodlands, 20% in 100-ha woodlands, and 10% in 1,000-ha woodlands (Grant and Berkey 1999). In Rhode Island red maple swamps, there was no relationship between forest size and catbird abundance (Golet et al. 2001). The catbird was considered area sensitive in Missouri. The smallest forest it was observed in was 5.6 ha. Hayden et al. (1985) estimated that forests would have to be larger than 340 ha to reach 100% occurrence. Because the catbird is associated more with shrubby habitats and avoids nesting within forests except where there are openings, it is not surprising that its abundance declines with increasing forest size. It is more relevant if the catbird requires large shrubby patches. This does not appear to be the case, although it has not been well documented. Corbat et al. (1988) concluded that the catbird was not area dependent in Pennsylvania where it was common in regenerating 1-ha clear-cuts. The catbird occasionally nests in solitary hawthorns in pastures (Nickell 1965) and frequently in small patches of shrubs around dwellings indicating that it is not area sensitive.

Most Ontario nests were in living shrubs, trees, and vines. Nine were in dead woody vegetation, 2 were supported by cattails, 1 was in a brush pile, 1 was on a vine-covered trellis, and 4 were in

fallen trees. One nest was on or very near the ground in a tangle of vines near the base of a beech tree. Nest trees were typically small or saplings. Deciduous shrubs, trees, and vines (37 species, 81.9% of nests) were preferred to coniferous trees and shrubs (8 species, 18.1% of nests). Species most frequently selected for nesting were hawthorn (57 nests), grape vines (23), raspberries (23), willow (21), apple (20), white cedar (19), spruce (18), and dogwood (17). Nests were positioned at all heights within trees and shrubs and there was a tendency to locate nests centrally near the trunk rather than distant from it. Nests were usually well concealed in upright crotches, on horizontal branches, or occasionally between 2 adjacent upright tree trunks. Nests were 0.3-4.9 m from ground, with most 1.1-1.8 m up (Peck and James 1987). Nickell (1965) found 200 nests in Rondeau Park; 65.3% were in grape canopies exposed to full sunlight and growing over thickets of small beech, sugar maple, basswood, tulip tree, elm, ash, and birch to a maximum height of approximately 4.6 m. Nearly all other nests were in forks between thinner coverings of grape. Of the Rondeau nests, 66.0% were in wild grape an average of 2.3 m above ground, 7.0% were in beech an average of 1.6 m up, 4.5% were in sugar maple an average of 2.2 m up, 3.5% were in hawthorn an average of 1.6 m up, 3.5% were in gray dogwood an average of 1.9 m up, 3.0% were in hophornbeam an average of 2.2 m up, and 12.5% were in miscellaneous species. The average height of 175 nests was 2.2 m (range 0.8-5.2 m). One nest in Parry Sound District was 4.9 m from the ground in a jack pine (Mills 1981).

A new nest is usually built for each brood but rarely a nest from the previous year may be reused. The catbird has been known to usurp Brown Thrasher nests and use old Northern Cardinal nests (Horn et al. 2007; Marshall et al. 2001; Nickell 1965; Potter 1988). Nests are typically in deciduous shrubs and trees that are mostly living but occasionally dead, and seldom in coniferous species. Dominant species used for nesting are grape, hawthorn, gray dogwood, tartarian honeysuckle, and elderberry. Nests in marshes or thicket swamps are often in shrub willows, buttonbush, Carolina rose, highbush blueberry, meadowsweet, and winterberry holly. At the margins of water, nests are often in dogwoods and elderberries. Several Michigan nests were in shrubbery overhanging water including swamps, lagoons, streams, and lakes. Distance of nests from shore averaged 54.9 m for swamps, 2.1 m for lagoons, 0.9 m for streams, and 3.4 m for lakes. Any deciduous shrub or tree species may be used for nesting, but those that have several vertical stems or branches, such as gray dogwood and honeysuckle, are greatly preferred. More linear and open species, such as staghorn sumac and prickly-ash, tend to be used only when an adjacent plant provides cover. Of almost 4,000 Michigan nests, 14.8% were in gray dogwood, 13.8% in tartarian honeysuckle, 11.3% in hawthorn, 8.2% in grapes, 5.8% in common elderberry, 3.5% in Japanese barberry, 3.4% in privet, 2.5% in shrub willows, 2.2% in American hazel, 2.0% in mock orange, 1.8% in ninebark, 1.6% in lilac, 1.6% in highbush blueberry, 1.4% in forsythia, 1.2% in prickly-ash, 1.2% in Carolina rose, 1.2% in cultivated roses, 1.2% in white spruce, and 1.0% in American plum. Other nest species supporting 0.3-1.0% of nests (in descending order of importance) were blackberry, bittersweet, buttonbush, elm, cultivated spirea, nannyberry, meadowsweet, red raspberry, black spruce, crabapple, winterberry holly, apple, white cedar, winter honeysuckle, Virginia creeper, silky dogwood, beech, nightshade, hophornbeam, sugar maple, Norway spruce, and American yew; an additional 73 woody species each supported less than 0.3% of nests. Only 1 nest was found in a herbaceous species: meadow-rue. At Delta Marsh, Manitoba, over 50% of nests were in Manitoba maple although it constituted only 25% of the available trees. Sandbar and peach-leaved willow represented 55% of the available

trees but were seldom used for nesting. In Iowa, 72% of nests were in deciduous shrubs, 11% in deciduous saplings, 14% in deciduous trees, and 2% in coniferous trees; none were in forbs or grass. Two Ohio nests were built on the ground despite other suitable nest substrates being present: 1 nest was in a cavity in a tree and 2 were in marsh vegetation. In British Columbia, 91 of 93 nests (98%) were in deciduous shrubs or small trees, usually in dense tangles of vegetation. Forty-seven percent of nests were in wild roses, 25% in lilacs, 7% in grape, 4% in red-osier dogwood, and 4% in willows; 20 other species of shrubs and small trees supported nests. In Iowa, most nests were in gooseberry, multiflora rose, and prickly-ash, but also in elm, red mulberry, and honey locust. Rose was used more than its availability and was most commonly used later in the season; elm and mulberry were used only later in the season. Gooseberry was used most commonly for nesting, especially early in the season and was used in proportion to its availability. Prickly-ash was used less than its availability. All nests in this species were concealed by other woody species. A moderate amount of vegetation density in the immediate vicinity of the nest and edge habitat are apparent requirements. In Pennsylvania, nest sites had higher woody stem density than randomly selected sites. In Michigan, 45% of nests were at an edge. Most nests are hidden from above but many are easily visible from below and at least 1 side. The nest is situated where it offers good visibility for the sitting female and the male anywhere in the immediate vicinity of the nest. Nests have been reported on the ground (rarely) to more than 15 m from the ground, but most are 1-2 m up. The mean height of 4,572 nests was 1.5 m (Brackbill 1950a; Campbell et al. 1997; Gabrielson 1913; Graber et al. 1970; Gross in Bent 1948; Johnson and Best 1980; MacKenzie et al. 1982; Nickell 1965; Schill and Yahner 2009; R.J. Smith et al. 2020; Stauffer and Best 1980).

The male guards the nest and expels other birds and small mammals from this area. Territory size in London averaged 0.32 ha. Two territories in Illinois were 0.06 and 0.45 ha; territories in Georgia and Bermuda were 0.20-0.41 ha. Home range sizes have not been quantified, but are much larger. Birds have been documented traveling 73 m to obtain nest material and 1 pair was seen regularly 183 m from the nest. Catbirds may fly several hundred metres to feed in undefended areas where there are no territorial disputes among birds. Active nests may be close to each other. Two Illinois nests were 14.6 m apart; 2 Ontario nests were within 18 m of another nest (Brewer 1955; Graber et al. 1970; Nickell 1965; Peck and James 1987; Slack 1976; R.J. Smith et al. 2020).

Natal philopatry is low. Nickell (1965) banded more than 1,000 nestlings in Michigan over 16 years and only 2 returned for a return rate of approximately 0.2%. In Ohio shrublands, 3 of 304 juveniles (1%) returned to the natal area (Lehnen and Rodewald 2009b). In New Jersey old-field habitat, 11 of 765 young (1.4%) returned to nest (Suthers 1988). In Iowa, 0 of 32 nestlings returned (Johnson and Best 1980). In New York, 7% of nestlings returned to breed in the natal area. The mean distance from natal nests to the first nests of returning juveniles was 358 m (R.J. Smith et al. 2020). Schlossberg (2009) estimated natal philopatry at 2% based on a sample of 389 from 3 studies.

Adult site fidelity is higher. Schlossberg (2009) calculated that the return rate of adults averaged 23% based on a sample of 576 from 4 studies. In London, 17 of 51 males (33.3%) returned; 7 returned twice and 1 returned 3 times. Eighteen of 58 females (31.0%) returned and 6 returned twice. Combining the sexes, the return rate was 32%. The return rate was strongly influenced by sex and slightly by reproductive success, but not by age of birds, which were all after-hatch-year birds (Darley

et al. 1977). In Ohio shrublands, 8 of 189 adults (4.2%) returned to the same site. There was some evidence that shrubland birds dispersed to younger patches, but they did not seem to move to larger patches (Lehnen and Rodewald 2009b). R.J. Smith et al. (2020) stated that 12% of adults returned to breeding sites in New York and Johnson and Best (1980) reported a return rate of 40% in Iowa. There are several reports of individuals or pairs returning to the same area to nest, often in the same territory or very close. Birds have been known to nest in the same area for as long as 5 years (Brackbill 1950a; Gill 1935, 1936; Graber et al. 1970; Gross in Bent 1948). In London, the rate of return ranged from a high of 64% for males that had nested successfully the previous year to a low of 35% for unsuccessful males and females. No bird that deserted its first territory of a season returned to it in subsequent years. For successful males, there were no differences in return rates to first and second territories held in a single year. No unsuccessful females returned to the last territory but 4 of 7 unsuccessful males did. Only 6 females returned to their previous territory and 4 of these retained the same mate (Darley et al. 1977). In New York, birds tended to return to the territory that they held last (Gill 1935). In Iowa, 3 returning males occupied territories 0 m, 180 m, and 280 m from their previous territories; distances for 3 females were 110 m, 350 m, and 420 m (Johnson and Best 1980).

Some birds retain the same territory for all nests within a season; others desert the first territory (Darley et al. 1971; Gill 1935). Successive nests in London were usually within 50 m of each other if the territory was retained. When a territory was abandoned, the birds often disappeared completely or re-established a territory more than 100 m distant from the first. In all cases, the second territory was not within the home range of the birds while they were on their first territory. Deserting pairs moved distances of 150-450 m. A single male moved 600 m and a pair moved to an adjacent territory 50 m away. Both members of a pair typically deserted together. Causes of territory desertion were failure of a female to appear on the territory, death of a mate, and nest destruction. Most desertions occurred after laying had begun and always after at least partial loss of the eggs. Birds exhibited an inconsistent response to nest loss: some deserted the territory, some remained, and some individuals deserted 1 year and remained another after similar losses. Approximately 38% of birds shifted territories within a season and some of the shifts were by pairs. There was a tendency for seasonal faithfulness to territories and partners (Darley et al. 1971).

Limiting Factors

Eggs have been reported in Ontario nests from early May to mid-August, with most present in June and the first 3 weeks of July (Peck and James 1987). London birds initiated egg laying between 13 and 24 May over 4 years. Initiation of egg laying was related to air temperature. In a year when the mean average temperature in the first 2 weeks of May was 14.5ºC, egg laying was initiated on 13 May. When the average temperature during this period was 4.5ºC, egg laying began on 24 May. The last eggs in the latest nests at London were laid between 7 and 14 July (Scott et al. 1987, 1988). In Algonquin Park, nests are under construction from late May to early June, eggs are present from late May to late June, nestlings are present from mid-June to late July, and dependent fledglings have been observed from early July to late August (Tozer 2012).

Nest building begins 7-10 days after arrival and usually takes 5-6 days; later nests are built quicker. Laying normally begins 1-3 days after the nest is complete, but may begin as soon as the

lining is complete or be delayed for as long as 6 days after completion. In 1 case, an egg was laid the day after the nest was completed and egg laying was delayed until the 6th day in another nest. At London, the time between pair formation to laying of the first egg averaged 10 days. One egg is laid per day. Some incubation occurs with the laying of the second egg, but full incubation is reached when the last or penultimate egg is laid. The incubation period of 24 Ontario nests was 11-15 days, mostly 12-13 days. Elsewhere, incubation periods of 12-15 days have been reported (average 12.9 days). Hatching periods between successive eggs may vary considerably among broods suggesting irregular incubation. The nestling period is 9-15 days, but mostly 11-13 days (average 11.3 days in Michigan). At London, the time elapsed between initiation of egg laying to fledging was 24-25 days for 3-egg clutches, 26-28 days for 4-egg clutches, and 29 days for a single 5-egg clutch. It typically took 15 days between fledging and initiation of a second brood, so it was an average of 42 days to fledge a 4-egg clutch and prepare for a second. The average interval between fledging and laying of the first egg of the second brood was 7.6 days in Iowa and 10.8 days in Michigan for an average of 36 days to produce 1 brood and prepare for another. Overall, intervals of 2-19 days have been reported between fledging and laying the first egg of the second brood. The average time between loss of a nest and laying of the first egg in 41 replacement clutches in London was 5.05 days. Intervals were 5-8 days for losses during laying, 3-7 days during incubation, and 3-6 days during brooding (Balogh et al. 2011; Campbell et al. 1997; Darley et al. 1971; Gabrielson 1913; Graber et al. 1970; Gross in Bent 1948; Johnson and Best 1980, 1982; Nickell 1965; Peck and James 1987; Scott et al. 1987, 1988; R.J. Smith et al. 2020; Whittle 1923).

In most of its range, the catbird raises 2 broods and 3 broods may be attempted in the southeastern states. Double-brooding has been confirmed in Ontario, Quebec, and British Columbia. At the University of Western Ontario campus, only 3 pairs attempted second broods and these were among the 4 earliest to produce a brood. If the first nest is unsuccessful, it is unlikely that birds would have sufficient time to raise a second brood. Renesting is common if a nest is lost. Replacement nests are more likely to occur if the loss occurs early in the season. At London, 8 of 11 birds (72.7%) that lost nests in the last week of June renested, 2 of 3 (66.7%) that lost nests in the first week of July renested, and 0 of 10 that lost nests in the second week of July renested. Clutches of 1-6 eggs have been reported in Ontario, with 4 eggs most frequent. In London, clutches of 2-5 eggs occurred, but 2-egg clutches may have been due to partial loss of the clutch. Mean clutch size was 3.9 eggs 13 May to 2 June, 3.5 eggs 3-22 June, and 3.1 eggs 23 June to 12 July. During the early period, most nests (67.9%) contained 4 eggs, 17.0% had 3 eggs, 13.2% had 5 eggs, and 1.9% had 2 eggs. In the middle period, clutch sizes were 47.3% 3 eggs, 43.6% 4 eggs, 5.5% 5 eggs, and 3.6% 2 eggs. In the last period, 77.8% of clutches had 3 eggs, 11.1% had 2 or 4 eggs, and there were no 5-egg clutches. Clutch sizes decreased by about 1 egg between May and July, but the change was not abrupt because some females had second clutches of the same size as the first. Annual production depends on the success of the first nest because a successful nest may provide sufficient time to raise a second brood, and earlier nests are likely to produce more young than later nests. In Illinois, clutches averaged 3.7 eggs in May and June and 3.1 in July and August. Similar declines in clutch size with season were reported in Michigan and Iowa. Late nests in Iowa were smaller during a drought year than in a year with normal precipitation. In New York, clutch size averaged 3.24 eggs in years with a high density of catbirds compared with 3.60 in a year with low density. Mean clutch

sizes in the east have been reported as 3.2-3.8 eggs. Differences in reported clutch sizes may be due in part to the proportion of early versus late nests in the sample. Western clutches tend to be larger with means of 3.9 in Manitoba and 4.1 in British Columbia (Campbell et al. 1997; Gill 1935; Graber et al. 1970; Gross in Bent 1948; Johnson and Best 1980; Lent 1992; Nickell 1965; Peck and James 1987; R.J. Smith et al. 2020; Vincent and Bombardier in Gauthier and Aubry 1996; Weir 2008).

The age at first breeding is 1 year and the catbird breeds annually thereafter (R.J. Smith et al. 2020). It is typically monogamous, but 2 cases of bigamy have been documented. A male in Iowa defended 2 nests 160 m apart separated by an active territory (Johnson and Best 1980). Another male in Pennsylvania defended 2 nests 69.5 m apart and there did not appear to be any intervening territories. The nests were in an area that appeared to have the highest densities of shrubs, thorny vegetation, and fruiting species within the study area (Hanley et al. 2007; Johnson and Best 1980). The pair bond is usually retained for both broods and replacement clutches within a year. If 1 member of a pair is lost, remating typically occurs. Occasionally birds divorce after the first brood and select different mates. Usually a new mate is chosen each year, but pairs may occasionally remate in subsequent years. In London, both members of 12 of 56 pairs (21.4%) returned and 4 of the returning pairs (33.3%) remated. In each case, the pair had nested successfully the previous year and retained the same territory throughout the year. Remating requires that both birds return at about the same time or the male is likely to mate with another female (Brackbill 1950a; Darley et al. 1971, 1977; Gill 1935; R.J. Smith et al. 2020).

The catbird forages from the ground to treetops. In Georgia and Bermuda, 50% of foraging occurred on the ground, 42% on foliage, 7% on bark, and 1% by flycatching. Foraging techniques included 96% gleaning, 3% hovering, and 1% flycatching. It has been observed flicking leaves from the eavestrough of a house to obtain food and it also turns over leaves on the forest floor to feed. It is an opportunistic feeder that may regularly visit electric lights at dawn to eat attached insects. It foraged at night under a stadium light where one made a 10-m sally to hawk an insect. It may also feed regularly at night on moths under artificial lighting. It has been observed searching marsh vegetation for emerging dragonflies and may feed heavily on moths during migration using a flush-chase technique. The catbird has been known to peck the eggs of other bird species and ate the contents of a Chipping Sparrow egg. In an experiment near Ottawa, catbirds broke eggs throughout their nesting cycle and were more likely to break eggs of other species than their own. They were more likely to peck cowbird eggs than those of conspecifics and pecked eggs rather than young when both were present in a nest. Unpalatable eggs were not pecked. Catbirds appeared to break eggs to eat their contents and to prevent parasitism of their nests (Gross in Bent 1948; Lebbin et al. 2007; Nickell 1965; Rodewald and Kearns 2011; R.J. Smith et al. 2020; Spooner et al. 1996).

Nestlings in first nests are initially fed mostly insects although they may be offered some fruit later, but young in later nests are fed much more fruit. Young in first nests are fed about 95% insects. At 1 nest young were fed June beetle adults and larvae, cutworms, flies, crickets, grasshoppers, geometer and sphinx moth caterpillars, and small amounts of cherries and blackberries. At another nest, food provided to young included 16.6% flies; 6.7% grasshoppers; 23.8% adult and larval moths and beetles (weevils and June, click, and tiger beetles); and 1.5% fruit (raspberries and gooseberries). At 1 nest, young were fed small geometer caterpillars and flies within 1 hour of hatching, and one

was fed a mayfly. Almost half the food provided to young consisted of flies, grasshoppers, beetles, and moths. Young may be fed large adult moths such as cecropia, prometheus, and sphinx moths. A small frog was fed to young. Fruit consumed by young includes those of dewberry, red and black raspberries, mulberries, black cherry, chokecherry, and tartarian honeysuckle. Where feeders are provided, adults may feed nestlings raisins and small suet chunks (Gabrielson 1913; Graber et al. 1970; Nickell 1965; R.J. Smith et al. 2020).

In spring, the diet of the catbird is predominantly insects and spiders, with increasing amounts of fruit eaten as the season progresses. The percentage of fruit in the diet is 20% in spring, 60% in summer, 81% in autumn, and 76% in winter. In May, Illinois birds consumed animal matter almost exclusively, predominantly ants, caterpillars, crane flies, ground beetles, and spiders. Beginning in June, fruit became increasingly important, and it fed on newly emerged dragonflies which appeared to be an important food. Other insects it eats regularly included beetles, grasshoppers, midges, moths, and cicadas. An analysis of 645 stomachs found that 44% of the diet consisted of animal matter. About 75% of this was ants, beetles, grasshoppers, and caterpillars. Of the vegetation consumed, about a third was cultivated strawberries, raspberries, and blackberries. Wild fruits included those of cherries, dogwoods, black gum, elderberries, greenbrier, spicebush, black alder, and sumac. Another analysis of 192 stomachs found that the diet was comprised of 55% vegetation: 18% cultivated fruits, 35% wild fruits, and 2% miscellaneous vegetation. Of the animal food, beetles comprised 24% of the entire diet, ants were 10%, caterpillars and miscellaneous animals were each 5%, grasshoppers were 4%, millipedes and spiders combined were 4%, and bugs were 2%. In May, about 66% of the diet consisted of ants, millipedes, June and ground beetles, and caterpillars. At the end of June, grasshoppers and crickets were important at 10% of the diet, but were rarely eaten earlier; consumption of them dwindled to almost nothing after June. By August, the amount of insects in the diet was only 1%, but an increase occurred again in September. Miscellaneous animal foods that the catbird has eaten include slugs, honey bees, aphids, gypsy moth caterpillars, skin beetles, trout fry from a hatchery, carpenter ants, ash borers, leaf beetles, leafhoppers, treehoppers, jumping plant lice, and sawflies. Several anthropogenic foods may be consumed such as suet, raisins, apple slices, walnut kernels, cheese, bread, milk, corn flakes, puffed wheat soaked in milk, mushrooms, garbage, boiled potato, fried fish, beef stew and soup, and peanuts. Other fruits it consumes are those of holly, honeysuckle, autumn olive, nightshade, guelder-rose, nannyberry, Virginia creeper, common elderberry, southern arrowwood, sweet gale, pokeweed, sassafras, poison ivy, buckthorn, mountain-ash, bittersweet, mulberries, grapes, and hawthorns. In Michigan, spicebush berries were the preferred fruit of autumn migrants. In southern Manitoba, it eats willow flowers early in the spring and rarely grain (Beal 1897a; Graber et al. 1970; Gross in Bent 1948; Holt 1918; Oguchi et al. 2018; R.J. Smith et al. 2020; Whittle 1923). In Illinois, all birds ate fruit. In the first year, the fruit diet consisted of 82% elderberries and 18% spicebush; in the second year it was 74% grapes, 24% poison ivy, and 2% Virginia creeper; and in the third year it was 100% grapes. Ninety-three percent of frugivory occurred in forest gaps and it fed more on solitary fruit-bearing shrubs (62%) than clumps of shrubs. It concentrated on 1 or 2 fruit species each year, and the species selected were not usually the same in different years (Malmborg and Willson 1988). Stutchbury et al. (2005a) studied frugivory on red elderberry by the catbird and found that it foraged at only 5.9%

of sites and on 5.7% of visits. They concluded that the low level of frugivory was probably due to its low abundance in the forest.

Cowbird parasitism is seldom documented because the catbird is an ejector of parasitic eggs. Egg ejection is often almost immediate, but some eggs are tolerated for 2-3 days before they are removed. Birds in the west appear to be more tolerant of parasitism; a lower percentage of eggs are ejected and the reported incidence of parasitism is higher. Rarely, the catbird may bury a cowbird egg in the nest lining. Reported parasitism rates are 20 of 1,241 Ontario nests (1.6%), only 1 record in Illinois, 8 of more than 3,000 Michigan nests (0.3%), 1 in 60 (1.7%) in another Michigan study, 5 of 183 British Columbia nests (2.7%), 4 of 35 nests (11.4%) in an Illinois arboretum, and 5.2% of 58 Kansas nests. There are fewer than 10 documented records of catbirds successfully fledging a cowbird, including 1 nest in Windsor, so parasitism of catbird nests is not very profitable for cowbirds. Cowbirds may remove a catbird egg prior to laying their own egg, so this may affect productivity of the catbird. In Ohio, it was estimated that 1.2% of catbird eggs were lost from the population as a result of parasitism (Campbell et al. 1997; Graber et al. 1970; Gross in Bent 1948; Johnson and Best 1980; Lowther 1997; McGeen and McGeen 1962; Nickell 1958; Peck and James 1998a; Rasmussen et al. 2009; Rivers et al. 2010; Rothstein 1974, 1975; R.J. Smith et al. 2020; Woodward 1976). In London, 7 of 16 nests (44%) were parasitized including 3 of 8 first nests and 4 of 8 replacement clutches. Three of the 7 parasitized nests had lost a catbird egg. This is the highest rate of parasitism reported for the catbird, but is probably more indicative of the actual rate. Despite being the highest rate of parasitism documented for the species, catbird nests were parasitized significantly less than other species in the study area. The nest-guarding behaviour of males may reduce parasitism (Scott 1977).

Certain human habitat alterations have been beneficial for the catbird but others have been detrimental. Initial forest clearing created much new habitat. Clear-cutting and other forest management may be beneficial by converting unsuitable forested habitat into early successional areas. Holmes et al. (2004) did not document the catbird in woodlots with no recent history of timber harvesting in the Carolinian Forest Region of Ontario. It was present in woodlots where diameter-limit cuts and selective thinning had occurred. In 1 of the 2 years of study, its abundance was negatively correlated with the amount of residual basal area. In New York, it colonized clear-cuts within 2 years of harvest and increased annually until the sixth year after cutting, when the study was terminated. Urbanization may have been beneficial earlier when lots were much larger and trees and shrubs were retained to a large degree. Modern urbanization results in habitat loss because lots are very small with minimal woody cover. There is also a tendency to clean up urban areas by removing shrubs and mowing. Typically no forest management is undertaken in urban woodlots so that these eventually become mature with limited shrub and sapling growth and become unsuitable for catbirds. Intensification of agriculture has resulted in the loss of many hedgerows. Road widening and improvements also frequently result in the loss of shrubby vegetation on roadsides. Rights-of-way cut through forests for electric transmission lines and pipelines and the regular maintenance to halt succession is beneficial. Considerable habitat has been lost due to maturation of abandoned agricultural fields and planting of coniferous plantations. Habitat for the catbird probably started to decline in Ontario in the mid-1950s due to agricultural intensification, and losses have continued more rapidly due to additional agricultural intensification,

urbanization, road improvements, maturation of old fields, and establishment of plantations (Corbat et al. 1998; Keller et al. 2003; Nickell 1965; R.J. Smith et al. 2020; Vincent and Bombardier in Gauthier and Aubry 1996).

In North Carolina, the catbird increased significantly as the number of houses and buildings within 200 m of the centre of a woodlot increased. It was 1 of only 5 species that increased with housing density (Lumpkin and Pearson 2013). In Washington, DC, 61% of fledglings died before reaching independence. Predation accounted for 79% of mortality. Lower survival at 2 of the 3 sites was probably due to higher densities of gray squirrels and domestic cats, and potentially rats. Forty-seven percent of known predation events were attributable to cats. One site appeared to provide good nesting habitat whereas the other 2 sites were sinks. Urban habitats present significant variation in habitat suitability for breeding catbirds (Balogh et al. 2011).

In urban woodlots in Chicago, abundance of the catbird was positively correlated with abundance of exotic honeysuckle species. It appeared to be attracted by the arching structure and tall cover provided by honeysuckles (Schneider and Miller 2014).

In Pennsylvania and New Jersey over a 15-year period, hemlock declined from 56% of the total basal area to 46% due to the hemlock woolly adelgid, resulting in an increased understorey of deciduous shrubs. The catbird increased, probably in response to the openings in the canopy and increased shrub coverage (Toenies et al. 2018).

Farwell et al. (2019) studied the effect of shale gas infrastructure (well pads, access roads, and pipelines) on the Gray Catbird in contiguous forest in West Virginia. It demonstrated no significant response to any of these features.

The catbird may be affected by environmental contaminants. In Illinois, it disappeared from an area treated with heptachlor and the population appeared to be depressed the following year, possibly due to a shortage of food. It has been suggested that pesticides used in orchards and gardens may have contributed to its decline (Graber et al. 1970; Vincent and Bombardier in Gauthier and Aubry 1996).

Cold and wet weather in spring may delay the onset of nesting (Darley et al. 1971). This may reduce the average clutch size for the season and fewer birds may have time to raise a second brood. High winds cause a significant proportion of nest failures. Nests are not attached to stems or limbs so they are vulnerable to being dislodged by wind (MacKenzie et al. 1982; R.J. Smith et al. 2020).

The catbird is vulnerable to being struck by vehicles because it typically flies low and often nests on roadsides (Gross in Bent 1948; R.J. Smith et al. 2020).

Price (2004) predicted that the breeding range of the Gray Catbird might contract in southern Ontario if the average summer temperature increased by 2°C.

Status

The catbird undoubtedly increased significantly with forest clearing associated with European settlement. Prior to this, it was probably confined to shrub growth at forest edges along streams and marshes, clumps of shrubs in open marshlands, and the understorey of more open woodlands (Nickell 1965). McIlwraith (1894) considered it a common summer resident and Baillie and

Harrington (1937) concluded that it was a common summer resident north to Sudbury and southern Kenora District. In Elgin County, it was a very common breeder in 1891 and 1954 and common in 2000 (Lancaster et al. 2004). During the first atlas, the range of the catbird was confirmed to cover most of the Great Lakes–St. Lawrence and Carolinian forest regions and there were scattered records from the Boreal Forest Region and southern Hudson Bay Lowland (Curry in Cadman et al. 2007; Wilson and McRae 1993). Greatest abundance occurred south of the Canadian Shield. Curry (in Cadman et al. 1987) concluded that numerous squares containing abandoned farmland near the southern edge of the Shield probably supported in excess of 1,000 pairs. James (1991) considered the catbird a common summer resident in the south, locally rare north to Kenora and Timmins, and a vagrant to southern James Bay and Big Trout Lake.

The second atlas demonstrated that there had been no change in the breeding distribution of the catbird except for a range extension in a band north of Lake Superior and Sudbury. Once again, breeding evidence was obtained in the Moosonee area. Its probability of observation did not change province-wide between atlases, but a significant decrease occurred in the Great Lakes–St. Lawrence Forest Region. The greatest decrease occurred in the Shield and may have been due to succession of shrubby areas into forest. It was most abundant south of the Shield and occurred in almost every square. Two areas of high density occurred in a wide band north of Lake Erie from Rondeau to Niagara Region (much of the Carolinian Forest Region), and in southeastern Ontario from the Peterborough area along Lake Ontario and the St. Lawrence River to the Brockville area (Curry in Cadman et al. 2007).

Breeding Bird Survey data for 1970-2021 indicate that the catbird decreased at annual rates of 0.000539% in Canada and 0.588% in Ontario. For 2009-21, it increased at annual rates of 1.66% in Canada and 0.395% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

The young are dependent upon the adults for 12-14 days after fledging. In Washington, DC, fledglings were attended for an average of 18.9 days. Adults attended female fledglings for a significantly shorter period (18.3 days) than the 21.0 days spent attending male fledglings (R.J. Smith et al. 2020).

Fledglings and postbreeding adults leave the territory a few hours to 5-8 days after the young leave the nest. They often congregate in shrubby riparian areas or other thickets near water (Akresh et al. 2009; Nickell 1965; R.J. Smith et al. 2020). During the postbreeding period, the capture rate of the Gray Catbird in West Virginia clear-cuts was negatively correlated with the amount of ripe fruit. Important habitat parameters were basal area, stem density, and vertical complexity (McDermott and Wood 2010). In Minnesota, Streby et al. (2011b) captured only 1 catbird in regenerating clear-cuts during the breeding season, but caught 36 adults and 36 fledglings during the postbreeding period. In Ohio, Vitz and Rodewald (2006) captured 37 adults and 186 juveniles in regenerating clear-cuts during the postfledging period. In Pennsylvania during the postfledging period, Stoleson (2013) captured 38 adults and 67 juveniles in clear-cuts and 1 adult and 0 juvenile in mature forest with a dense understory. In Missouri, Porneluzi et al. (2014) netted birds during the postfledging period in an oak-pine-hickory forest 2-15 years after it was clear-cut. Only a single catbird was captured during this period.

MIGRATION

Migration appears to be strictly nocturnal. Adult males arrive first in spring followed shortly by adult females, and older birds typically pair with each other. Yearling males are the next to arrive and yearling females are the last arrivals. In Pennsylvania, males did not arrive before females but adults arrived before yearlings. In southern Ontario, the catbird arrives in late April or early May with peak numbers occurring in mid-May. In the southern Shield, average arrival is mid-May but it does not occur until late May at Moosonee. Autumn migration is well underway in September, with most birds leaving the province by late September or early October. Stragglers may persist until mid- to late November (Black and Roy 2010; Curry 2006; Darley et al. 1971, 1977; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

In Pennsylvania over an 18-year period, there was no change in spring temperature, but the amount of rain received in May increased. Spring arrival of the catbird advanced by 6.6 days per decade (R.J. Smith et al. 2023).

Similar habitat is used during migration as during the breeding season, except that greater use may be made of forested habitat (Campbell et al. 1997; R.J. Smith et al. 2020). During spring migration in Pennsylvania, Smith and Hatch (2008) netted significantly more catbirds in shrub than forested habitat. Also in Pennsylvania, it was associated with more fragmented landscapes during both spring and autumn migration. Its abundance was negatively correlated with forest patch size during spring migration (Keller and Yahner 2007). During spring migration in Wisconsin and Minnesota, there was no difference in its abundance in floodplain and upland forests (Kirsch et al. 2013). During autumn migration in New York, detections of the Gray Catbird increased with increasing numbers of species of fruiting shrubs (Mudrzynski and Norment 2013). Oguchi et al. (2018) studied its usage of exotic and native shrublands in Michigan during autumn migration. Exotic shrublands were dominated by autumn olive, nonnative honeysuckles, and multiflora rose; native shrublands were dominated by gray dogwood, winterberry holly, and spicebush. Capture rates of catbirds were significantly higher in native shrublands and were 3.74 and 4.32 times higher in 2 years. Native shrublands were actively selected as habitat and were used 32% more frequently than expected. The minimum stay duration averaged 18.3 days (range 1.0-50.0 days). Time spent by habitat included 2.5 days in exotic shrublands, 4.7 days in native shrublands, 0.6 day in open habitat, 0 day in marshland, and 1.1 day in woodland. It consumed spicebush berries significantly more in native than in exotic shrublands; spicebush was highly preferred in the diet. The 50% kernel home range of 9 individuals averaged 6.5 ha (range 1.1-15.8 ha); the 99% kernel range averaged 39.3 ha (range 8.6-89.7 ha).

In Florida, 21 of 1,779 catbirds (1.2%) banded during migration were site faithful. A higher percentage (23.3%) of birds was faithful to their wintering areas in subsequent years (Somershoe et al. 2009).

One late autumn migrant in Algonquin Park fed on suet, bacon grease, and cereal. Natural foods consumed in autumn included fruits of winterberry holly and wild raisin (Tozer 2012). During autumn migration in New York, 20% of fecal samples contained Bella honeysuckle fruits, 20% contained fruits of red-osier and gray dogwood, and 55% contained common buckthorn fruits (Mudrzynski and Norment 2013).

In Michigan, Oguchi et al. (2017) studied the effects of stopping over in autumn in exotic shrublands compared with native shrublands. Fruits of nonnative shrubs such as autumn olive, common buckthorn, and honeysuckle have higher sugar and water content but lower fat and energy content compared with native species such as spicebush, gray dogwood, and Virginia creeper. Catbirds stopping over in exotic shrublands did not maintain their mass in 1 of 2 years. They had poorer immune status and lower plasma total carotenoids (which are immunostimulatory antioxidants) in that year compared with those stopping over in native shrublands. Antioxidant capacity was lower in both years for birds foraging in nonnative shrubs. Habitat quality may affect the health status of migrating catbirds.

During migration, the catbird is commonly killed by striking tall structures such as electric transmission towers, television towers, office buildings, and lighthouses. In Manhattan, it was among the top 20 species involved with collisions with buildings (Graber et al. 1970; Gross in Bent 1948; Leighton et al. 2002; R.J. Smith et al. 2020). In the United States, the catbird was more vulnerable to striking buildings than average. For all building types combined, it was 12.8 times more likely to strike a building than the average for birds. It was 20.7 times more likely than average to strike a 1-3 storey residence, 23.2 times more likely than average to strike a low-rise, and 23.9 times more likely than average to strike a high-rise (Loss et al. 2014).

In Pennsylvania, an outbreak of the viburnum leaf beetle resulted in almost complete mortality of the southern arrowwood, which was formerly the third most abundant shrub. Prior to the infestation, spring migrating catbirds gained significant mass after sunrise, but no weight gains occurred after the infestation (Smith and Hatch 2017).

The catbird is common during migration in Ontario. Daily numbers tend to be lower in autumn, probably due to the more protracted migration period (James 1991).

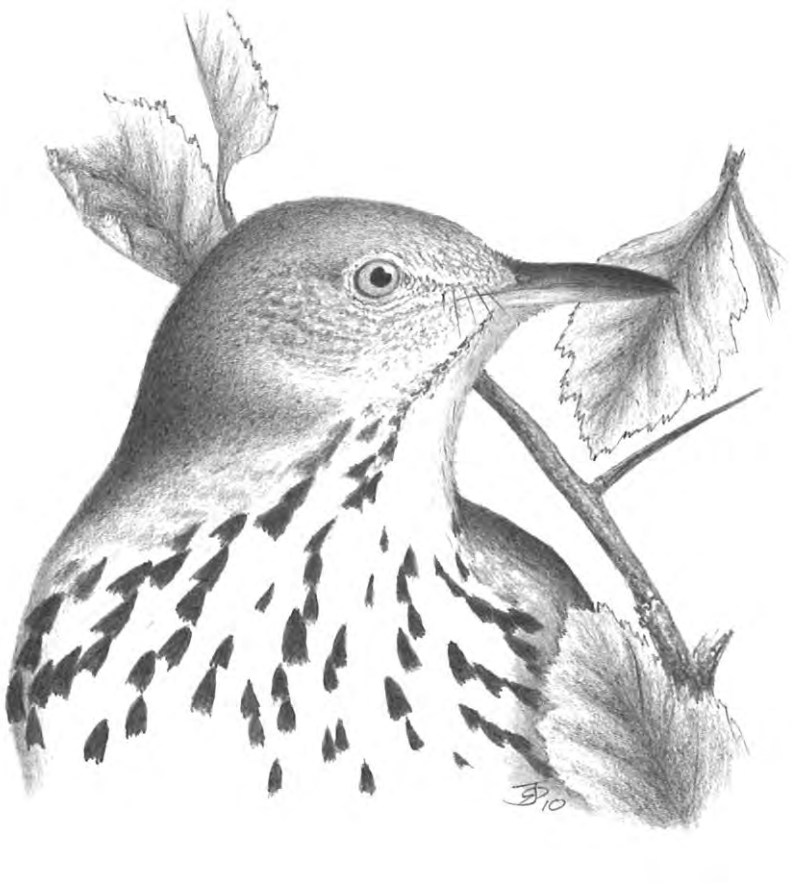
WINTER

The catbird is rare in winter north to the Toronto area, although there are a few winter records from the Kingston and Presqu'ile areas. One spent the entire winter south of Cambridge only to expire just prior to the normal spring migration period (Neil Sandilands, personal communication). Prior to the 1990s, catbirds were seen in only 33% of winters in the Hamilton area, but now one and sometimes several are seen each winter. This was attributed to a combination of milder winters and more observers. In Niagara Region, there are 2 December records and 5 January records and it has been seen on 19 Christmas Bird Counts (CBC) collectively from St. Catharines and Niagara Falls (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

CBC data indicate that the catbird increased in Ontario 2.73% annually 1970-2021 and 5.96% 2009-21 (National Audubon Society 2022).

Brown Thrasher

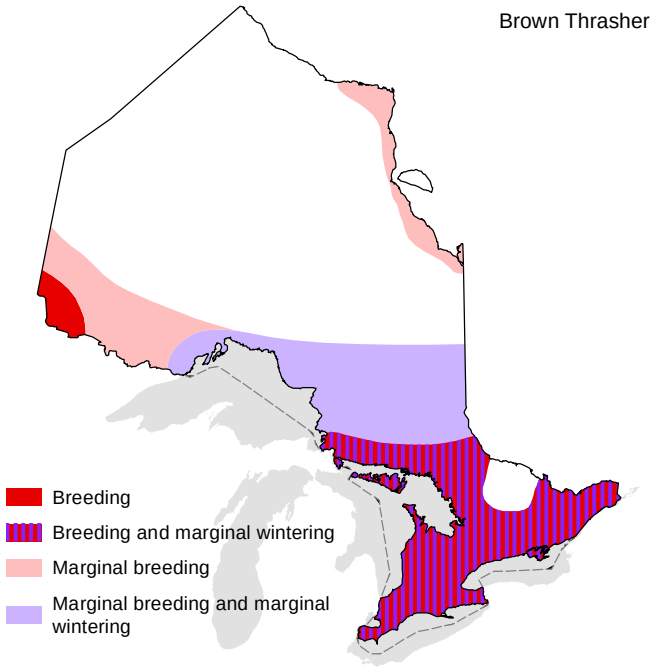
Toxostoma rufum



BREEDING SEASON

Habitat Requirements

In Ontario, the Brown Thrasher breeds in a variety of open and early successional habitats. Most nests (54.0%) were in open rural habitats, including hawthorn meadows (25.9% of nests), in overgrown farm fields and pastures (24.5%), in orchards and vineyards (1.6%), in willow swales (0.8%), in gravel pits (0.8%), and in river floodplains (0.4%). A total of 18.2% of nests were in woodlands, including 6.7% in mixed woods, 4.7% in deciduous woods, 3.4% in coniferous woods, and 3.4% in unspecified woods. An additional 27.7% of nests were in miscellaneous habitats including along fencerows and road and railway rights-of-way (16.6%); in residential gardens (6.3%); in other manicured areas such as cemeteries, parkway medians, golf courses, fairgrounds, and parks (2.0%); on sand dunes (2.0%); at edges of marshes (0.4%); and on limestone savannahs (0.4%). Woodlands selected for nesting were open in character. Many woodland nests were at edges, clearings, and hydro cuts, or near shorelines. Dry areas were much preferred to wet sites (Peck and James 1987).



In jack pine stands near Gogama, where the Brown Thrasher is near the northern extent of its range, James and Peck (1995a) detected it at 1 site where it was associated with open shrubby areas in pine and mixed forests. Near Parry Sound, it was absent in pure jack pine stands and occurred in low densities in open, mixed pine-hardwood stands. All had 25% or less canopy cover and some deciduous cover with openings associated with bedrock outcrops or logging (James 1979a). In Algonquin Park, it was rare in open woods and thickets (MacLulich 1938). Mills (1981) concluded that it preferred drier brushy areas in Muskoka and Parry Sound districts; McIlwraith (1894) reported the same from the Hamilton area. In Durham Region, it nested in a young pine plantation that was still dominated by shrub willows, in an old field dominated by apple trees and hawthorns with an understorey of grass, and in a sugar maple forest sloping down to a white cedar–balsam fir–spruce swamp. This stand was open with a dense undergrowth of raspberries and bittersweet nightshade (Speirs and Orenstein 1975). In eastern Ontario, nesting habitat includes early successional areas such as overgrown fields, deciduous thickets, woodland edges, and young second growth. It avoids nesting close to human habitation but a few pairs nested within a Kingston cemetery and on conservation lands within the city (LaForest 1993; Weir 2008). In Ontario, it has nested in a tamarack swamp (Rodrique and Tardif in Gauthier and Aubry 1996).

In southern Ontario, the Brown Thrasher was more abundant on conventional than organic farms, but not significantly. The only statistically significant relationship was with the presence of hedgerows. It also tended to be associated with pasture, riparian and upland woods, and habitat heterogeneity. It was negatively associated with large isolated trees, field size, use of herbicides, grassy strips between fields that often contained fences, and road, railway, and hydro rights-of-way (Kirk et al. 2011).

In the east, the Brown Thrasher inhabits thickets, hedgerows, small openings in forest clearings, and forest edge. In the Midwest, it commonly breeds in fencerows, shelterbelts, and woody draws. In the east, it favours underbrush and hedgerows in dry, well-drained habitat. It has a marked preference for young second growth with a well-developed shrub layer. It also occurs in agricultural habitat such as old fields, berry plantations, and orchards; in woodland edges; in suburban and rural habitat; and occasionally near human habitation. It is scarce in suburban and urban habitat where it may occur in cemeteries, parklands with shrubby or young second growth, and on university campuses. In many areas, it avoids suburban and urban areas and is more likely to occur in these

habitats in the Midwest. In Illinois, it showed a marked preference for hedgerows and other roadside or field-edge vegetation, thickets, and shrub-grown areas. It nested in woodlands, but only at edges and not in the interior. Edges of large forest blocks were seldom used, with smaller woodlots preferred. It was as closely tied to edges such as hedgerows as any Illinois bird species, and the habitats that it favoured were those that were least available. In 2000 in Illinois, it was most abundant in shrub and savannah habitats, occurring in lower densities in upland forest, grazed grass, low-density developed, and developed open space habitats. It was rarely documented in corn and idle grass habitats. The forests it used were small and linear. The most apparent habitat requirement is shrubby cover where thorny or dense plants are particularly favoured for nesting. In addition to these key nesting habitats, the Brown Thrasher may nest in gardens, orchards, swamps, moderately grazed pastures, open woods, pine and oak barrens, shelterbelts and wooded draws, riparian woodlands, tallgrass prairies with isolated patches of trees, small openings in forest cover, blueberry plantations, oak savannahs, and young conifer plantations. In Wisconsin, it is a characteristic species of pine and oak barrens, nesting there equally or more commonly than in any other native community. The thrasher may nest in a variety of forest types including northern hardwoods, deciduous swamps and lowland stands, aspen-birch, pines, mixed woods, and green ash stands. In Quebec, it is common in open deciduous woods but rare in mixed forests. It occurs in low density in these stands where it is associated with seedling-sapling stages, young burns or cuts, or older stands that have open canopies with considerable woody undergrowth (Back 1979; Beal et al. 1916; Bent 1948; Campbell et al. 1997; Capen 1979; Cavitt and Haas 2020; Erwin 1935; Gentry et al. 2006; Graber and Graber 1963; Graber et al. 1970; Haas 1998; Heagy and Best 1983; Leighton et al. 2002; Mossman and Hoffman 1989; Mossman et al. 1991; Murphy and Fleischer 1986; Noon et al. 1979; Raynor 1976; Rodique and Tardif in Gauthier and Aubry 1996; Rumble and Gobeille 1998; Samson 1979; Taylor and Taylor 1979; Temple et al. 1979; Vickery et al. 1994; Walk et al. 2011).

In North Carolina, the Brown Thrasher was negatively correlated with tree canopy coverage at the 200-m scale. As canopy cover increases, shrub cover decreases. It was not correlated with the amount of exurban development within the landscape (Gilbert and Ferguson 2019). In North Dakota, it preferred areas with 9-40% tree cover (Cunningham and Johnson 2019).

Due to its predilection for shrubby habitat, the Brown Thrasher is usually associated with early successional habitats. Speirs and Orenstein (1975) considered it an early successional species in Ontario. In New York, it declined over a 35-year period on a successional plot that transitioned from an open agricultural field to second-growth forest. It was absent throughout the study in a forested plot but numbers remained constant in a Christmas tree plantation that was maintained in an early succession stage (Brooks and Bonter 2010). In New Jersey, it was present in fields that were 20 years old, but absent in 10- and 40-year-old fields (Suthers 1988). Temple et al. (1979) stated that it was associated with mid-seral mixed woods in the northeast, but reported it in only 1 of 16 woodlands. It occurred in higher densities in late than early seral stages of green ash woodlands in South Dakota. Late seral stages contained high densities of chokecherries that may have provided food and a suitable nesting substrate (Rumble and Gobeille 1998).

Cade (1986) prepared a habitat suitability index (HSI) model for the Brown Thrasher. It occupied a wide range of cover types but densities were highest in dense woody vegetation associated with

shrub thickets, hedgerows, forest edges, or mid-successional forests. The most consistent habitat characteristic around song perches in Missouri was a litter depth of 1-2 cm. Habitat characteristics associated with forest edges, overgrown grasslands, or old fields that were used were 350-2,450 stems smaller than 2.5 cm per ha, 24-1,000 stems larger than 2.5 cm per ha, 55-95% litter coverage, and a canopy height of 4-18 m. In Louisiana bottomland forests, it occurred mainly at heights of 0.6-7.6 m, but was commonly observed at all other heights. Early successional woody fields in Arkansas supported highest densities where there was 25% tree cover, 519 trees larger than 7.6 cm diameter at breast height (DBH) per ha, and 11,243 understorey stems 7.6 cm DBH or smaller and 1.4 m or more tall per ha. In North Dakota, territories had fewer trees (245 compared with 445 per ha) and lower percent canopy cover (19.5% compared with 32.7%) than unoccupied areas. At 115 Brown Thrasher locations in Iowa, the density of stems 5 cm DBH or larger averaged 391 per ha (range 14-2,700) and the density of stems smaller than 5 cm DBH averaged 1,370 per ha (range 16-20,400). Presence of deep, non-acidic humus on the ground is associated with an abundance of invertebrates. This is best provided by early successional deciduous trees and shrubs with low carbon to nitrogen ratios in their leaves. The model assumed that shrub and forest stands with 10,000-30,000 woody stems 1.0 m or taller per ha, 10-30% canopy cover by trees 5 m or taller, and 80% or more litter cover at least 1 cm deep provided optimal habitat. Suitability decreases when the woody stem density is less than 10,000 or greater than 30,000 stems per ha, when the tree canopy cover is less than 10% or greater than 30%, or when the litter coverage is less than 80%.

Thomas et al. (1977) summarized habitat usage by the Brown Thrasher in Massachusetts suburban areas. They considered this habitat marginal for it. Its abundance was correlated with deciduous tree volume at heights of 1.8-3.0 m and 3.3-4.6 m, and deciduous shrub volume at heights 4.9-6.1 m, but none of these associations approached significance. The most important layer was 0-6.1 m. It was negatively correlated with deciduous tree volume at heights 6.4-7.6 m indicating that canopies taller than 6.1 m decreased habitat suitability.

The Brown Thrasher does not appear to be an area-sensitive species and frequently nests in narrow, linear habitats such as hedgerows. In Mississippi, it nested in 10-m wide borders around fields but was absent when borders were 30 m or more wide or lacking (Conover et al. 2009). The minimum mean width of wooded riparian habitat that it used in Iowa was 40 m (Stauffer and Best 1980). In South Dakota, the area of the smallest shelterbelt that was occupied was 0.3 ha (Cavitt and Haas 2020). In New Jersey, it was absent in woodlots smaller than 0.8 ha and rare in those smaller than 4 ha (Cavitt and Haas 2020). In Maine, it was negatively associated with grassland patch size but positively associated with the presence of trees. Larger areas were more intensively managed for blueberry production; the relative proportion of shrubby habitat declined with increasing patch size (Vickery et al. 1994). There do not appear to have been any studies done on the response of Brown Thrashers to different sizes of shrubby fields.

Ontario nests were both elevated (75.2% of nests) and on the ground. Most elevated nests were in shrubs, trees, and vines, with a few on fallen trees, branches, and brush. One nest was on a fence among vines and another was in a limestone crevice 1.7 m from the ground. Deciduous trees and shrubs (27 species, 89.3% of nests) were selected for nest sites more frequently than coniferous trees and shrubs (5 species, 11.7% of nests). Species chosen most frequently for nesting were hawthorns

(70.1% of nests), grape and other vines (9.6%), white cedar (5.0%), apple (4.3%), rose (4.0%), lilac (3.7%), and pines (3.3%). Nests in trees and shrubs were mostly in crotches but some were on horizontal branches. They were randomly situated from near the trunk to away from it and at various levels. A few were supported between vertical main stems and 1 tree nest was under a fallen piece of bark. Elevated nests were 0.2-6.7 m from the ground, with most 0.9-1.5 m up. Ground nests were under or near the bases of shrubs, trees, and vines (63.5% of nests); under branches, brush, and fallen trees (10.4%); under plants, dead weeds, and long grass (12.2%); under ends of logs (7.0%); and under boards and picnic tables (2.6%). Single nests were found under a rail fence, inside a wire guard on a young apple tree, between 2 blades of a disc-harrow, and beside a rock. Some ground nests were in depressions; some were concealed in grasses but a few were exposed. One nest was built on top of what appeared to be an old robin's nest (Peck and James 1987). Sheppard et al. (1936) observed that clumps of hawthorns appeared to be favourite nesting sites in Niagara Region.

In eastern North America, 25-50% of nests are on the ground. Ground-nesting is rare further west, probably due to the presence of several species of large snakes that are potential nest predators. Ground nests are usually near shrubby cover, often at the base of a shrub, or among tufts of grass. In prairie habitat, many ground nests are under fences. Dense shrubs are preferred for above-ground nesting, particularly thorny species. The Brown Thrasher has been reported nesting in hawthorn, gooseberry, greenbrier, rose, honey locust, lilac, grapevine tangles, forsythia, honeysuckle, red cedar, sumac, American plum, rough-leaved dogwood, small elms, euonymus, and privet. In Kentucky, 50% of nests were in small sumacs entangled with honeysuckle vines and 21% were in rose bushes. In Kansas, 27% of nests were in American plum, 27% in rough-leaved dogwood, 20% in small elms, 9% in honey locust, 5% in winter honeysuckle, and 3% in gooseberry. In Iowa, 77% of nests were in shrubs, 3% in deciduous saplings, 16% in deciduous trees, and 3% in coniferous trees. Most nests are in thickets or clearings but they may rarely be near buildings. Nests are occasionally placed in brush piles. One Tennessee nest was in a crack at the top of a post at the edge of a thicket. A bird house with the roof raised was used for nesting in 2 consecutive years. Nests tend to be near the ground, with an overall height range of 0-10.5 m, mostly within 2 m of the ground. Nests may be placed higher up as the season progresses. Thrashers frequently reuse old nests from previous years but rarely reuse nests that were used in the same season (Bent 1948; Cavitt and Haas 2020; Cavitt et al. 1999; Erwin 1935; Graber et al. 1970; Potter 1988; Rodrique and Tardif in Gauthier and Aubry 1996; Snow 1994; Stauffer and Best 1980; Tyler 1994).

Limited information is available on territory size. In Illinois forest-edge habitat, territories averaged 0.6, 1.1, and 1.1 ha over 3 years. Territories were larger when the population was low and smaller when the population was high. In Kentucky, territories were 0.5 ha to less than 1.0 ha. Urban-nesting thrashers in Tennessee tended to adopt buildings, driveways, sidewalks, and hedges as territorial boundaries. Once boundaries were established, the activities of a pair were almost entirely confined to the territory. The Brown Thrasher may compete with the Gray Catbird and has been documented ejecting its eggs and usurping the nest (Bent 1948; Cavitt and Haas 2020; Erwin 1935; Graber et al. 1970).

Limited information is available on natal philopatry and adult site fidelity. Graber et al. (1970) noted that at least some juveniles and adults returned in Illinois, but had no quantitative data. South

Carolina thrashers tended to build repeatedly in the same vine, shrub, or sapling, either for successive nests in a single season or for single nests in successive seasons. The birds were not banded, so it was unknown if the same individuals were involved (Potter 1988). In North Dakota, 8 of 392 young (2%) returned to nest, but no returning birds nested in their natal shelterbelt. The average natal dispersal distance to the first breeding site was 4.9 km (range 3.8-8.9 km; Haas 1995, 1998).

In North Dakota, return rates of adults were related to nesting success the previous year. For successful birds, 36% of males and 24% of females returned for an overall return rate of 30%. For birds whose nests failed naturally the previous year, return rates were 17% for males, 9% for females, and 13% overall. Return rates for birds whose nests had been experimentally failed were 12% for males, females, and overall. The return rate of birds that nested successfully was significantly greater than for those whose nests had failed when results for the sexes were combined. The return rates for females did not vary significantly for successful and unsuccessful birds. Of successful birds returning between years, 3 moved 50 m, 1 moved 150 m, 1 moved 500 m, and 1 moved more than 750 m; for unsuccessful birds, 7 moved 50 m, 1 moved 150 m, 1 moved 550 m, 2 moved 650 m, and 3 moved more than 750 m. Differences between nesting outcome and dispersal distance were not significant (Haas 1998). Among years, 66% of males and 71% of females remained in the same shelterbelt in North Dakota; 97% of males and 95% of females were at the same site, 3% of males and 5% of females moved to a wooded draw, and no birds moved to another site. Distance moved between nests in subsequent years averaged 259 m (range 0-1,200 m; Haas 1995). Of birds that renested after either a successful or unsuccessful nest, 81% did so in the same shelterbelt, 98% remained in the same site, and only 1 left its original site to breed in a wooded draw. Thrashers moved a mean distance of 86 m within a breeding season (range 7-464 m; Haas 1995, 1998).

Limiting Factors

Eggs have been found in Ontario nests from the last week of April until the third week of July, with most reported from the last week of May until mid-June (Peck and James 1987). A nest in York Region contained 2 young on 7 August suggesting a later egg date (Peck and James 1998a). In Algonquin Park, eggs are present from late May to mid-June; nestlings are present from early June to mid-July (Tozer 2012).

Nest building takes 4-14 days, but averages 3.8-4.2 days with a typical range of 2-8 days; most Tennessee nests took 3-4 days to build. Nests built early in the season take longer to construct. In Kansas 3-4% of nests were old. Nest reuse saved 3-8 days in nest construction time; clutches in old nests were initiated an average of 17.4 days earlier than those in new nests. Eggs are laid an average of 2 days (range 1-5 days) after nest completion. The female may start building the nest for the second brood 2-5 days after the first brood fledges. One egg is laid a day and incubation begins with the laying of the last egg or possibly earlier because asynchronous hatching may occur. The incubation period is 10-14 days with averages of 11.5 days in Kentucky, 12.5-13 days in Illinois, and 13.6 days in Kansas. Twenty-two Ontario clutches took 10-14 days to hatch, with 19 hatching in 11-13 days. Eggs in first clutches tend to hatch synchronously, but late-season nests usually hatch asynchronously over more than a day. Young fledge when they are 9-14 days old, but most leave after 10-11 days (average 10.5 days in Kentucky and Kansas). Young may be fully feathered and able

to leave the nest at age 9 days, an adaptation that may help reduce rates of nest predation (Bent 1948; Cavitt and Haas 2020; Cavitt et al. 1999; Erwin 1935; Gabrielson 1912; Graber et al. 1970; Heagy and Best 1983; Murphy and Fleischer 1986; Peck and James 1998a).

The Brown Thrasher may raise 1 or 2 broods annually. Double broods have been confirmed in Ontario, but there is no evidence of double brooding in Quebec. The egg-laying curve for Illinois suggests that most birds raise a single brood. In Kansas, birds at 1 study area raised 2 broods; those at another site were single brooded. In North Dakota, 2 broods were raised only occasionally. Renesting typically occurs if a clutch is lost. Second clutches may be laid in either the same or a new nest, but replacement clutches are usually in the same nest. Clutches of 2-7 eggs have been reported in Ontario, with most containing 4 eggs. Only 1 clutch each of 6 and 7 eggs was reported; it is possible that more than 1 female contributed to these nests. Elsewhere, clutches of 2-7 eggs have been reported. Nearly all clutches contain 3-5 eggs and mostly 4. Two-egg clutches are rare and may represent nests where some egg loss has occurred. One Kentucky clutch of 6 eggs and 1 Illinois clutch with 7 eggs were known to have been laid by 2 females. Clutches of 5 eggs are more common during the peak laying period or early in the season, and at more northerly latitudes. Two Kansas studies reported slightly larger clutches in late May than in early or late-season nests; another study found no seasonal variation. In Illinois, most April and May clutches have 4 eggs; June and July clutches have 3 eggs. Clutches of 5 eggs are more common in the northern portion of that state. In some years, large clutches are particularly prevalent in Illinois, but the reason for this is unknown (Bent 1948; Cavitt and Haas 2020; Erwin 1935; Graber et al. 1970; Murphy and Fleischer 1986; Peck and James 1987; Rodrique and Tardif in Gauthier and Aubry 1996).

The age at first breeding is 1 year and presumably breeding occurs annually thereafter. Birds are typically monogamous, although 1 male apparently attended 2 females. Pairs usually remain together for the entire breeding season. At least 1 case of divorce has been documented and this occurred after successfully rearing a brood (Bent 1948; Cavitt and Haas 2020).

The Brown Thrasher usually forages on the ground or a short distance above it. Foraging is usually undertaken by searching through leaf litter for insects and fallen seeds and berries. Occasionally, it obtains insects from below the surface of the soil by pecking or hammering its bill into the ground. It also picks fruit off trees, seeds off herbaceous plants, and occasionally flycatches from an elevated perch. It may carry nuts away in the beak to open elsewhere. Even during summer, it may visit bird feeders and bring its young along. Because it is wary of humans, it visits only those feeders where there is considerable shrubbery nearby (Cavitt and Haas 2020; Dunn and Tessaglia-Hymes 1999; Graber et al. 1970). One bird waded in water as deep as its breast feathers to feed on water striders (Hodges 1948). A female ran twice at a robin and drove it away from an earthworm that it had begun to pull up (Van Tyne 1948). Royall (1995) observed thrashers pursuing and capturing fireflies on a lawn.

The dominant foods given to nestlings at an Iowa nest, in decreasing order of abundance, were mayflies, grasshoppers, moths, and cutworms. Other food items included crickets, June beetles, dragonflies, butterflies, centipedes, other beetles, spiders, caterpillars, flies, earthworms, bugs, ants, and wireworms. Cherries, nuts, and raisins placed near the nest were fed to the young. In Kentucky, 25.2% of items fed to nestlings consisted of flies, 24.0% were beetle or fly larvae, 19.6% were

grasshoppers, and 12.0% were adult beetles. In Kansas, adults fed nestlings sumac berries and blackberries (Cavitt and Haas 2020; Gabrielson 1912; Heagy and Best 1983).

Beal et al. (1916) examined the contents of 266 stomachs from the southeastern United States. The diet consisted of 62.6% animal matter and 37.4% vegetable matter. No single item appeared to be favoured. Beetles were most frequently consumed and comprised 18.1% of the diet. They were eaten throughout the year but were a little more prevalent in the diet from March to June. Ants comprised 1.4% of the diet, surprisingly low given that the Brown Thrasher feeds predominantly on the ground; bees and wasps were 0.9% of the diet. Bugs comprised 1.5% of food items; most were stink bugs. Caterpillars were eaten in every month except November and constituted 6.0% of food items. Almost all flies were eaten in November and they comprised 1.8% of the diet. Grasshoppers comprised 2.4% of the annual diet with a maximum of 8.5% in September. The diet also included 0.6% spiders, 2.2% millipedes, and 1.3% miscellaneous invertebrates such as crayfish, isopods, snails, and earthworms. Eleven stomachs contained bones of lizards, salamanders, or treefrogs. Wild fruit was eaten every month with an annual average of 19.9% of the diet with a peak of 46.0% in September; January and February were next in abundance for wild fruit. Thirty species of wild fruits were eaten with the most abundant being blueberries, huckleberries, holly berries, elderberries, pokeweed, hackberries, Virginia creeper, and black gum. The Brown Thrasher also ate fruits of bayberry, sumacs (including poison sumac), pine, and sweetgum. Fruit was eaten from April to December with an annual average of 12.4% and most (53.2%) consumed in July. These included raspberries or blackberries, currants, grapes, cherries, and strawberries. It is likely that most were taken from uncultivated plants. Mast comprised 23.7% of the diet and was chiefly acorns. Mast was eaten every month except August, but mostly in autumn and winter with the peak of 57.4% in November. Grain comprised 2.6% of the diet and was almost all corn with a little wheat and oats; most was evidently waste grain. In Illinois, beetles were important in the diet in spring but the thrasher also ate earthworms, seeds, and grain; corn was especially important in April. From June on, fruit was more important in the diet; it was documented feeding on pokeweed and barberries. At feeders, nut meats were a favourite, including cracked black walnuts; it also ate sunflowers (Graber et al. 1970). It has eaten the fruits of mulberries and Canada moonseed (Breiding 1946; Holt 1918). It occasionally eats small frogs, snakes, and crabs (Cavitt and Haas 2020).

The Brown Thrasher is the largest regular host of the Brown-headed Cowbird. Parasitism rates vary considerably geographically and may vary annually in a given location. It is an egg rejecter, or at least an intermediate egg rejecter, ejecting some eggs from nests. Eggs were rejected from 25 of 26 experimentally parasitized nests in 1 study. In North Dakota, 33% of cowbird eggs in naturally parasitized nests were removed by thrashers; 58% of experimentally parasitic eggs were removed. Because of egg rejection, reported rates of parasitism are probably lower than actual rates. There is 1 report of a thrasher building the nest up over a cowbird egg and 2 reports of 3-4-day-old cowbirds disappearing from nests in which young thrashers remained. In Ontario, 18 of 768 nests (2.3%) were parasitized. Parasitism rates reported elsewhere range from 0% to 37.5%, but most are 12% or less. In North Dakota, the rate of parasitism was 12-36% when cowbird eggs lost to rejection were considered. In North Dakota, parasitized nests fledged a mean of 0.7 and a median of 2 fewer fledglings than unparasitized nests. Many parasitized nests do not successfully fledge any cowbirds

(Cavitt and Haas 2020; Graber et al. 1970; Haas and Haas 1998; Lowther 1985, 1991, 1997; Moore 1956; Nickell 1955; Peck and James 1998a; Rivers et al. 2010; Rothstein 1975).

Habitat loss is the most significant limiting factor for the Brown Thrasher. The initial clearing of forest cover and early farming practices were beneficial. Now the shrubby habitats that it requires are scarce and declining due to a number of factors. These include enlargement of farm fields and removal of hedgerows, road improvements and removal of roadside vegetation, reduced areas of orchards and more manicuring in them, natural succession, planting coniferous plantations, and urbanization (Cavitt and Haas 2020; Curry 2006; Graber and Graber 1963).

The Brown Thrasher is vulnerable to environmental contaminants. Adults have been found dead in fields treated with dieldrin or heptachlor. Nestlings in pecan groves treated with organophosphate or carbamate pesticides showed reduced rates of mass increase and decreased survival rates (Cavitt and Haas 2020; Graber et al. 1970).

Raynor (1976) partially attributed the decline of the Brown Thrasher on Long Island, New York, to the increase in the Northern Mockingbird. During the period of decline, there was little change in habitat except for some natural succession. When the mockingbird first colonized the area, it occupied residential areas that were little used by thrashers. It then spread into all habitats except forest interior. Mockingbirds continued to increase and replace thrashers at feeders, berry-bearing plants, and other food resources. The aggressive nature of the mockingbird probably allowed it to dominate and displace the thrasher, although direct conflicts between the species were not observed.

The Brown Thrasher does not appear to adapt well to human activities. In Illinois, thrasher populations were high in residential areas early in the 20th century, but are now low (Graber et al. 1970). It now seldom occurs in residential areas and is not common near rural residences even when suitable habitat is present. In suburban areas of Massachusetts, however, Thomas et al. (1977) found no indication that human density, dogs, or cats had any significant effects on thrashers but the habitat was marginal for the thrasher. Because it often nests close to the ground along roads, it is vulnerable to being struck by vehicles. It was 1 of the 8 most common birds struck by cars around Peoria, Illinois, and the 5th most frequent roadkill near Urbana, Illinois (Cavitt and Haas 2020; Graber et al. 1970). Nests may be abandoned if they are disturbed by humans during the laying stage. Flagging of nests by researchers increased predation by the American Crow (Cavitt and Haas 2020).

In Georgia, the Brown Thrasher benefitted slightly from burns that opened up the canopy in hardwood stands. It was absent on control plots and forests subjected to low-intensity burns, with less than 5% canopy loss. In medium-density burns causing 5-20% canopy mortality, it was absent 1-2 years after fire and present at a density of 1 per km^2 3-6 years after the burn. It occurred at the same density 1-6 years after fire in high-intensity burns that killed 20-50% of the canopy (Klaus et al. 2010).

DesGranges and Morneau (2010) concluded that the Brown Thrasher was sensitive to climate change in Quebec.

Status

The breeding range of the Brown Thrasher probably expanded considerably after forest clearing by European settlers. McIlwraith (1894) noted that it was not as abundant as the Gray Catbird and was somewhat local in distribution. There were considerable areas of suitable habitat where it was absent but it was a common summer resident in the Hamilton area. Baillie and Harrington (1937) concluded that it bred almost entirely south of Lake Nipissing and Ottawa and considered it a fairly common breeder. They reported earlier records from Manitoulin Island and Thunder Bay, but had no confirmed breeding records from these areas. Sheppard et al. (1936) reported that it was not particularly common in the Niagara region and was local in occurrence. In 1891 in Elgin County, it was an uncommon summer resident that appeared to have decreased greatly in the past 5 years. By 1954, it was considered a breeder that was less abundant than the catbird. In 2000, it was a local and uncommon breeder (Lancaster et al. 2004). In the Hamilton area, it occurred in every square during the second atlas, but there were fewer than there were 50 years ago (Curry 2006). It was common in the Kingston area during the 19th and 20th centuries (Weir 2008). At Presqu'ile, the general consensus was that it had declined in the park due to natural succession (LaForest 1993). Mills (1981) reported that it was decidedly scarce in some regions of Muskoka and Parry Sound districts. Breeding occasionally occurred in the Hudson Bay Lowland (Wilson and McRae 1993). The first atlas showed a wider breeding distribution than that reported by Baillie and Harrington (1937). It bred north to Sault Ste. Marie, north of Sudbury, near Thunder Bay, in the western portion of Rainy River District and southern portion of Kenora District, and there was 1 record from North Point north of Moosonee. The apparent range expansion may have been due to abandonment of marginal agricultural land, but continuing natural succession may have been inducing declines even by the time the first atlas was conducted. Its range was discontinuous in the Canadian Shield, and it was notably absent from the heavily treed Algonquin Highlands and other uncleared areas of the Great Lakes–St. Lawrence Forest Region (Curry in Cadman et al. 1987). James (1991) considered the Brown Thrasher a common summer resident in the south, rare and local in the north to Kenora and Timmins, and a vagrant north to the Moosonee area.

The second atlas revealed that very little change in the distribution of the Brown Thrasher had occurred since the first atlas. It occurred regularly north to the Sudbury and Sault Ste. Marie areas and in Rainy River District, with scattered records north to Winisk. It continued to be virtually absent in heavily forested regions of the Great Lakes–St. Lawrence Forest Region in the Shield, particularly in the Algonquin Highlands. Its probability of observation declined significantly province-wide and in all regions except the Hudson Bay Lowland. Although there was a nonsignificant increase in this region, it continued to be rare and sporadic there. Declines were probably attributable to natural succession, hedgerow removal, forest growth, and establishment of coniferous plantations. It was most abundant south of the Shield. Highest densities occurred in a band from Elgin County northwest to Lake Huron, in a broad band south of the Shield from Lake Simcoe south to Lake Ontario and eastward beyond Ottawa, along the Ottawa River east of the Algonquin Highlands, and south of the base of the Bruce Peninsula. These areas still support extensive areas of shrubby growth. Low densities were found in agricultural areas such as the extreme southwest, the Niagara Peninsula, and the urban areas of Hamilton east through Toronto (Curry in Cadman et al. 2007).

Breeding Bird Survey data for 1970-2021 indicate that the Brown Thrasher decreased at annual rates of 1.12% in Canada and 1.25% in Ontario. It decreased at an annual rate of 0.187% in Canada and increased at an annual rate of 1.029% in Ontario 2011-21. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young remain in shrubbery near the nest for several days. The adults and fledglings remain together for about 19 days, but the young may remain in the territory for as long as 45 days. During the postbreeding season, fledglings moved an average of 0.2 km (range 0-5.4 km; Haas 1995, 1998). When a second brood is attempted, the female assists in raising the first young for only a few days and they are the responsibility of the male thereafter. When the female does not attempt a second brood, brood division occurs with each adult caring for half the brood. In these cases, the territory may be divided (Cavitt and Haas 2020).

In regenerating clear-cuts in Ohio, Vitz and Rodewald (2006) captured 8 adults and 37 juveniles during the postfledging period. It is possible that the thrasher bred within these clear-cuts, but birds may also have moved from other nesting locations once the young fledged. In Missouri, Porneluzi et al. (2014) netted birds during the postfledging period in an oak-pine-hickory forest 2-15 years after it was clear-cut. Only a single Brown Thrasher was captured.

MIGRATION

The Brown Thrasher is a short-distance, partial migrant that migrates nocturnally. It is usually solitary during migration, although 2-4 may occasionally be found together in suitable habitat patches. It may migrate with Gray Catbirds and various species of sparrows. A bird banded in Ontario was recovered in Maine the following winter and another Ontario-banded bird was encountered in New England 4 years later (Brewer et al. 2018; Cavitt and Haas 2020; Graber et al. 1970).

Males arrive 7-10 days earlier in spring than females. Arrival in Ontario is in mid- to late April, with migration extending into mid-May. In the Hudson Bay Lowland, the thrasher occurs annually, usually as a spring overshoot, between early May and 6 June. Autumn migration may begin in late August in the Hudson Bay Lowland, with a record of a migrant at Shagamu on 28 August. It is typically gone from the province by the end of September with stragglers persisting until late October (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008; Wilson and McRae 1993).

During migration, the Brown Thrasher may occur in hedgerows, along railway rights-of-way, in mature deciduous forests, and in urban parks and gardens, particularly those with fruit-bearing plants and feeders (Cavitt and Haas 2020).

The Brown Thrasher may strike television towers and other tall structures during migration. It tends to be less vulnerable to this than many other species and represented only 0.1% of mortalities at Illinois towers during autumn migration (Cavitt and Haas 2020; Graber et al. 1970).

At Long Point Bird Observatory, the Brown Thrasher experienced a significant decline of 3.3% per year 1961-88. It was 1 of 7 species that showed a weak, nonsignificant increase in 1 decade (the

1960s) combined with highly significant declines in other decades (12.0% in the 1970s and 3.1% in the 1980s; Hussell et al. 1992).

James (1991) considered the Brown Thrasher a common migrant.

WINTER

Root (1988) concluded that temperature and vegetation were the primary factors associated with the winter distribution of the Brown Thrasher. In autumn, most move to areas where the average January temperature is above –4°C. All areas of high winter concentrations are where the temperature rarely drops below freezing. It is a snow avoider associated with areas where there are frequent changes between presence and absence of snow (Keyser et al. 2022).

Habitats selected in winter are similar to those used during the breeding season. The Brown Thrasher may occur in dense riparian thickets, brushy woodland edges, fencerows, gardens, yards, cultivated areas, vine-covered thickets, brier patches, hedgerows, urban areas near feeders, and in sheltered areas with heavy woody growth. It may prefer thickets near water. In Texas, it preferred dense riparian thickets and woodlands. Foraging occurred at sites with well-developed overstoreys and rarely in open areas with no canopy cover. In Alabama, it occurred mostly in successional shrub and sapling areas in openings (Bent 1948; Cavitt and Haas 2020; Fischer 1981a, 1981b; McClure et al. 2013a).

Wintering birds establish territories soon after their arrival in September and October. Birds are very sedentary in these territories and highly aggressive toward any intruders. In Texas, 27% of banded thrashers returned the following year. All were found in the vicinity of their initial point of capture, suggesting that returning birds use the same winter territories each year (Fischer 1981a, 1981b).

During winter in the Hamilton area, the thrasher ate seeds and fruits and sometimes frequented bird feeders (Curry 2006). Bent (1948) reported that acorns are an essential part of the winter food and that it favoured sumac berries in December. In Texas, it foraged by tossing aside the leaf litter with its bill and occasionally pecking and probing into the ground. Ninety-five percent of all foraging activity was on the ground with some foraging occurring in clusters of dead leaves in trees or on berries of trees (Fischer 1981a, 1981b). When snow covers the ground, it may visit feeders. Early in the 1900s, it was a rare visitor to feeders but it is now a regular visitor to feeders and birdbaths, especially in the south. Favourite foods at feeders are mixed seeds, bird puddings, and millet and it infrequently eats black-oil sunflowers and cracked corn and drinks water. It may occasionally eat hulled sunflowers, milo, wheat, suet, peanut butter mixes, baked goods, and whole corn (Dunn and Tessaglia-Hymes 1999).

Severe winter weather may cause mortality of the Brown Thrasher. One was found dead in Alberta when January temperatures dropped to –35°C. After a severe winter storm in Illinois, 1 dead thrasher was found. Prior to the storm, the density of thrashers was 9.4 per km² in bottomland forest; density declined to 1.5 km² after the storm, a decline of 84.2%. It was absent in upland forest and urban residential areas before and after the storm. The decline was probably due to high mortality. It may be vulnerable there because it is a ground forager at the northern extent of its range (Cavitt and Haas 2020; Graber and Graber 1979).

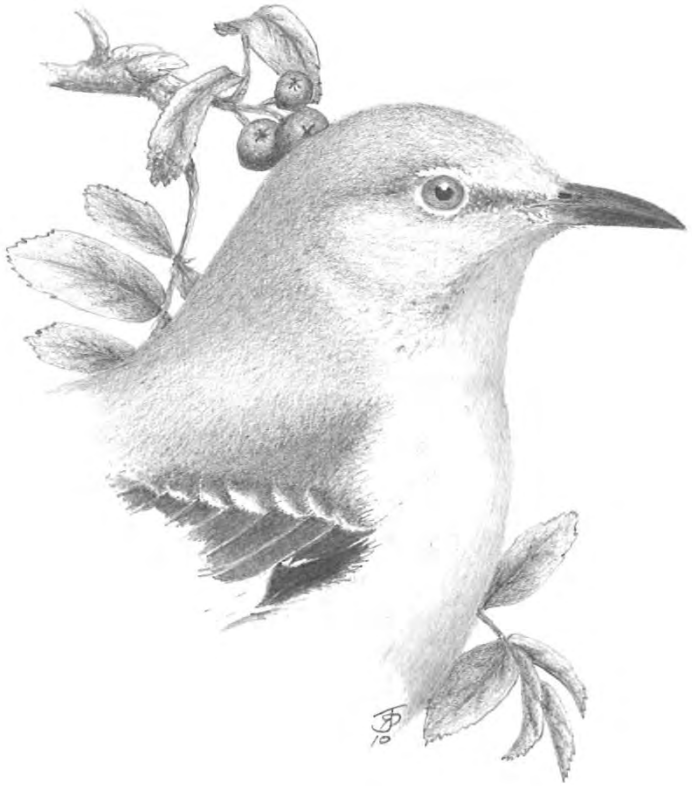
The Brown Thrasher appears to be extending its winter range northward, possibly in response to warmer weather or provision of bird feeders. It is now very local in winter north to the Great Lakes area where it is mostly reported from urban areas with feeders or thickets with abundant berries (Cavitt and Haas 2020). Graber et al. (1970) concluded that it was possibly wintering in Illinois in greater numbers than previously.

James (1991) considered the Brown Thrasher a rare winter resident in Ontario, occurring mainly in the south but occasionally north to Thunder Bay and Kirkland Lake. Since the 1950s in the Hamilton area, 1 or 2, or rarely several, have spent the winter (Curry 2006). From 1964-2007, it was found near Kingston during December in 15 years and remained throughout 8 winters (Weir 2008). In Elgin County, it is rare in winter and usually remains there only until early winter; it has been observed on 20% of Christmas Bird Counts (CBC) conducted since the late 1940s (Lancaster et al. 2004). In Niagara Region, there are 9 January records and 5 February records (Black and Roy 2010). One survived the winter at Huntsville (Mills 1981).

CBC data for Ontario indicate that the Brown Thrasher decreased at annual rates of 4.24% 1970-2021 and 4.04% 2009-21 (National Audubon Society 2022).

Northern Mockingbird

Mimus polyglottos

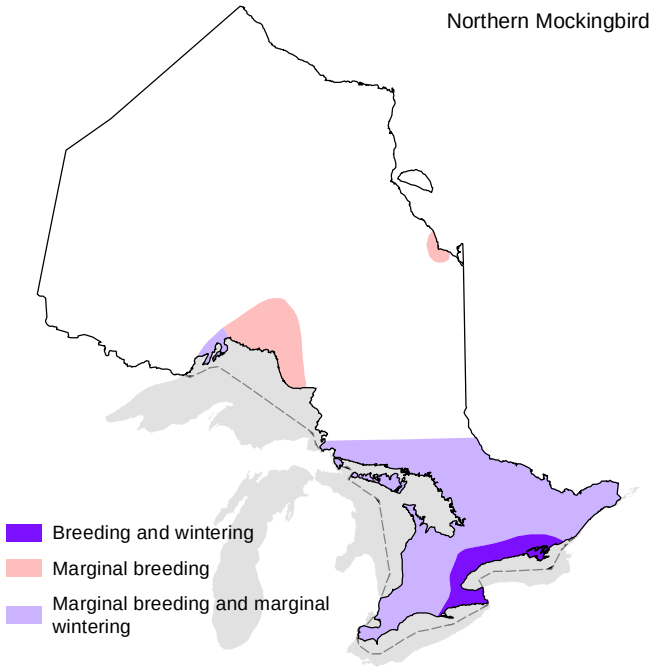


BREEDING SEASON

Habitat Requirements

In Ontario, the Northern Mockingbird has nested in rural fields, pastures, orchards, and floodplains (43.4%); residential gardens and cemeteries (28.3%); shrub- and tree-covered sand dunes (10.0%); coniferous woods and plantations (8.3%); deciduous woods (6.7%); and 1 nest each in a shrubby border of a marsh and a park campground. Wooded areas used for nesting tend to be more open than closed (Peck and James 1987). In the Greater Toronto Area (GTA) in the 1930s, breeding tended to occur in rural areas beyond the urban fringe. The current GTA range largely coincides with the urbanized area with only a handful of territories on or north of the Oak Ridges Moraine. Fifty-three percent of territories were in industrial areas. It showed a strong preference for linear features such as railways and, to a lesser extent, hydro corridors. Density was greatest in large industrial areas west of the airport and in Mississauga and Etobicoke. Many urban parks, cemeteries, and suburban areas that would be suitable habitat elsewhere are unused or rarely occupied (Smith and Poon 2006).

Throughout its range, the mockingbird is associated with human-altered areas. It reaches its greatest abundance in suburban and urban areas where it prefers lawns with scattered trees and



shrubs, particularly those that bear fruit. Hedges may be particularly attractive to it. It occurs in small towns, old suburbs, landscaped cemeteries, golf courses, vacant lots, school yards, and university campuses. In rural areas, it is associated with farmsteads, hedgerows, edges of thickets bordered by pastures and cultivated fields, orchards, woodlot edges, and prairie-like areas. In Illinois, it was much more tolerant of open-field conditions than the Gray Catbird. It was found in sandy prairie areas more than the Brown Thrasher and may have an affinity for sandy areas, but occurs in a wide range of soil types. In Illinois, it was much more common in hedgerows than any other habitat; densities were higher in rural than urban habitats. Forest interior is avoided but forest edge may be used, although it is not particularly favoured. It occurs in willow thickets, clearings and edges in forested areas, logging slash, coastal beaches, and garbage dumps in British Columbia. In the Kingston area, it occurs in more open and built-up areas in a 20-km band along the St. Lawrence River and Lake Ontario (Campbell et al. 1997; Crowell et al. 1982; David in Gauthier and Aubry 1996; David et al. 1990; Doughty 1988; Farnsworth et al. 2020; Graber and Graber 1963; Graber et al. 1970; Joern and Jackson 1983; Laskey 1962; Leighton et al. 2002; Sprunt in Bent 1948; Weir 2008).

The mockingbird prefers narrows strips of vegetation to wide strips or no vegetation. In Mississippi, it was absent in field margins with no vegetated borders or with borders 30 m or more wide, but was common in 10-m wide borders (Conover et al. 2009). Its overall probability of occurrence in Maryland and Delaware riparian forests was 48% and was significantly greater in narrow than wide forests: 65% in 50-m wide forests, 56% in 100 m, 37% in 200 m, 21% in 300 m, and 1% in 800 m (Keller et al. 1993).

Areas with short grass are preferred to those with tall grass. Tall-grass habitats support a significantly lower density of mockingbirds (Roth 1979).

Mockingbirds roost predominantly in deciduous shrubs, trees, and vines. These may be very close to human habitation. One roosted in a shrub near a window and 1 pair roosted in a garage over winter but moved to a rose vine when the weather became warmer (Laskey 1935, 1936).

Nests reported to the Ontario Nest Records Scheme were in living trees, shrubs, and vines, with deciduous species (62.1% of nests) preferred to conifers. Tree species used most frequently were hawthorn (20 nests), cedar (11 nests), spruce (4 nests), maple (4 nests), and pine (4 nests). Nests were well concealed and randomly positioned in crotches and on branches near or at the trunk, or at the end of horizontal or drooping branches. They were usually supported by upright branches. Nest

heights ranged from 0.3 to 4 m, with most 1.1-2.0 m up (Peck and James 1987, 1998a). Of 663 nests in the GTA, 59% were in small conifers with 44% in small spruce. Small spruce in landscaped areas initially provide good nesting habitat but are abandoned once they mature. Nests early in the season were often in honeysuckle. They were highly conspicuous because nesting was initiated prior to leaf-out (Poon and Smith 2005; Smith and Poon 2006). Two nests were on artificial structures in the Toronto area. One was 1.1 m from the ground on a pipeline valve within a chain-link fence enclosure. The other was on wire mesh hanging below the eavestrough of a shed (Smith 2024).

In addition to the plants that supported Ontario nests, nests have been found in rose vines and shrubs, hackberry, sycamore, privet, sassafras, grape, catalpa, greenbrier, trumpet creeper, mulberry, snowberry, plum, pear, Virginia creeper, ash, elm, basswood, locust, and rough-leaved dogwood. In Tennessee, 53.8% of nests were in conifers, including white cedar, spruce, pine, and red cedar. Red cedar was favoured and supported 33% of nests. Nest building started before leaf-out with almost all early nests in coniferous vines and saplings. Later nests may be in deciduous trees and shrubs and be higher off the ground. The percentage of higher nests began to increase in May with leaf-out and progressively increased into June and July. Nest height changed seasonally in Illinois also, with average nest height just under 1.5 m in April and May and almost 2.1 m June through August. A seasonal increase in nest height has been reported from many areas, but there is no change in nest heights in other areas. Most nests are 1-3 m from the ground, with extremes of 0.3-19 m. In Tennessee, 76% of nests were 1-2 m from the ground, 18% were 2-5 m up, and 5% were lower than 1 m. One nest was in a gourd designed for Purple Martin nesting. It was nailed under the eaves at the peak of a small shed. Others were under the eaves of a well house, in a leafless grape vine, in a leafless shrub at a wire fence, on the ledge of a grape arbour, on a protruding tree root in a creek bank, in a section of a 2-compartment nest box on a fence post, in a pile of fence rails, in a cavity in a tree, in a bluebird box, and in the top of a hollowed-out fence post covered with vines (Campbell et al. 1997; Crowell et al. 1982; Farnsworth et al. 2020; Graber et al. 1970; Joern and Jackson 1983; Laskey 1935, 1962; Murray 1958; Sprunt in Bent 1948; Turcotte 1995).

Both sexes defend a territory against other mockingbirds of the same sex. Territoriality declines in July or early August, depending upon when young fledge from the last nest and the moult begins. In Tennessee, where birds held territories year round, the boundaries shifted slightly each nesting season in response to food supplies and presence of suitable roosting and nesting sites. In California, exactly the same boundaries were retained. In California, 5 breeding territories were 0.25-0.55 ha. Food was provided by humans in these territories so they may have been smaller than normal. Florida breeding territories averaged 1.27 ha (range 0.41-2.00 ha). Texas territories ranged from 0.66 to 2.53 ha. Territories of 2 Tennessee birds were about 2 ha, but the space occupied in any given time never exceeded half that size. Even in areas of dense population along railways in the GTA, pairs tended to be 200-300 m apart. The closest nests were 73 m apart and this was considered exceptional, possibly due to a lack of suitable nest sites. Spacing between pairs along Illinois roadsides was about 85 m. Mockingbirds rarely leave their territories except during the transitional period between winter and breeding seasons (Farnsworth et al. 2020; Graber et al. 1970; Laskey 1935, 1962; Michener and Michener 1935; Smith and Poon 2006).

No mockingbird is known to have nested on its natal territory, but at least 2 females have done so on adjacent territories. Young appear to disperse at least several territories away, but no detailed studies have been done on this. After dispersal from the natal territory, juveniles attempt to establish autumn territories. Those that are successful may nest near their natal area; others may disperse as far as 320 km. In California where it is a permanent resident, only 11% of birds banded as juveniles were recovered after 1 year. In Tennessee, 2 juveniles were captured 1.6 km from where they had been banded, 1 was recovered at its nest 5.2 km away, and 2 were retrapped where they had been banded. Of over 900 nestlings banded near Nashville, 5 (approximately 0.6%) were recovered 32-320 km away; the total range of distance for recoveries was 0.5-320 km (Doughty 1988; Farnsworth et al. 2020; Laskey 1936, 1962; Michener 1951; Michener and Michener 1935).

Mockingbirds in the southeast and west tend to be permanent residents and remain on the same territory for life. No adults banded in Nashville were ever recovered outside that city. Site fidelity of northern migratory populations is unknown. In Ontario and Quebec, individual territories may only be occupied in 1 or 2 years. In Ontario, there is considerable turnover in territories year to year because of changing habitat, such as young spruce becoming too large to be attractive for nesting. Some territories persist for several years in the GTA, but it is unknown if they are occupied by the same individuals. In Quebec, individual territories are rarely occupied for more than 2 years so occurrence at most sites is highly irregular. These birds probably winter in the northern United States where they would have to compete with resident birds defending food supplies. Many may not survive which may explain why few return to breed at the same locations (David in Gauthier and Aubry 1996; David et al. 1990; Farnsworth et al. 2020; Laskey 1962; Smith and Poon 2006; Whittle 1922).

Limiting Factors

Eggs have been found in Ontario nests from the last week of May until mid-August, with most present from mid-June to mid-July (Peck and James 1987). In the GTA, some mockingbirds began nesting in mid-April; 14 April was the earliest egg-date (Poon and Smith 2005). Nest building may take as long as 14 days or as little as 2 or 3 days. Nests started early in the season tend to take longer to finish. Nests for subsequent broods are usually completed in 2 or, most often, 3 days. Some birds start laying as soon as the nest is complete; others may wait 3 or 4 days. Eggs are laid at the rate of 1 a day, although a day may rarely be skipped. Incubation is sporadic until the clutch is complete. Females may delay incubating the second clutch to feed larger broods from first nests. The incubation period of 8 Ontario clutches was 11-13 days. Overall, incubation periods range from 9 to 15 days, but are mostly 12-13 days. Eggs may hatch synchronously or asynchronously but typically all hatch within a 24-hour period. The nestling period is 10-15 days but usually 12-13 days. Nest building for the subsequent brood may start as soon as 2 days after the first young fledge. In Illinois, an entire nesting cycle from nest building to fledging took 33-36 days (Breitwisch and Gottleib 1992; Breitwisch et al. 1986a; Doughty 1998; Farnsworth et al. 2020; Graber et al. 1970; Laskey 1935, 1962; Michener and Michener 1935; Peck and James 1987; Sprunt in Bent 1948; Zaias and Breitwisch 1989).

In Ontario, the mockingbird typically raises 2 or 3 broods (Peck and James 1987; Poon and Smith 2005). This is normal throughout its range, although 1 Tennessee bird was confirmed raising 4 broods. Renesting is common if a clutch is lost. Usually a new nest is built for each brood but

occasionally nest materials may be taken from an old nest. One pair used the same nest for its second and fourth broods. Due to high predation rates and the number of broods raised, the mockingbird builds a minimum of 3 nests a year and often as many as 5 or 6. Clutches of 2-5 eggs have been reported in Ontario, with most containing 4 eggs. Overall, clutches of 2-7 eggs have been reported, with clutches larger than 5 eggs rare. Mean clutch sizes range from 3.5 to 3.9. In Tennessee, 63% of nests contained 4 eggs, 23% contained 3 eggs, and 14% contained 5 eggs. The peak for 3- and 4-egg clutches was in April; most 5-egg clutches occurred in May. Usually only a single 5-egg clutch was found per season in this population, but there were 11 in a year when May and June temperatures were 4ºC above normal. Clutch size does not appear to decline as the nesting season progresses (Farnsworth et al. 2020; Graber et al. 1970; Laskey 1935, 1962; Sprunt in Bent 1948; Zaias and Breitwisch 1989).

It is likely that all yearling females breed. Males are physiologically capable of breeding at age 1 year, but many are not successful in attracting a mate. Even yearling males that successfully defend a territory may not become mated. The sex ratio is male biased, so populations may contain significant numbers of nonbreeding males. The mockingbird is typically monogamous, but there are several reported cases of bigamy. Bigamy often occurs in response to the loss of a neighbouring male leaving the female without a mate, but it may also occur when adjacent territories are occupied by a pair or an unmated male. Bigamy is suppressed by the aggressiveness of females toward each other. Bigamous males tend to have larger than average territories so that females can keep further apart, and they tend to be more aggressive in defending their territories than monogamous males. Because males build the base of the nest, a bigamous male can influence the timing of nesting of his females so that there is minimal overlap in the feeding of the broods. When the broods do not overlap, the male helps to feed both of them, but if 2 broods are present at the same time, the male feeds only one. Bigamy appears to be opportunistic, with some males being bigamous in consecutive years; others alternate between monogamy and bigamy. A case of polyandry was reported from North Carolina. A female ranged over the territories of 2 males and nested in both territories and exhibited this behaviour over 4 years. The female often took food from 1 territory to feed nestlings in the other territory. Some pairs have been together 6-8 years, but it is uncertain if there is any persistence of pair bonds in subsequent years in northern migratory populations. Most pairs remain together during a breeding season, but divorce and mate switching occasionally occur. Although mate switching often occurs as a result of nest failure, females may assess mates by evaluating adjacent territories before electing to mate with one of the males. This may occur even if she has been mated to one of the males for a long time. In North Carolina, 12% of females copulated with a male and then renested with another. In 1 year, 22% of females switched territories after active courtship with 1 male (Breitwisch et al. 1986b; Derrickson 1989; Doughty 1988; Farnsworth et al. 2020; Fulk et al. 1987; Laskey 1962; Logan 1991, 1997; Logan and Rulli 1981; Zaias and Breitwisch 1989). Extra-pair copulations have been documented in Florida. Many broods had more than 1 father and a few had more than 1 mother (Farnsworth et al. 2020).

Both adults and juveniles capture arthropods on or near the ground, take fallen fruit from the ground, and pick fruit from trees and shrubs. Medium- to large-bodied (3 cm) ground-inhabiting vermiform larvae were commonly taken by adults but rarely caught by juveniles. Both adults and

juveniles captured prey by spotting it from perches and flying to make the capture. Juveniles frequently picked fruit from trees and met a significant proportion of their daily nutritional requirements from fruit, a food easier to obtain than arthropods (Breitwisch et al. 1987). In Texas, mockingbirds used 3 main foraging techniques: aerial hawking, ground hawking (watching for prey from an elevated perch and flying to the ground to capture it), and gleaning. Birds in areas of tall grass fed significantly more in shrubs and in the air than those in more typical foraging habitat of short grass. Foraging substrates were 64% on the ground and herbaceous species, 23% in shrubs, and 13% in air in tall-grass areas and 93% on the ground and herbaceous species, 4% in shrubs, and 3% in air in short grass. Foraging techniques in the ground-herb layer were 18% gleaning and 82% ground hawking in tall grass and 87% gleaning and 13% ground hawking in short grass. Hawking techniques were 23% aerial and 54% ground in tall grass and 9% aerial and 12% ground in short grass. Tall, dense grasses and forbs caused mockingbirds to use aerial perches and above-ground substrates instead of gleaning from the ground-herb layer (Roth 1979). There are cases of the mockingbird successfully capturing prey after wing-flashing (quickly opening and closing the wings while simultaneously spreading the tail). It may pick fruit while perched in a tree or shrub, but occasionally hovers while picking fruit. It may occasionally cling to tree trunks in woodpecker fashion when preying upon arthropods on trunks and has been observed drinking sap from recently pruned deciduous trees. It may knock cicadas to the ground by hitting them with the wings and chest before grabbing them in the bill (Fairfield and Fairfield 1997; Farnsworth et al. 2020).

Eighty-five food items collected from nestlings in Texas consisted of 64.3% orthopterans (25.6% nymphs and 38.7% adults), 11.5% lepidopterans (9.3% larvae, 2.2% adults), 13.2% other insects, 9.8% spiders, and 1.2% snails. In British Columbia, adults fed young juneberries, cabbage white butterflies, and crickets. The amount of fruit delivered increases with time. Overall, nestlings are fed a mixture of arthropods (82%) and fruit (19%). Initially, they are fed arthropods almost exclusively, including spiders, dragonflies, grasshoppers, crickets, beetles, moths, butterflies, and ants. Twenty-five to 30% of food fed to older nestlings is fruit. In Florida, young may also be fed small lizards. A similar diet is provided to fledglings (Breitwisch et al. 1986a; Farnsworth et al. 2020; Fischer 1983; Laskey 1962; MacKenzie et al. 1995).

Beal et al. (1916) summarized the contents of 417 mockingbird stomachs from the southeastern United States. They contained 47.8% animal matter and 52.2% vegetable matter. Most animal food was consumed in May (85.4% of food eaten that month); the most vegetation consumed was in December and January (86.6% both months). The food items indicated that most food was obtained from the ground. Grasshoppers appeared to be the preferred animal food (average of 14.9% of food items, increasing to 43.3% in July but with only a trace in February). It also ate locusts and crickets. Caterpillars comprised 9.5% of the diet and were eaten every month with peaks in August (23.9%) and to a lesser extent in May, with the fewest eaten in October. Hymenopterans comprised 7.5% of the diet (4.5% ants and 3.0% bees and wasps). Bugs and flies were seldom eaten. Spiders comprised less than 2% of the diet every month except October. Mockingbirds also ate a few millipedes, crayfish, isopods, and snails, plus lizards and a small snake. Fruits most commonly consumed were those of hollies, greenbriers, blackberries, pokeweed, elderberries, mulberries, and black gum. Fruit comprised 3.4% of the diet, and was either raspberries or blackberries that were consumed from

May through August. It is most likely that these were taken in the wild rather than in gardens. It occasionally ate grapes. The remainder of the vegetation consumed was of no great importance in the diet and included various weed seeds; sumac berries of various species, including poison sumac; flower petals; and vegetative rubbish. In Ontario, fruit may be more important in the diet given that invertebrates are not very available in winter. Breitwisch et al. (1987) stated that the overall diet of the mockingbird was 35% fruit June through August and 67% in September and October. During the breeding season, the proportion of invertebrates in the diet is almost 85% compared with 13% in winter. Other fruits that may be consumed are those of privet, bittersweet, hackberry, hawthorn, apple, yew, crabapple, hophornbeam, barberry, guelder-rose, poison ivy, Virginia creeper, red cedar, black alder, and nightshade (Doughty 1988; Farnsworth et al. 2020; Graber et al. 1970; Laskey 1936; Sprunt in Bent 1948; Whittle 1922).

The Northern Mockingbird is a fairly rare host of the Brown-headed Cowbird. Peck and James (1998a) reported that 0 of 107 Ontario nests were parasitized, but Poon and Smith (2005) found 9 cases of parasitism in 483 GTA nests (1.9%). It appeared as though all cowbird eggs were laid in May and 8 of 9 cases of parasitism occurred before 22 May. The parasitism rate in May was 4.5%, considerably lower than other species nesting in the area. During April and May, cowbirds have a limited range of hosts in the GTA, predominantly the American Robin and House Finch. The robin is a known egg rejecter and no cowbirds ever fledge from House Finch nests because of the unsuitable diet of seeds fed to nestlings. By late May, more host species become available and the cowbird can select more suitable hosts than the mockingbird. Abandonment occurred at 6 of the 9 parasitized nests; eggs were initially accepted at 2 nests before they were abandoned. No cowbird young fledged from any of the nests. The mockingbird is an intermediate rejecter, ejecting 60-68% of foreign eggs. Most birds are either acceptors, ejecting 0% of eggs, or rejecters, ejecting them all. It is one of very few species that shows an intermediate reaction. Rejection rates vary seasonally and were 50% in March and April in Louisiana and 82% in May to July. Parasitism rates were 0% in Louisiana (607 nests) and Texas (222 nests), and 4.0% and 8.7% in Oklahoma (50 and 23 nests, respectively), but the mockingbird is 1 of the 24 most parasitized species in Kansas. In Oklahoma, it appeared as though both mockingbirds and cowbirds fledged from parasitized nests (Peer et al. 2002; Quinn and Tolson 2009; Wolfe 1995).

Because most Ontario mockingbirds nest in urban areas, habitat loss is not a significant issue. Removal of hedgerows along roads and between fields has the potential to remove suitable habitat for rural mockingbirds. This has been identified as an issue in Illinois (Graber and Graber 1963).

Several habitat features may affect nesting success of the mockingbird. These include height of grasses and forbs, degree of isolation of the nest shrub or tree, amount of cover over the nest, and nest location within shrubs. In Texas, nesting success in ground vegetation with dense cover (99% at ground level and 37% at 0.6 m) was significantly less than in short and sparse cover (81% at ground level and 14% at 0.6 m). Density of mockingbirds was significantly lower in areas of tall vegetation; no young were produced from first nests, and no attempts were made to renest. Approximately 13-22% of birds nesting in short vegetation successfully reared first broods, and birds continued to nest throughout the summer (Roth 1979).

In Louisiana, nests in isolated patches of vegetation suffered significantly less predation than those in continuous strips of vegetation. Linear corridors provided cover for the large snakes that were the primary predators, and probably other predators. A high density of vegetation around the nest may have marginal antipredator value if it includes a combination of very dense patches interspersed with open corridors. The percent reduction in light transmission above the nest was the best predictor of the number of days that young survived in the nest. Dense canopy over a nest increases the likelihood of young fledging (Joern and Johnson 1983).

In Florida, nests in low shrubs or placed low in shrubs were more successful than nests higher up. Nests at the juncture of a branch and the trunk were more successful than those along a branch or among twigs or leaves (Farnsworth et al. 2020).

In Florida, urban mockingbirds started nesting earlier and produced significantly more fledglings than rural birds. Survival rates of young were greater in urban areas. Residential birds tended to remain on their territories year round. Urban birds were more likely to return to the same territory the following year if they were successful at nesting. Successful and unsuccessful females nesting in pastures and wildlife preserves showed little difference in their probability of returning. Their return rate was similar to that of unsuccessful urban females. Rural populations were sinks, parking-lot populations were sources, and residential populations were sources in 2 of 3 years. It was considerably more abundant in urban than rural habitats (Stracey and Robinson 2012).

In Florida, Stracey et al. (2014) studied the effects of light pollution on the mockingbird. As light levels increased, there was a significant increase in feeding time past sunset. Although light pollution created conditions bright enough to allow it to feed young later into the night, this did not increase brood size. Birds at brightly lit parking lots fed nestlings later than those in sites with no artificial lighting, but those in residential areas did not. This suggests that there may be a threshold of light required to elicit later feeding.

In Florida, Walters et al. (2019) studied the response of the mockingbird to urban noise. As background noise increased, there were significant declines in its song of syllables in the 1-3 kHz range and significant increases in those 3-5 kHz in frequency. There was no difference in use of syllables greater than 5 kHz in noisy environments. It altered its song in response to noise and was adapted to inhabiting noisy environments.

In South Carolina, mockingbirds declined and almost disappeared in agricultural lands dominated by cotton, but there was no decline in areas of corn, tobacco, and soybeans, or in urban or suburban areas. This may have been due to the aerial spraying of pesticides on cotton plantations (Stewart 1974).

Cold, wet weather in spring or early summer may result in nest abandonment; even half-grown nestlings may perish (Farnsworth et al. 2020; Graber et al. 1970; Poon and Smith 2005). Although the mockingbird is fairly tame and will allow humans to approach closely, nests may be abandoned if they are disturbed during incubation. Once the eggs hatch, mockingbirds are tolerant of disturbance (Farnsworth et al. 2020).

In some areas, the mockingbird may be affected by the 13- and 17-year cycle of cicadas. It may experience a population dip the year before local emergence of cicadas, suggesting that it increases after emergence of adult cicadas and then gradually declines (Farnsworth et al. 2020).

Price (2004) predicted that the range of the mockingbird could increase in southern Ontario if the average summer temperature increased by 2ºC.

Status

The Northern Mockingbird is a recent arrival in Ontario. The first record was from Chatham in 1860 and a pair was observed in Hamilton in 1883. As late as 1937, only 4 nests had been found, 3 in Essex County and 1 in Haldimand; the first nest was at Amherstburg in 1906. It spread gradually into Ontario during the 20th century as part of a continent-wide expansion of the northern limits of its range. Most early records were from the extreme southwestern portion of the province, with 12 occurrences in Ontario between 1900 and 1920. The pattern shifted during the 1920s with scattered, isolated records across a broad front of southern Ontario. The first records for the GTA were in the 1930s, with one spending the winter of 1935-36. The first nest was documented in 1936. Early colonization was slow with several years between successive sightings. There was a slow and erratic increase in sightings through the 1940s with a more pronounced increase after about 1954. It was still rare in the province in the 1950s, but some birds were pioneering and nesting further north, including on Manitoulin Island and at Ottawa, Moosonee, and Sioux Lookout. In the 1960s, it was still rare in the GTA and in Niagara, with the first breeding for Niagara documented in 1961. The area from Vineland to Niagara Falls was populated in the 1960s. During the late 1970s, there were increasing numbers in central and northern Ontario including on Manitoulin Island and in Algoma District. Breeding was confirmed at Moosonee in 1979. It began to occur more regularly in the Hamilton area beginning in 1953, with a gradual expansion both by pioneering males in spring and postbreeding dispersal in autumn. The first record for Elgin County was in 1948, with 3-10 reports annually since 1990, except for 2 years when none were seen. The first record in the Kingston area was prior to 1915, with the next records in 1936 and 1955. Starting in 1962, it was found there every year and numbers rose steadily annually; the first nest was reported in 1966. The first record from Muskoka District was in 1959 and breeding was confirmed in 1975. During the first atlas, the mockingbird was well established in the Niagara Peninsula, although its contiguous range ended at Hamilton. There were only 10 squares with breeding evidence for the GTA. It was found in 29 contiguous squares in Niagara and occurred in scattered areas south of the Canadian Shield, with some records in the southern Shield and northern records from Cochrane, Moosonee, Thunder Bay, and Kenora. In the south, there were minor concentrations in the region from Prince Edward County to Kingston and near Ottawa (Baillie 1967; Baillie and Harrington 1937; Curry 2006; Curry in Cadman et al. 1987; de Vos 1964; Lancaster et al. 2004; McIlwraith 1894; Mills 1981; Poon and Smith 2005; Smith and Poon 2006; Weir 2008; Wright 1921). James (1991) considered the mockingbird an uncommon permanent resident in the Niagara Peninsula, rare and irregular elsewhere in the south, and occasional north to Thunder Bay and Moosonee.

The second atlas demonstrated that the mockingbird had increased in abundance and expanded its range since the first atlas. Its probability of observation increased significantly province-wide and in and south of the Canadian Shield. It extended its contiguous range in Niagara to include

the entire region and the urbanized area south of the Oak Ridges Moraine as far east as Bowmanville. There was a consolidation of range in the Prince Edward County to Kingston area. It also bred in Chatham-Kent and in Haldimand County along the shoreline of Lake Erie. Elsewhere, its distribution was scattered. There were additional records from the north from Sudbury, east of Lake Nipigon, and at Moosonee. Its greatest abundance occurred in Niagara Region and, to a lesser extent, the GTA (Smith and Poon in Cadman et al. 2007).

The main expansion into the GTA did not begin until the early to mid-1990s. The estimated number of breeding territories in the GTA during different periods was 1921-30, 0; 1931-40, 4: 1941-50, 3; 1951-60, 9; 1961-70, 15; 1971-80, 23; 1981-90, 51; 1991-2000, 247; 2001-05, 1,591. Of the total of 1,943 territories recorded in the GTA, only 352 (18.1%) were documented prior to 2001. During the early 2000s, numbers more than doubled over those of the 1990s, especially for Peel, Toronto, and York. During the second atlas, breeding was confirmed in every urbanized square in the southern half of the GTA. The population was estimated at 640 adults comprised of 200 confirmed pairs, about 40 additional pairs, and approximately 160 single birds (Smith and Poon 2006).

The increase in population of the mockingbird in Ontario is consistent with increases throughout its range. It was rare in New England between 1900 and 1920 but increased markedly there. It first occurred in Illinois in the 1880s with a major surge in population in the last half of the 20th century. Some range expansions and population increases may have been due to repopulation of areas where numbers had been decimated by selling mockingbirds for caged song birds. Populations continue to expand northward and are predicted to continue to do so (Doughty 1988; Farnsworth et al. 2020; Wright 1921).

Breeding Bird Survey data indicate that the mockingbird is decreasing. Population trends 1970-2021 were annual decreases of 1.27% in Canada and 1.7% in Ontario. The 2011-21 trends were annual decreases of 4.97% in Canada and 6.61% in Ontario. The long-term results were highly reliable for Canada and of medium reliability for Ontario; the short-term results were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young may not be able to fly until about 8 days after leaving the nest. In Florida, about half of fledglings could fly 5 days after leaving the nest. In 1 year, all could fly 8 days after fledging, but all did not fly until 13 days after fledging another year. For as long as 2 weeks, the young remain close to each other, often within a metre. The parents provide food to the young for 3 weeks after they leave the nest, at which time the young leave the natal territory. Care of fledglings from the first brood ends abruptly when the next clutch hatches. No brood division occurs in early broods but it may occur in the last brood. In some cases, the final brood may be cared for entirely by one of the parents. Young from the last brood of the year remain on the natal territory an additional 2-4 weeks (Farnsworth et al. 2020; Zaias and Breitwisch 1989, 1990).

Most fledglings jump to the ground upon fledging and remain low in shrubs or small trees for 1-2 days before climbing to greater heights. In Florida, the mean height of 4-day-old fledglings above ground was 5.2 m. Later, fledglings descend to the ground and initiate the foraging techniques used by adults. Fledglings spent 89% of their time perched in vegetation. They were not

more concealed by vegetation when they were young. They spent 31% of their time in vegetation partially or completely hidden from view (Breitwisch and Gottleib 1992; Zaias and Breitwisch 1989).

Fledglings are driven from their natal territory 1-2 days after the next clutch hatches. After dispersal, some juveniles attempt to establish territories. Others form flocks and forage in areas between territories held by adults (Breitwisch and Gottleib 1992; Farnsworth et al. 2020; Laskey 1962).

MIGRATION/AUTUMN

It appears as though most, but not all, northern birds are migratory, but even some southern residents may move considerable distances in autumn or winter, returning to their territories after a brief absence. In the GTA, about 25% of birds remained on a territory year-round; the remainder either migrated or dispersed. Dispersal within the GTA appears to be mainly along railway and hydro corridors. Of 881 territories in the GTA, 559 (63.5%) were breeding season only, 120 (13.6%) were winter only, and 202 (22.9%) had records in both seasons. This suggests that many birds withdrew from their breeding territory to initiate a territory elsewhere, making local movements of a few kilometers rather than undertaking full-scale migration. The Toronto Islands and Leslie Street Spit have yielded numerous May records and there are no breeding season records for these areas. These birds are presumably spring migrants. Prior to 2000, there was a pronounced spring peak in Toronto and Durham Region with a less defined peak in Halton and Peel. The peak is even more pronounced in Northumberland County. These peaks are highly suggestive of regular spring migration. Long Point Bird Observatory data do not provide strong support for autumn migration. In Elgin County, where there are only 2 nest records, there are several spring records between 10 April and 9 May; autumn records are from 28 August to 29 November. Some birds arrive there in early October and remain over winter, staying until late April. In Hamilton, there were numerous May and November observations in the 1950s and 1960s. In Algonquin Park, where there has been no evidence of nesting, the mockingbird is a regular but rare visitor that occurs predominantly in spring from mid-April to early May. Birds may travel as far as 800 km between breeding and autumn or winter territories. It appears as though all Quebec mockingbirds are migratory. It is absent from February to April, with a sudden increase in May and peak numbers in June and July. In interior British Columbia, spring migration is suggested by a peak in May and many birds apparently leave in August and September. Even in Tennessee and Illinois, there are peaks of observation in late April and May and again in autumn from August through November. In Maryland and Delaware, it is considered a short-distance migrant rather than a resident. It appeared in northern Illinois from September to November where there were few breeding pairs suggesting that postbreeding dispersal may include northward movements. Rare collisions with television towers suggest that it is a nocturnal migrant (Campbell et al. 1997; Curry 2006; David in Gauthier and Aubry 1996; David et al. 1990; Doughty 1988; Farnsworth et al. 2020; Graber and Graber 1963; Graber et al. 1970; Keller et al. 1993; Lancaster et al. 2004; Laskey 1935; Smith and Poon 2006; Sprunt in Bent 1948; Tozer 2012).

Habitat used in autumn and winter is similar to that used during the breeding season: suburban and urban areas, industrial areas, and edge habitat or linear corridors in rural areas. Most birds are associated with human habitation or development. Habitats with an abundance of fruit are essential in autumn and winter (Graber et al. 1970; Hailman 1960a; Laskey 1936).

In autumn, there may be major shifts in the areas inhabited. Adults may begin their moult a short time after the young of the last brood fledge, often in late July (Zaias and Breitwisch 1990). At this time, defence of the breeding territory ceases and there may be large influxes of birds to areas with feeders or large amounts of food that were previously defended by 1 or 2 pairs. Territorial behaviour is reasserted in late September and is intense because birds attempt to establish a territory that will be used throughout autumn and winter. In southern resident populations, the pair may remain intact and stay year-round on the breeding territory. In the northern portion of its range, birds tend to have separate breeding and autumn-winter territories. Of 23 North Carolina birds holding autumn territories, 15 had resided on the same territory at least 1 year, 7 were new to the area and acquired a territory, and 1 shifted its territory within the same general area. Autumn-winter territories may be held by juveniles, females, and males. Many juveniles are successful in establishing territories between areas defended by adults; these are often used for breeding. Other juveniles either are unsuccessful in establishing a territory or do not attempt to do so, and congregate in flocks. Females may establish territories distant from those of their previous mate or may defend a small territory adjacent to their mate, often within a small portion of the breeding territory. Both mated and unmated males may defend autumn-winter territories. Either sex may abandon a territory at any time due to insufficient food resources, or annex adjacent unoccupied territory. Territorial birds may band together to eject intruding birds attempting to take food resources (Farnsworth et al. 2020; Hailman 1960a; Laskey 1935, 1962; Logan and Wingfield 1990; Michener and Michener 1935).

Autumn territories are required to protect food resources and may be smaller than those defended during the breeding season. In Tennessee, males' territories were about 0.6 ha in area compared with 0.3 ha for females. A single territory in Virginia was 0.45 ha. In North Carolina, sizes of territories in September were an average of 0.53 ha 1 year (range 0.37-0.72 ha) and 0.39 ha (0.26-0.57 ha) in October another year (Hailman 1960a; Laskey 1936; Logan 1987; Michener and Michener 1935).

In autumn and winter, other frugivorous species may be attacked and driven from the territory. Specific resources, such as a fruit-laden tree, may be vigorously defended. Mockingbirds in South Carolina defended holly trees against other species, with aggression directed most to those that were potential competitors for food. The mockingbird has been known to kill Cedar Waxwings while defending a fruit tree (Hedrick and Woody 1983; Laskey 1935; Moore 1978).

Mockingbirds may forage in groups in fruit-bearing trees in late autumn. Birds tend to arrive simultaneously from all directions, usually shortly after a series of calls that may act as a signal. Foraging in groups may overwhelm birds defending the tree and reduces the chances of any individual bird being chased away by the defender (Merritt 1980).

The mockingbird is rare in Ontario during migration and rare to locally uncommon in autumn where birds are still on territory. Fifty-one were seen on the 1991 autumn count in Hamilton (Curry 2006).

WINTER

The mockingbird tends to avoid areas with snow in winter. Frozen ground without snow is an important predictor of its presence (Keyser et al. 2022). Winter habitat is similar to that used at other times of the year. Birds typically remain on the territories they established in autumn throughout the winter. In Tennessee, there was considerable wandering by wintering birds during January and February. Three birds moved 4.8 km away during winter and one returned. In Florida, winter birds may wander from the territory, presumably as pairs, and return in 1-4 weeks, but this behaviour was not documented in Pennsylvania or Maryland (Farnsworth et al. 2020; Graber et al. 1970; Laskey 1935).

The winter territory is established around food resources, particularly fruit. Although food resources decline through the winter, birds are usually able to remain at the same site all winter. Three territories in New York were 0.35, 0.89, and 1.65 ha. Despite the disparities in size, the territories had similar numbers of rose bushes (68-80), area covered by fruit bushes (460-495 m^2), and fruit bush surface area (1,100-1,600 m^2). Birds appeared to assess the amount of food resources to determine the required territory size, with most territories containing a similar amount of food resources regardless of the territory size. The size of territories changed over winter, but there was no consistent pattern of increase or decrease in size. Territory size fluctuations appeared to be unrelated to food supply. The initial size of 5 territories was 0.35-1.65 ha (Safina and Utter 1989). Logan (1987) noted changes in winter territory sizes in North Carolina. Over 2 years, December territory sizes averaged 0.24 ha both years (range 0.09-0.56 ha). December territories were 49.1% the size of September territories and 64.3% the size of October territories. Territory size increased in January to the size they were in early autumn. Changes in territory size were highly irregular. In 1 year, all territories shrunk in December. In another year, some decreased, some did not change, and others increased. The consistent decrease in territory size occurred only in the colder year. Smaller territories may minimize energy expenditure because less activity is necessary to patrol the territory. Michener and Michener (1935) also noted that winter territories were smaller and fluctuated in size. The smaller size might be due to withdrawal to areas with the greatest food supply or due to giving up some of the territory to the female. Winter territories of 4 females were 0.25 ha, later reduced to 0.19 ha; 0.03 ha, later increased to 0.10 ha; 0.06 ha, later increased to 0.25 ha; and 0.03 ha. Territories may have been smaller because the authors provided abundant food to the mockingbirds. In Florida, winter territories averaged 0.31 ha November to January (range 0.08-0.59 ha). Territory sizes increased slowly to 0.37 ha (range 0.14-0.55 ha) by mid-March and 0.74 ha (range 0.15-2.61 ha) by the end of March (Farnsworth et al. 2020). In Tennessee, 1 male had a feeding range about 300 m long (Laskey 1936).

Fruit of the multiflora rose is one of the most favoured winter foods of the mockingbird. In the GTA, presence of multiflora rose was one of the best predictors for finding mockingbirds, but only 12% of territories contained this plant. In Nova Scotia, 1 in about every 25 multiflora rose clumps contained a mockingbird in winter. The northward range expansion of the Northern Mockingbird has largely been attributed to planting of multiflora rose. It maintains a slight positive energy balance when feeding on multiflora rose. Without this fruit in winter, it is unlikely that it could maintain a positive energy balance. There is evidence that it moves away from residential areas

without roses in mid-winter (Castrale and Donaldson 1986; David et al. 1990; Farnsworth et al. 2020; Graber et al. 1970; Smith and Poon 2006; Stiles 1982).

In Ontario, the mockingbird rarely visits winter feeders and relies mostly on natural foods, but many of these are nonnative species. It has fed on multiflora rose hips, sumac seeds, frozen apples still on the tree, fallen pears, and Boston ivy berries. It may also take scraps from dumpsters (Sheppard et al. 1936; Smith and Poon 2006). One near Branchton spent many mornings over a 3-week period in a small roadside common buckthorn eating the berries until they were depleted (personal observation). In Boston, Whittle (1922) observed a female feeding on the ground under a hickory tree and presumed that it was eating the nuts. Important fruits were those of pokeweed, juneberry, hophornbeam, barberry, holly, guelder-rose, and crabapple. Other fruits reported in the diet are hawthorns, figs, plums, elderberries, red cedar, mountain-ash, hackberry, Japanese honeysuckle, and viburnums. Of 1,845 food items eaten by a single bird, all were fruit: 31.5% multiflora rose, 65.6% sumac, 2.4% Japanese honeysuckle, 0.4% viburnums, and 0.1% red cedar. By dry weight, it ate 72.9% rose and 19.8% sumac with 66.6% of calories obtained from rose and 26.3% from sumac. A second bird ate 76.4% rose, 86.7% of the calories consumed. Fecal pellets from a third bird contained 547 rose seeds, 65 Japanese honeysuckle seeds, and 2 red cedar seeds, with rose representing 89.1% of the diet (Laskey 1962; Leighton et al. 2002; Stiles 1982; Wright 1921).

The mockingbird visits about half the feeders within its range. Nearly twice as many feeders are visited in urban and suburban areas as in rural areas. Most feeders are visited in the coldest months. Favourite feeder foods are peanut butter mixes, fresh and dried fruit, bird puddings, and water. Infrequent choices are mixed seeds, all kinds of sunflowers, hulled peanuts, pet food, suet, baked goods, and sugar water (Dunn and Tessaglia-Hymes 1999). In the GTA, it has eaten suet, raisins, chopped grapes, chopped apples, and rarely seeds. Other items consumed at feeders are apples, holly berries from a wreath, asparagus berries, bittersweet berries, and cherries. Usually only 1 bird visits a feeder at once, although there may occasionally be 2 or 3. Adults are dominant over juveniles, so fewer of them attend feeders (Doughty 1988; Dunn and Tessaglia-Hymes 1999; Graber et al. 1970; Laskey 1936; Michener 1951; Michener and Michener 1935; Smith and Poon 2006).

The mockingbird is restricted in winter to areas that have an average minimum January temperature of at least −7°C. All areas of higher concentration have average minimum January temperatures of at least −1°C (Root 1988). In Ontario and British Columbia, it withstands colder temperatures than these (Campbell et al. 1997; Smith and Poon 2006).

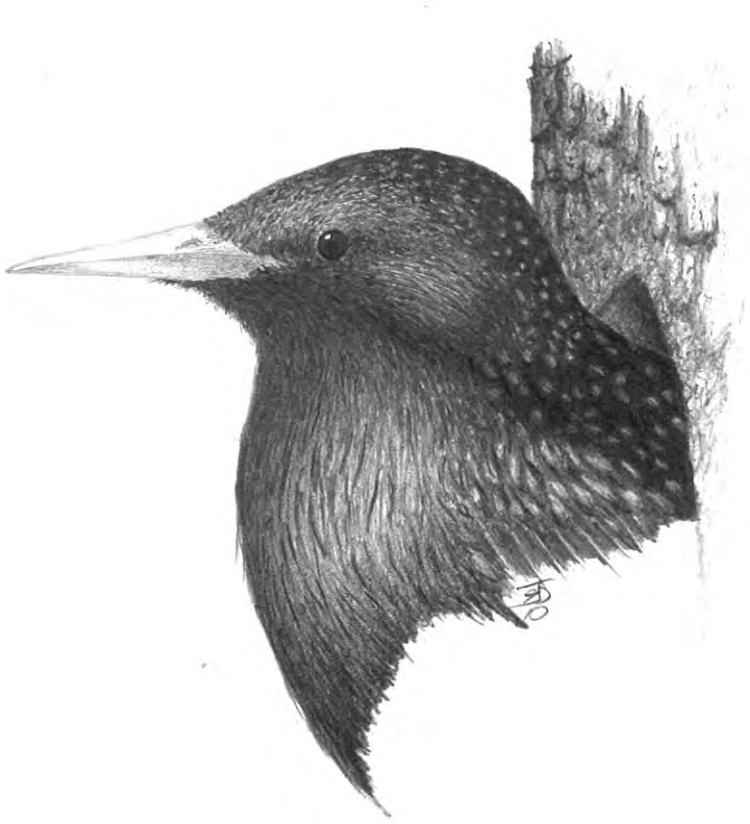
Severe winter weather may cause significant mortality of the mockingbird, particularly of juveniles that are unable to secure a winter territory. This may also be true of northern migratory birds that have to compete for food resources with southern resident birds in winter. Some birds that wintered in Niagara Region in the 1960s disappeared after a severe ice storm in mid-January. On the Ozarks Plateau, severe winter weather was a factor affecting its winter occurrence; it was adversely affected by severe storms in the mid- to late 1970s. After severe winter weather in Illinois, birds shifted to residential habitat where they survived because of feeders and shrub plantings. The density of birds per km² in urban residential areas was 3.25 before the storm and 27.75 afterwards (Farnsworth et al. 2020; Graber and Graber 1979; Smith 1986b; Smith and Poon 2006).

Wintering birds first appeared in the province much later than breeding birds. The first record of wintering was in London during the winter of 1922-23, 2 overwintered in Hamilton 1927-28, and the first Niagara record of overwintering was in 1931-32. The first record on the Hamilton Christmas Bird Count (CBC) was in 1941, but the mockingbird was not recorded consistently on this count until 1965. On the Peel-Halton CBC, there was an initial increase starting around 1990 and more substantial increases around 1995 and around 1997-98 for the Toronto count. An increase was not noticed in Richmond Hill, Kleinburg, and Oshawa until the 2000s (Curry 2006; Sheppard et al. 1936; Smith and Poon 2006). The mockingbird is still a rare winter resident in Ontario. Smith and Poon (2006) estimated the winter population in the GTA at 120 birds, 25% of the breeding population.

CBC data for Ontario for 1970-2021 indicate that the Northern Mockingbird increased at an annual rate of more than 3.15%. The trend 2009-21 was an annual decrease of 8.18% (National Audubon Society 2022).

European Starling

Sturnus vulgaris

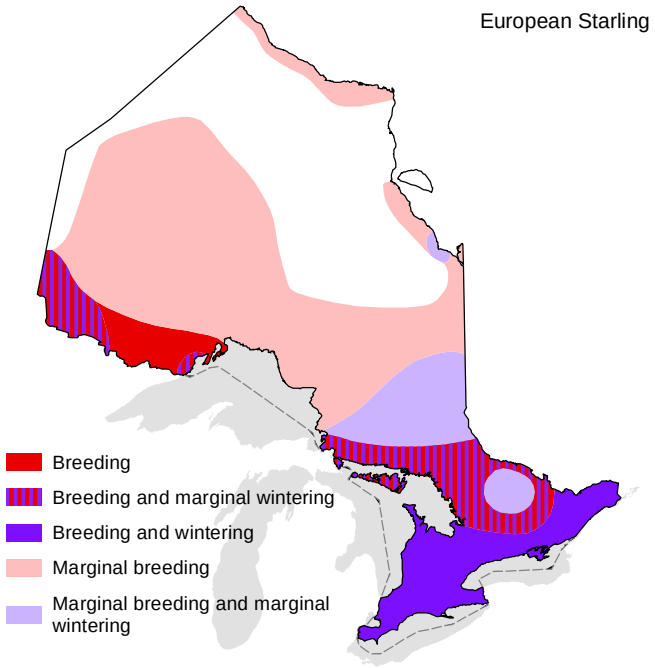


BREEDING SEASON

Habitat Requirements

In Ontario, the European Starling has nested in deciduous, mixed, and coniferous woods and swamps (30.1% of nests); in farmlands, including fields, pastures, orchards, and gravel pits (27.8%); in urban and rural populated areas, including gardens, streets, cottage areas, campgrounds, cemeteries, and golf courses (22.0%); along roadsides, floodplains, shorelines, and edges of canals (10.7%); in beaver ponds, marshes, wet meadows, and muskeg and bog areas (6.5%); on sand dunes and banks (1.9%); and on cliffs (0.9%). One nest was in a building in dry tundra. Dry areas were used more frequently than wet areas. The number of sites in wet areas was indicative of the presence of dead trees for nesting (Peck and James 1987).

The pattern of colonization in Ontario and other areas gives an indication of the starling's habitat preferences. Urban areas and towns were settled first. In many areas, its distribution is still strongly linked to areas of human concentrations. In the Hudson Bay Lowland and Boreal Forest Region, it is primarily restricted to human settlements and structures. In extensively forested areas, it may occur along highways but avoids forests (Baillie and Hope 1943; Campbell et al. 1997; Cotter et al. in



Gauthier and Aubry 1996; Graber and Graber 1963; James 1980; Kalinowski and Johnson 2010; Kalmbach and Gabrielson 1921; Lumsden 1980; Smith 1957; Wilson and McRae 1993). The second area inhabited was rural villages and farms where it nested primarily in cavities in houses, barns, and other structures. In rural areas, larger river valleys and lowland areas were populated first. Next it moved into smaller woodlots where it nested in trees with natural cavities or woodpecker holes. The last areas inhabited were isolated towns and human-made structures in extensively forested and tundra habitats, major highway corridors through extensive forests, and clear-cuts and burns with residual snags. A key habitat component is presence of extensive areas of short grass for foraging such as lawns, hayfields, old fields and meadows, and pastures. For grasslands to be suitable there must be nearby cavities for nesting. It avoids large expanses of non-grassland habitat such as extensively forested areas, muskegs, and areas north of the treeline. Highest densities occur in urban and agricultural areas (Baillie and Hope 1943; Cabe 2020; Campbell et al. 1997; Cramner-Byng 1990; Erskine 1977; Kalinowski and Johnson 2010; Kalmbach and Gabrielson 1921; Peck 1972; Schueler et al. 1974).

In Timiskaming District, Lumsden (1980) studied the distance from mowed or agricultural land that starlings nested in boxes designed for Common Goldeneyes. The furthest it nested from a cleared area was 503 m. This may be the maximum distance that it is able to carry enough food to nourish a brood. The percentages of available nest boxes used at different distances from suitable open habitat were: 0-100m, 84.6%; 100-200 m, 91.7%; 200-300 m, 69.2%; 300-400 m, 53.3%; 400-500 m, 53.8%; 500-600 m, 10.0%; 600-700 m and 700-2,000 m, 0%. In Muskoka and Parry Sound districts, it occasionally nests in trees in beaver ponds (Mills 1981). In wooded tracts in Durham Region, it was associated mostly with stands with open canopies. Highest densities occurred in woodlots that contained old beech trees, which were favoured nest sites (Speirs and Orenstein 1975).

In southern Ontario, there was no difference in the starling's abundance on organic and conventional farms. Its presence was significantly associated with farmsteads. It was negatively correlated with spring grain, pasture, and hay, although only the latter relationship was significant (Kirk et al. 2011).

In Quebec, the starling nests in cliffs exposed to sea spray along the Gaspé coast (Cotter et al. in Gauthier and Aubry 1996). In Wisconsin, it is a rare breeder in pine and oak barrens (Hoffman et al. 1991). In Iowa riparian areas, it was most abundant in floodplain woodlands followed by savannah, scrub, upland woodland, and wooded edge (Stauffer and Best 1980). In British Columbia, the most

frequently selected nesting habitats were associated with human settlement (50%), forest (38%), and grassland. Within broad habitat types, 54% of nests were in rural, suburban, or urban settings; 18% were in woodlands; and in grasslands (Campbell et al. 1997). In most areas, it reaches higher densities in urban than agricultural areas. Near Saskatoon, it has become a rural species with few, if any, occurring within the city (Leighton et al. 2002). In California, it was most abundant in oak savannahs with grass cover, intermediate in abundance in oak woodlands, and least abundant in oak savannahs with shrub cover and montane hardwoods (Wood et al. 2013).

At the landscape level, the European Starling preferred areas that were 10-29% forested in North Dakota (Cunningham and Johnson 2019).

Although the starling may occur in shrubby openings and disturbed areas in the interior of large forests, it occurs predominantly at edges of small woodlots when it uses forested habitat. Small, open-canopied tracts and edges are preferred for nesting and most nests are within 15 m of edge. In many areas, even edges of extensive forests are avoided. In South Dakota, densities were 2.7-7.0 times greater in small, isolated woodlots than in large, contiguous, riparian forests. In the mid-Atlantic states, its abundance was significantly negatively correlated with woodland size. Its probability of detection was 62% in 0.3-ha woodlots, 50% in 1-ha woodlots, 35% in 3.2-ha woodlots, 25% in 10-ha woodlots, 15% in 32.0-ha woodlots, and 10% in 100-ha woodlands with a gradual decline to 1-2% in 3,200-ha woodlands. In Maryland and Delaware, its probability of detection declined significantly with width of riparian forests. Probability of detection was 50% in 50-m wide forests, 49% in 100-m wide, 37% in 200-m wide, 26% in 300-m wide, and 2% in 800-m wide forests. In the mid-Atlantic states, its abundance was positively associated with moisture gradient, foliage density between 2 and 3 m, the number of trees larger than 3 cm diameter at breast height (DBH), and the number of tree species at the counting point. In Colorado floodplain forests, it was associated with areas with a high density of trees with a large DBH. In Durham Region, it was considered a late-successional species; in northern hardwoods in the northeast, it occurred most frequently in mature stands. Its association with large trees and older stands is due to its requirement for cavities for nesting (Aitken et al. 2002; Gentry et al. 2006; Keller et al. 1993; Mossman and Hoffman 1989; Noon et al. 1979; Robbins et al. 1979; Sedgwick and Knopf 1990; Speirs and Orenstein 1975).

All but 2 Ontario nests were in elevated holes or recesses. One nest was in a broken limb on the ground and another was in a wooden cable spool on the ground. Of 1,546 nests, 62.9% were in trees, stubs, and stumps; 36.0% were in bird boxes; 27.3% were in buildings; 18.8% were in fence posts; 8.7% were in mail boxes; 6.3% were in utility and flag poles and pipes; 1.4% were in miscellaneous human-made objects; 1.0% were in cliffs and banks; 0.5% were in bridges and dams; and 0.2% were in raptor nests. Both living (58.3% of nests) and dead (41.7%) trees were used for nesting. Deciduous trees (21 species, 91.8% of nests) were preferred to conifers (5 species, 8.2% of nests). Tree species used most often were elm (26.3% of nests), maple (25.4%), apple (16.7%), birch (12.3%), willow (10.0%), and poplar (9.3%). Most tree nests were in natural cavities or new or old woodpecker cavities. Nests were both inside and outside buildings. They were in human-made structures such as signs, radiators, gas tanks, pumps, air vents, air conditioners, and an aircraft. One nest was in a boiler tank that was half submerged in a lake. Three nests were in Bank Swallow tunnels. Single nests were reported in each of the sides of Red-tailed Hawk, Osprey, and Bald Eagle nests.

Nest sites were often reused; 1 tree cavity site was used in 17 of 20 years. Nests in trees were 0.3-23 m from the ground, with most 2.4-6 m up. Nests in buildings were 1.2-18 m from the ground, with most 2.7-6 m up. A nest in a sandbank tunnel was 30 m from the ground (Peck and James 1987).

Nest cavities tend to be in trees that are larger than average in the habitat that is being used. In New Jersey, the starling nested almost exclusively in 50-100-year-old silver maples that lined city streets. Only once the number of trees declined did birds start nesting in buildings. Tree cavities are preferred to those in buildings when they are available. Cavities used by starlings are similar to those used by the Northern Flicker, Red-headed Woodpecker, Red-bellied Woodpecker, and Great Crested Flycatcher, probably due in part because many nest cavities are usurped from the 3 woodpecker species (Campbell et al. 1997; Hutto and Gallo 2006; Sedgwick and Knopf 1990; Stauffer and Best 1980, 1982; Suthers 1978). Near Kingston, it exhibited no preference for orientation of cavity entrances (Rendell and Robertson 1994a). It shows a decided preference for nesting in deciduous trees and prefers cavities in branches to those in tree trunks. In some areas, it nested mostly in living trees and in other areas mostly in dead trees. When using woodpecker cavities, it has a strong preference for cavities that still have bark around the entrance and that face downward, thereby minimizing water flow into the cavity and giving the nesting bird an advantage when facing potential competitors or predators. Nest cavities in trees are usually 3-7.6 m from the ground. In British Columbia, height of nests not in nest boxes ranged from the ground to 75 m, with most 2.1-6.0 m up. Cavities in open areas are required. Along the British Columbia coast, it nests in natural cavities and woodpecker holes in pilings, often over water. It also nests in cavities in telephone poles, concrete power poles, and fence posts (Aitken et al. 2002; Bent 1950; Cabe 2020; Campbell et al. 1997; Erskine and McLaren 1976; Hutto and Gallo 2006; Ingold 1989; Kalmbach and Gabrielson 1921; Sedgwick and Knopf 1990; Stouffer and Best 1980).

The starling readily uses nest boxes and appropriates boxes designed for bluebirds, Tree Swallows, Purple Martins, American Kestrels, and waterfowl (Wood Duck, Bufflehead, Common Goldeneye, and Hooded Merganser). Gibo et al. (1976) provided nest boxes for starlings in 7 different habitats in Mississauga: in an arboretum, old field, orchard, pine stand, oak-maple stand, and on poles in the centre of an old field. The pine and oak-maple stands did not contain any grassy areas suitable for foraging but there were lawns and fields within 100 m. The seventh habitat was a suburban area. Boxes in the centre of an old field were preferred and the arboretum had fewer nests than expected. Boxes in the centre of the old field had the highest survival rate, so starlings may have been selecting nest sites that were less likely to suffer predation. In Kentucky, it preferred boxes affixed to isolated trees or poles or located on edges of isolated, small, wooded areas within pastures. It tended to avoid boxes on edges of larger wooded areas and dense overgrown hedgerows. It was also less likely to use nest boxes associated with cropland such as corn or wheat (Twedt and Oddo 1984). It cannot access boxes designed for bluebirds or Tree Swallows that have a circular diameter smaller than 3.8 cm (Bent 1950; Davis et al. 1986; McComb et al. 1987). The starling preferred wooden Purple Martin houses (1.8% occupancy rate) over aluminum houses (0.3%; Jackson and Tate 1974). In boxes designed for kestrels and goldeneyes, it showed a strong preference for boxes measuring 33 cm from the bottom of the entrance hole to the floor of the box over those measuring 24.5 cm or 18 cm. Goldeneye boxes with 6.3 cm entrances were used; those with 12.5 cm entrances were

avoided. In another study, 3 entrance-hole sizes were available in goldeneye boxes: 13 by 10 cm, 10.5 by 8 cm, and 7.5 by 6 cm. Of 42 pairs of starlings, 35 chose the smaller entrance hole, 7 the medium-sized hole, and 0 the large entrance. Starlings showed a strong preference for boxes painted black inside. The cavity entrances in kestrel and duck boxes are much larger than what the starling prefers, which may partially explain its preference for deep boxes with black interiors (Erskine and McLaren 1976; Lumsden 1976, 1986).

The starling nests on or in a variety of human-made structures, especially buildings. Savard and Falls (1981) studied its nesting preferences in several Toronto neighbourhoods. Although it occasionally nested in trees, most nests were in crevices and holes in buildings. Openings around eaves and eavestroughs accounted for 79% of nest sites. In Don Mills, vent holes between bricks of the attic provided 75% of nest sites and the remainder were around eaves and eavestroughs. Two pairs nested in dryer vent holes and had to lift up the small door closing the vent to access their nests. Nests averaged 6.83 m above ground in areas with 2-storey homes and 4.15 m in plots with 1-storey houses. The overall average nest height was 6.92 m. Nesting occurred more often in areas with 2-storey houses which may have been a reflection of more nest sites. It may prefer higher nest sites and preferred to nest at greater heights than the House Sparrow. The starling preferred to nest in buildings in Vancouver. Two nests were in tree cavities, 1 was in a nest box, and 62 were in buildings. The mean height of nests was 6.2 m with most nests in 2-storey buildings and apartment buildings rather than 1-storey buildings (Weber 1975). Nests have been found in chimneys, church steeples, silos, grain elevators, oil drums, posts, poles, holes in haystacks, cavities among rocks or piles of stones, and cliffs and earthen banks (Bent 1950; Campbell et al. 1997; Feare 1984). Several starlings nested in a Bank Swallow colony in a Maryland gravel pit (Robbins 1985).

Unusual nest sites include in old magpie nests, on fire escapes, hay tracks, barn doors, and in open boxes erected for pigeons. The starling occasionally nests on the ground when no elevated sites are available in sites such as old rabbit holes, under loose stones along shores, in cracks in the ground, in heaps of stones, in an indentation in an area of sloping ground, and in old tins and boxes in rubbish heaps. It rarely nests in the open outside a cavity in conifers, dense clumps of bushes, or in ivy (Kalmbach and Gabrielson 1921; Kessel 1957).

The starling defends only a small area around the nesting cavity. The territory may be limited to the nesting hole itself, but usually includes a 25-50 cm radius about the hole. Very early in the nesting season, a radius of 10 m around the nest site may be defended. Prior to egg laying, defence of the nesting cavity is intense, with many battles occurring. These may be severe, even resulting in the death of a combatant. Early in the breeding season, it may oust Northern Flickers and Eastern Bluebirds from their nesting cavities and even kill them. Once territorial boundaries are settled, aggression declines. Nest boxes with 10 compartments were never occupied by more than 1 pair, suggesting territoriality. Nonetheless, starlings may nest close to each other, with 30 pairs reported nesting in a church steeple, as many as 9 nests in a single silver maple tree, and 5 in a willow tree. Away from the nest cavity, starlings are very gregarious. Males may share singing perches distant from the nest, feeding areas are undefended, and it spends most of its time within flocks or at communal roosts (Bent 1950; Chapman 1925; Feare 1984; Gutzwiller and Anderson 1986b; Kessel 1957; Peck and James 1987; Suthers 1978).

The starling maintains a small home range immediately prior to nesting through incubation, but expands it during the nestling period. Early in the nesting period, the male remains within 100 m of the nest, decreasing to less than 60 m during laying and only 30 m during incubation. The female usually starts with a home-range radius of more than 100 m. Although the female's range contracts somewhat, it continues to remain larger than that of the male (Dunnet 1955; Fischl and Caccamise 1985; Kessel 1957).

Of 1,111 nestlings at Ithaca, New York, 33 (3.0%) returned: 21 at Ithaca (1.9% of the number banded) and 10 more than 32 km away. A few returned to the natal area to breed, but most did not. Birds have been found breeding 320-400 km from their natal site. In New Jersey, 10 of 78 young (12.8%) returned to the natal area. An analysis of banding recoveries in the Great Lakes region revealed that 30% of hatching-year birds were recovered in subsequent breeding seasons more than 50 km from their natal site and about 12% dispersed more than 200 km. Most remained within 130 km of the nest site until November when migration began. The mean recovery distance for hatching-year birds was 80 km, significantly more than for adult birds (Cabe 2020; Dolbeer 1982; Dunnet 1955; Kessel 1953a; Suthers 1978).

Once an adult breeds, it tends to remain in the same general area to breed for the remainder of its life. In New York, 22 of 68 females (32.4%) nested in the same nest box in consecutive years. Sixty-three (92.6%) moved less than 0.8 km from their previous nest site; only 5 (7.4%) moved more than 0.8 km (range 1.6-4.0 km). One female used the same box in 4 consecutive years and another did so for 3 years. Another female shifted her nesting site about 0.5 km between each of 4 consecutive nesting seasons. Approximately half the breeding females of 1 season returned the next year. The annual mortality rate is approximately 50%, so it is likely that all living females returned. In New Jersey, 0 of 558 adult birds banded outside a town moved into the town to breed. In a breeding colony isolated 3 km from the nearest breeding starlings, 60-70% of the breeding adults in any given year were immigrants. Banding recoveries of adults in the Great Lakes area demonstrated that the mean distance between banding and recovery sites was 15 km for males and 10 km for females. This indicated that adults usually return to near their previous nesting site (Cabe 2020; Dolbeer 1982; Kessel 1953a, 1957; Suthers 1978).

Limiting Factors

Eggs have been found in Ontario nests from the second week of March until mid-July, with most present in the last 3 weeks of May (Peck and James 1987). In Algonquin Park, eggs occur from mid- to late May, nestlings are present from late May to late June, and dependent fledglings have been observed from mid-June to late July (Tozer 2012). Lougheed and Graham (1985) found a nest at Long Point that contained young on 10 March and estimated an egg date of 24 February.

Resident males begin prospecting for nest cavities in August of the previous breeding season and may roost in them over winter to defend the cavity. In February, both sexes, but particularly males, start visiting cavities to inspect them (Kessel 1957; Stewart 1976). The male identifies a number of suitable nesting sites, but the female ultimately selects the one that is used for nesting. The first nest of the season is built very leisurely. In New York, nest building begins during the third week of March but egg laying does not begin until mid-April. Nest building begins in earnest about a week before egg laying commences. Many nests are built within 2-3 days of egg laying and a nest

can be built in a day. One female built a nest in a mail box and laid an egg in it every day, the previous day's nest and egg having been removed (Cabe 2020; Clark and Mason 1985; Kessel 1957; Soulliere and Rusch 1996; Twedt and Oddo 1984). Egg laying may not be initiated for a few weeks after the nest is complete, but mostly soon after nest completion. Within a given area, egg laying for the first brood is highly synchronized, with all females initiating egg laying within a 3-4 day period. Temperature appears to be the primary factor determining when egg laying starts. In Guelph, egg laying started with a minimum of 11 days (range 11-16 days) of mean temperatures of 4.4ºC or higher. In New York, laying did not begin until mean temperatures had been above 4.4ºC for at least 17 days and remained above this temperature consistently for at least 12 days. In Kentucky, egg laying started after 12-20 consecutive days with a mean daily temperature higher than 4.5ºC. In British Columbia, the onset of egg laying was positively correlated with long-term temperatures between January and March. Photoperiod affects gonadal development and egg laying does not start in the north until there are 13 or more hours of daylight. Because temperature is a key factor in determining timing of egg laying, there is considerable annual variation. At Ithaca, dates of first eggs differed by as much as 19 days over 7 years (Collins and de Vos 1966; Dunnet 1955; Erskine and McLaren 1976; Feare 1984; Källander and Karlson 1993; Kessel 1957; Twedt and Oddo 1984). One egg is laid a day; rarely a day is missed. Females laying 5-egg clutches incubated 11.2% of the time on day 1 and began continuous incubation on day 3; those laying 4-egg clutches incubated 27.6% of the time on the first day and continuously on the third day (Kessel 1957; Meijer 1990, 1993; Romagnano et al. 1990; Stouffer and Power 1990; Wright and Cuthill 1992). The incubation period is typically 12-13 days. More variable incubation periods of 10-15 days have been reported in Ontario, with most eggs hatching in 11-13 days. Incubation periods of 10-13 days have been reported in British Columbia. Because of the variable onset of incubation, hatching may be asynchronous, especially in larger clutches, and may take place over 2 days. Often the last-born nestling dies of starvation; the brood size frequently averages 1 less than clutch size. Nestlings typically leave the nest when they are 21 days old, but some remain in the nest another day or 2 after the first young fledge. The range of ages when young may leave the nest is 19-25 days (Brown 1951; Cabe 2020; Campbell et al. 1997; Dunnet 1955; Kalmbach and Gabrielson 1921; Kessel 1957; Meijer 1990; Peck and James 1987; Ricklefs and Smeraski 1983; Stouffer and Power 1990). In British Columbia, a complete nesting cycle from lining of the nest to fledging took 41 days (Erskine and McLaren 1976). Adults that attempt to raise a second brood may start bringing new nesting material to the old nest as soon as a day after the first brood has fledged. First eggs of the second brood have been laid 1-2 days after the first young leave the nest, but 6-10 days is more typical. Egg laying for the second brood is not as synchronized as that for the first brood; 37-50 days may elapse between the laying of the first egg in the first and second clutches. Over 3 years, the intervals between the first egg in the first and second clutches were 46, 44, and 42 days at Guelph (Brown 1951; Collins and de Vos 1966; Dunnet 1955; Kessel 1953b, 1957; Stouffer 1991; Twedt and Oddo 1984; Yom-tov et al. 1974).

Double broods have not been reported north of latitude 48ºN, but are typical further south. To successfully rear 2 broods, a female must initiate nesting early during the first synchronized egg-laying period. The incidence of double clutches ranges from 0% to 70% of females in a given population, but 60-93% of females that successfully raise a first brood attempt a second; a rate of 92% was reported from Guelph. The percentage of females raising second broods varies annually in

a given area depending upon how soon suitable temperatures for initiation of egg laying occurs, weather (with few or no double broods during droughts), and food availability. In British Columbia, 38% of females attempted a second brood; 20% successfully reared a second brood. It has been suggested that 3 broods may occasionally occur, but the breeding season is generally too short to raise a third brood and females appear to be physically incapable of doing so. Renesting is common if a clutch is lost, usually within 2 weeks. The occurrence of second broods produces a bimodal egg-date curve. The late peak is a combination of birds that are raising their second brood and those nesting for the first time in the season. A small proportion of clutches are laid between the 2 main peaks, termed intermediate clutches. These are a combination of replacement clutches, clutches of additional broods of polygynous males, and late first clutches (Brackbill 1949; Cabe 2020; Campbell et al. 1997; Collins and de Vos 1966; Cornell and Williams 2016; Dunnet 1955; Erskine and McLaren 1976; Kalmbach and Gabrielson 1921; Kessel 1953b, 1957; Peck and James 1987; Pinxten et al. 1990, 1991a; Stouffer 1991; Twedt and Oddo 1984). Clutches of 2-10 eggs have been reported in Ontario with most containing 4 or 5 eggs; 1 nest contained 9 young (Peck and James 1987). At Guelph, first clutches averaged 5.6 eggs and second clutches averaged 5.0 eggs. Sixty-five percent of females laid smaller second clutches, 22% laid clutches of the same size, and 13% laid larger second clutches. Intermediate clutches averaged 5.2 eggs. The modal clutch size was 6 for first clutches and 5 for second clutches. First clutches of adults were larger (5.6 eggs) than those of yearlings (5.1 eggs), but there was no difference in size of second clutches (5.0 for adults and 5.1 for yearlings). The mean clutch size in Ontario is 5.10 compared with 5.15 eggs in eastern North America (Collins and deVos 1966). Overall, the typical clutch size is 3-6 eggs but clutches of 7 and 8 occur regularly, with overall clutch sizes of 1-11 eggs reported. In New York, 6 was the modal clutch size for first clutches with 5 eggs the second-most frequent; 4 eggs was the modal size for second clutches with 3 eggs a close second. Average clutch size of yearlings was 5.1 eggs compared with 5.6 eggs for adults. Clutch size typically declines with the season, but second clutches that are larger than first clutches occasionally occur. Six appears to be the optimum clutch size, with clutches of this size producing the most fledglings. Larger clutches produce fewer young due to problems incubating larger clutches or feeding more young. Increased brood size reduces the probability that the youngest chick will survive, with brood mortality higher in broods of 6 or 7 than in broods of 5. In New Jersey, mortality of nestlings from last-laid eggs accounted for 55% of all brood reduction. Mortality of these nestlings increased from less than 27% in broods of 3 and 4 to more than 75% in broods of 5 and 6 (Bent 1950; Cabe 2020; Dunnet 1955; Erskine and McLaren 1976; Kalmbach and Gabrielson 1921; Kessel 1957; Meijer 1990; Power et al. 1989; Stouffer 1991; Stouffer and Power 1990, 1991a; Twedt and Oddo 1984; Wright and Cuthill 1992; Yom-tov et al. 1974).

At least some birds breed in their first year, but more females than males breed as yearlings. Some first-year males are not physiologically capable of breeding. At Guelph, 13% of 295 breeding females were yearlings. The sex ratio is male biased, which may make it difficult for yearling males to defend a nest cavity and attract a mate. The proportion of yearling females breeding varies annually with the highest reported rate of 66% occurring in colonies that were newly created by installing nest boxes. Competition with older birds may be an important determinant of the number of yearlings that breed. At Guelph, 8 of 20 yearling females (40%) attempted second broods and 5 were successful. Populations typically contain large numbers of nonbreeding yearling males, but

also nonbreeding yearling females and adults of both sexes. This is due to a scarcity of suitable nest cavities (Cabe 2020; Clobert et al. 1987; Collins and de Vos 1996; Dunnet 1955; Kessel 1953b, 1957; Pinxten et al. 1990; Sandell and Smith 1997; Stewart 1976).

The mating system is predominantly monogamous, with the male assisting in incubation and care of the young. Polygyny occurs either irregularly or regularly. Most cases of polygyny were in populations nesting in boxes where nest sites were common. Males may defend as many as 10 nest boxes, usually within 50 m of the nest of the primary female. Males attempt to attract additional females while the primary female is in the nest-building or egg-laying phases. Some males have as many as 5 female mates. They may continue to attract new mates through the incubation and nestling phases. Although most polygyny occurs sequentially, it occasionally occurs simultaneously. Cases of 2 females mated to the same male nesting in the same box and sharing incubation and rearing duties have occurred even though there were adjacent unoccupied boxes. Males assist the primary female the most in raising young and may not help subsequent mates. In an attempt to avoid males becoming polygynous, females are aggressive toward other females and solicit copulations more frequently while the male is singing at other cavities. Mates may or may not be retained throughout the breeding season. Pairs rarely remain mated for more than 1 season. If a female loses her mate, she is capable of raising the brood on her own. If she is successful in remating, the new male may remove the existing eggs and start his own clutch with the female. Males that lose their mates usually abandon the nest. Because males do not incubate or brood at night, they are incapable of successfully hatching eggs and unlikely to fledge young, although some males successfully raised broods during periods of warm nights. If the male attracts a new female to the same nesting cavity, existing eggs are destroyed or buried by new nest material (Eens and Pinxten 1995a, 1995b; Feare 1984; Kessel 1950, 1957; Pinxten and Eens 1994; Pinxten et al. 1989a, 1989b, 1994; Sandell and Smith 1997; Smith et al. 1996; Stouffer et al. 1988; Wright and Cuthill 1992). Extra-pair copulations are rare, with 2.1-8.7% of young in New Jersey and Sweden populations not being related to their behavioural father. All occurred in second clutches, which are not as closely attended by males as first clutches. Males attempt to avoid cuckoldry by closely guarding their female during their fertile period, from 4 days prior to laying until the second day of the laying period (Hoffenberg et al. 1988; Pinxten and Eens 1997; Pinxten et al. 1987; Power et al. 1981; Smith and von Schantz 1993).

Intraspecific nest parasitism occurs. Males guard their females away from the nest, leaving the nest vulnerable to intraspecific brood parasitism. Most parasitic females are those that have lost a nest or did not originally have a nest. Many parasitic females subsequently lay and care for a clutch of their own. Parasitic eggs laid before the host has started laying are ejected, but those laid during the host's laying period are accepted. Some parasitic females may remove one of the host's eggs. Most parasitism occurs in first clutches although a few intermediate clutches may be parasitized; parasitism of late clutches is rare. Starting incubation with the laying of the third egg reduces the effectiveness of parasitism. Parasitic eggs laid once incubation starts may hatch late with the young having no chance of fledging. Parasitism increases clutch size but does not increase the number of fledglings produced. The number of young fledged may be lower than that of unparasitized nests. This occurs when parasitism results in the creation of a superclutch that the adults are unable to

care for adequately. Some females lay smaller clutches than the optimum size to account for parasitic eggs. In New Jersey, parasitism caused a 16% reduction in the number of host fledglings but did not reduce the number of nests that produced at least 1 host fledgling, suggesting that parasitism costs were minor. The rate of nest parasitism ranges from 0 to 46% in different populations. The rate does not appear to be related to the proportion of nest sites that are occupied unless they are all occupied (Cabe 2020; Hoffenberg et al. 1988; Kessel 1957; Lombardo et al. 1989a; Pinxten et al. 1991a, 1991b; Power et al. 1989; Romagnano et al. 1990; Stouffer and Power 1991b; Stouffer et al. 1987; Yom-tov et al. 1974).

When feeding nestlings, the adults of a pair may fly to different feeding areas. Feeding areas may be adjacent to the nesting areas or as far as 1.6 km away. Usually the same flight paths are used daily. Areas of apparently suitable habitat may be flown over to reach the preferred feeding area. During the breeding season, birds occasionally forage singly, but mostly in small flocks. In autumn and winter, flocks forage in lines as a unit across fields by leap-frogging or in circles or arcs that move outward radially. Preferred feeding sites are areas with short grass, particularly lawns, grazed pastures, feedlots, and mown hayfields. It usually avoids tall grass. In Maryland, 60% of foraging was in vegetation 2.5 cm tall, 20% at 5 cm, 10% at 7.5 cm, and 7% in vegetation taller than 7.5 cm. In Oregon, numbers of foraging starlings decreased significantly once cattle-grazing was terminated. The increased shrub coverage degraded foraging habitat. In New Jersey, 95% of starlings foraged in 5 habitat types: urban-suburban, soybeans, corn, feedlots, and old fields. Highest numbers occurred in urban-suburban habitats. It obtains most of its food from the ground, typically by probing in the soil to a depth of 2.5 cm for invertebrates. During the breeding season, about 95% of food is obtained in this manner or by picking food from the ground. On rare occasions, it may open and close its wings very rapidly to startle insects. In the postbreeding season, the starling commonly hawks insects in the manner of a flycatcher. Less frequently, it may soar aerially at heights of 20-60 m to forage on flying insects. Some engaged in this activity were feeding on box elder bugs but most feed on flying ants. It associates with cattle, picking maggots from their dung. It may peck insects from the legs of cattle and ride on the backs and heads of cattle and deer, presumably feeding on insects. It may kleptoparasitize the American Robin by driving it away from earthworms that it has captured. In summer, it may feed on corn by puncturing the kernels, removing the milky contents and leaving the pericarps. In North Carolina and Virginia, it fed on larvae of corn earworms and fall armyworm moths without damaging the corn. It missed no ears containing larvae and opened no ears that were without larvae. It has captured monarch butterflies on the wing and eaten them. In Niagara vineyards, damage to grapes by starlings is greatest at the edges where they fly from adjacent overhead wires and trees a short distance to the top of the vines, remove a single grape, and return to the perch to eat it. In vineyards, 22-30% of grapes at the edge were damaged compared with 5-20% 30 m from edge and 0.5-2.5% at 70 m. In the first 30 m, bunches of grapes near the top of vines sustained 3-4.5 times more damage than those at the bottom. In California, it regularly feeds on nectar of the coral tree (Bernhardt et al. 1987; Brackbill 1952b; Brooks 1952; Cayouette 1947; Dunnet 1955; Earnst et al. 2012; Feare 1984, 1993; Hailman 1959; Hodges 1950; Kalmbach and Gabrielson 1921; Murphy 1981; Somers 2010; P.A. Stewart 1973; Suthers 1978; Tucker 1950; Van Tyne 1946; Williamson and Gray 1975; Ziraldo 2010).

During the first few days, the adults bring the nestlings small caterpillars, grubs, and other insects, with larger insects brought as the young increase in size (Brown 1951; Kessel 1957). Kalmbach and Gabrielson (1921) examined the diet of 325 nestlings. The diet of young 1-5 days old consisted of 2.4% ground beetles, 3.9% June beetles, 5.6% weevils, 14.0% orthopterans, 45.3% caterpillars, 1.5% millipedes, 23.4% spiders, and 0.2% cherries and miscellaneous material. From 6 to 10 days of age, nestlings ate 11.6% ground beetles, 18.3% June beetles, 4.5% weevils, 11.2% orthopterans, 34.9% caterpillars, 5.3% millipedes, 3.6% spiders, and 3.4% cherries. Nestlings older than 10 days ate 7.7% ground beetles, 18.3% June beetles, 1.0% weevils, 9.0% orthopterans, 37.8% caterpillars, 6.4% millipedes, 3.3% spiders, and 4.8% cherries. As the young grow older, there is a decline in consumption of soft and easily digested foods. Most spiders (8.6% of the diet) are consumed in the first few days. The overall diet of nestlings consisted of 95.1% animal food, with the most prevalent food being caterpillars, along with a few moths and cocoons. These formed 38.2% of the diet, with a large proportion being cutworms. Beetles comprised 30.0% of the diet (almost half of which were June beetle larvae), and 11.3% was orthopterans (mostly crickets). No other insect orders comprised as much as 1% of the diet, with ants and stink bugs being most prevalent among these. Millipedes totalled 4.4% of the nestling diet compared with 33.0% for adults. Cultivated cherries (3.2% of food) were the only vegetable matter of importance. Lindsey (1939) reported that the diet of 139 nestlings in New York consisted of 95% animal matter and 5% vegetation. Beetles and their larvae formed 46.9% of nestlings' food with adult and larval June beetles comprising 27.0% of the food. Caterpillars comprised about 25% of the food of nestlings and these were dominated by cutworms. Orthopterans were important in the diet of nestlings, with a single species of cricket comprising 2.6% of the food. The predominant bugs eaten by both adults and nestlings were stink bugs and these occurred in the diet year-round.

Chapman (1925) considered the starling beneficial based on its diet. It is an effective destroyer of insect pests such as cutworms, grasshoppers, and weevils. Kalmbach and Gabrielson (1921) concurred and noted that its greatest damage was to cherries. Damage to peaches and pears was rare and they considered damage to grapes and corn trivial. In Ontario, Fleming (1927) concluded that the starling was economically beneficial but cautioned that it had the potential to do serious harm to fruit crops if it became abundant. Of 12 bird species that visit vineyards in Niagara Region, only the robin and starling are abundant enough to pose economic threats, and most damage to grapes is done by starlings (Somers 2010). The starling also has the potential to damage corn crops.

Three studies (Fleming 1927; Kalmbach and Gabrielson 1921; Lindsey 1939) collectively analyzed the contents of 3,214 adult stomachs. The diet consisted of 47.9-58.6% animal matter and 41.4-52.1% vegetable matter. Animal food was most important in April and May, constituting more than 90% of the diet. From spring through early autumn, animal food comprised a minimum of 50% of the diet, with lowest consumption from late autumn through winter. Beetles were the most important animal food (19.6-22.4% of food items), especially the clover leaf weevil which was the most abundant insect consumed. It also ate scarab, rove, click, ground, darkling, Colorado potato, lady, pill, clown, and leaf beetles. Short-horned grasshoppers and crickets were important and comprised 5.7-12.4% of the diet. They were particularly prevalent in the diet in August and September. Millipedes constituted 3.3-14.2% of the diet and were about half the items consumed

in April and May. Lepidopterans represented 3.2-6.0% of the annual diet. These were mostly caterpillars but some adults were eaten. Other insects eaten included hymenopterans (mostly ants), bugs (mostly stink bugs), and green bottle flies. Spiders represented 0.5-1.5% of the diet; snails represented 0.9% of the diet in 1 study. Miscellaneous animal foods included isopods and salamanders. The starling commonly eats seeds of ragweed and yellow foxtail. Mast and various grass and weed seeds are eaten in insignificant amounts. The predominant vegetable foods are fruits and items taken from human garbage. Garbage is important in winter and may constitute 35-50% of the diet. It includes coffee grounds, orange seeds, beans, and parings of various vegetables and fruits. Wild fruits confirmed in the diet include mulberries, juneberries, blackberries, elderberries, chokecherry, black cherry, black gum, Virginia creeper, bayberry, staghorn sumac, poison ivy, roses, dogwoods, apples, viburnums, and buckthorns. Corn and other grains were unimportant in the diet and were considered to be waste. In Quebec, vegetation comprised less than 0.1% of the volume of the diet 10-19 May (all barley), 10.6% 14-29 July (4.8% cherries, 2.4% vetch, 1.9% grasses, 0.8% water parsnip, 0.7% field bindweed, 0.1% barley), and 9.3% 12 August to 16 September (3.1% cherries, 4.1% barley, 1.3% oats, 0.8% bindweed, and less than 0.1% grasses). Animal food constituted 100% of the diet 10-19 May, 79% 14-29 July, and 89.3% 12 August to 16 September. From 10 to 19 May, the diet consisted of 17.2% millipedes, 75.9% beetles, and 6.9% ants; from 14 to 29 July, 43.3% beetles, 10.2% ants, 10.2% millipedes, 7.5% snails, 2.6% bristle flies, 2.6% owlet moths, and 2.6% plant bugs; and from 12 August to 16 September, 41.4% beetles, 15.9% orthopterans, 12.8% flies, 9.8% ants and wasps, 3.2% aphids, and 3.2% other bugs (Potvin et al. 1976). Other plant species in the diet in New Jersey included pokeweed, clover, and wheat. During development of roosts, the starling focused on a few insect groups. During the decline of roosts from mid-July onwards, the contribution of insects to the diet decreased and remained low through the decline. As roosting populations approached their maximum, it fed increasingly on plant material, including both natural and agricultural foods (Fischl and Caccamise 1987). It favoured hackberry fruits in autumn (Cabe 2020). In an Illinois woodlot, the fruit eaten 1 year was 20% grapes and 80% Virginia creeper and 77% grapes and 23% Virginia creeper the next year. All frugivory occurred in forest gaps rather than forest interior (Malmborg and Willson 1988). Captive birds strongly and consistently preferred the fruit of invasive species to those of native species. Autumn olive was preferred over winterberry holly and multiflora rose was preferred over Carolina rose. Only when choosing between glossy buckthorn and highbush blueberry did it select the native species and eat some of both choices. Of the nonnative fruits, the starling preferred autumn olive over multiflora rose or Asiatic bittersweet. The starling may be a factor in the spread of these and other nonnative plant species (La Fleur et al. 2007). In Algonquin Park, the autumn diet includes berries of mountain holly and winterberry holly (Tozer 2012).

The starling is a rare host of the Brown-headed Cowbird, with no cases of parasitism reported from Ontario. The cowbird egg was accepted in both cases in 2 nests that were experimentally parasitized. A 1973 observation of starlings feeding cowbird fledglings was only the third known incident of parasitism at that time. The rarity of parasitism may be because the starling is a cavity nester that aggressively defends its nest (Cabe 2020; Kessel 1957; Peck and James 1987; Thomas 1973).

Considerable competition takes place for nesting cavities. The starling is usually successful in ousting Tree Swallows, Carolina and Northern House wrens, bluebirds, and chickadees. House Sparrows may successfully defend their nest sites against the starling but often the starling is victorious. The starling may occasionally usurp nests of the Rock Pigeon, Purple Martin, and Great Crested Flycatcher. The most intense competition is between starlings and woodpeckers. The Northern Flicker is most affected by starlings who take over many of its cavities and may remove eggs or even kill adults. The Red-bellied Woodpecker nests at the same time and the starling is usually successful in usurping their nest cavities, although there are records of Red-bellied Woodpeckers killing and removing starling nestlings and taking over the cavity. The Red-headed Woodpecker nests later than the starling, so there are fewer conflicts between these species. Starlings may commit infanticide at other starlings' nests, presumably in an attempt to take over the nesting cavity (Baker and Payne 1993; Bent 1950; Erskine and McLaren 1976; Ingold 1989, 1994; Kalmbach and Gabrielson 1921; Romagnano et al. 1986; Stauffer and Best 1982; Stewart 1976).

The starling is experiencing habitat loss, with fewer available nesting cavities and a decline in the amount of suitable habitat. Nest boxes erected for bluebirds, wrens, and swallows are now designed so that the cavity entrance is too small to allow access to starlings. The number of farm buildings and silos is declining and wooden structures are being replaced with steel buildings that preclude entry and offer no external cavities. Old buildings in cities that had ornate cornices and ledges are either being refurbished or replaced with modern buildings. Most modern buildings have aluminum soffit and fascia with no cavities. Orchards are now well maintained with no decadent trees with cavities. Although urban sprawl creates more lawns for foraging, new subdivisions have no trees with cavities in them and the houses also are cavity-free. Most agricultural land is in row-crop production with considerably less area in pasture and hay. Most hay crops are dominated by alfalfa which grows quickly after cutting and therefore is suitable for foraging for only short periods.

Starling nestlings exposed to an organophosphate representative of a direct cholinesterase inhibitor had a significantly lower probability of survival than control birds. A total of 18.5% of treated nestlings died within 48 hours. The response was reversible in those that survived and did not extend into the fledgling stage (Stromborg et al. 1988). In an area with high selenium levels in California, there was no significant effect on hatching success or the embryos, with no abnormalities or defects detected (Santolo 2007). Parathion initially causes intoxication and death at higher doses (Rattner and Grue 1990).

The starling is much maligned because it roosts and flocks in large numbers. It and several species of blackbirds are treated at roosts in the United States in efforts to reduce numbers. A product called Tergitol was used 1974-92 but is no longer registered for use. It was an industrial detergent that made the birds' feathers pervious to water, robbing them of their insulating qualities. Treated birds subsequently died of hypothermia. Now, a nonpersistent organochlorine pesticide is used that shuts down birds' liver and kidney functions. Several million blackbirds and starlings are killed annually in the south and Midwest (McCracken 2003b).

Weather conditions can greatly affect productivity during the breeding season. Cold and wet weather may contribute to mortality of nestlings as may high temperatures in the nest cavity. Precipitation is an important reproductive variable because starlings feed by probing their beaks

into the soil. Dry years result in lower productivity because dry soil is harder to probe (Cabe 2020). In Texas, a thunderstorm with a downfall of large hail resulted in an estimated mortality rate of 26% (Hall and Harvey 2007). In Illinois, approximately 4% of birds died following a heavy rainfall with high wind and temperatures dropping suddenly below freezing (Bent 1950).

In the Midwest, the starling occurred in very low density when fire frequency was low, but increased substantially when the frequency of fires every 15 years rose from 4 to 7.3, the maximum recorded. Fires create snags and inhibit woody growth, enhancing conditions for foraging (Grundel and Pavlovic 2007b).

In Georgia, there was no difference in the number of fledglings produced by starlings nesting in rural and urban habitats (Guindre-Parker et al. 2025).

Status

The starling was introduced to North America from Europe. The current North American population originated from a release of 100 birds in New York's Central Park in 1890 and 1891. Its range spread north, east, and south from New York City and within 20 years it was known from Maine to Virginia. By the 1920s, millions were present. By 1952, it was found throughout southern Canada, the entire United States except southern Florida, and northeastern Mexico. It may still be slowly expanding and increasing along the southern edges of its range. Typical of a species expanding into new territory, it initially increased its population exponentially and then experienced a decline in numbers. Populations started to level off in New York, Ohio, and Massachusetts as early as the 1930s. In the east, the population declined by an estimated 75% from 1932 to 1942 (Bent 1950; Cabe 2020; Chapman 1925; Cotter et al. in Gauthier and Aubry 1996; Davis 1960b; Kalmbach and Gabrielson 1921; Kessel 1953a).

The first Ontario starling record was a flock of 4 or 5 seen in Niagara Falls in autumn 1914. In 1919, several were seen near Brockville, including some recently fledged young, but it was uncertain if the birds had nested in Ontario or across the St. Lawrence River in New York. The next record was in the winter of 1919-20 when a small flock was observed in St. Catharines. The first breeding record was in 1920 near Beamsville and nests were confirmed in Burlington in 1922 and Guelph in 1924. By 1922, it had reached Kingston, Toronto, Hamilton, and Chatham and the following year it appeared in Kitchener, London, and on the outskirts of Toronto. Nesting was confirmed in Toronto in 1926 and the population burgeoned there after birds started to remain year-round during the winter of 1929-30. It was first seen in Kingston in 1921 with confirmed breeding in 1926. The range of the starling was continuous across southern Ontario by 1925; by 1926, there were records from 75 locations and 32 counties. It reached Orillia in 1925, Muskoka in 1926, North Bay in 1927, and Port Sydney in 1926 and was well established in Muskoka and Parry Sound districts by the mid-1930s. Even shortly after its appearance, the starling was abundant. In autumn 1929, a flock of 5,000 was seen in Toronto and 3,000 were seen in London; 10,000 were seen in Brantford in the spring of 1930 (Baillie and Harrington 1937; Cramner-Byng 1990; Curry 2006; Fleming 1927; Mills 1981; Putman 1947; Saunders 1930b; Sheppard et al. 1936; Snyder and Baillie 1930; Weir 2008). Baillie and Harrington (1937) stated that it had become one of the most common birds in Ontario. At that time, it nested in suitable locations everywhere throughout southern Ontario north to at least Thunder Bay and Sudbury districts. It had been found as far north as Kapuskasing, Moose Factory, and York

Factory on Hudson Bay. In 1964, starlings were observed at radar site 415 near Cape Henrietta Maria and breeding appeared to have taken place (Peck 1972). Birds were first reported at Winisk in 1965 and the first nest was found there in 1967 (Lumsden 1980).

During the first atlas, the range of the starling covered the entire province, but with large gaps in distribution in the heavily forested Boreal Forest Region, the Hudson Bay Lowland, and the Algonquin Highlands. Presence in these areas was associated with towns or areas where there were buildings or other structures (Bowman in Cadman et al. 1987). James (1991) considered the starling an abundant permanent resident in the south, becoming a rare and local summer resident north to Winisk and Cape Henrietta Maria. Wilson and McRae (1993) noted that the starling was a common breeder in Moosonee.

The second atlas revealed that there had been no change in the breeding distribution of the starling, where it remained associated with human settlement and agricultural land. There was no change in its probability of observation province-wide, but there was a significant decline in the southern Canadian Shield, probably due to natural succession. Highest densities occurred in southwestern agricultural areas and in larger urban areas such as the Greater Toronto Area, Kingston, and Ottawa. Breeding Bird Survey (BBS) data demonstrated that Ontario south of the Shield and much of the United States Midwest, Pennsylvania, and New York have the highest starling densities on the continent (Cadman in Cadman et al. 2007).

Human alteration of natural habitats benefitted the starling and it quickly settled into agricultural and urban areas. It had a history of reaching its peak abundance in the third or fourth decade after its appearance, followed by a decline. Declines are continuing in much of its range due to modernization of buildings, less agricultural land in pasture and hay, and natural succession. Despite these declines, the starling continues to be an abundant breeding species in Ontario (Cabe 2020; Campbell et al. 1997; Cotter et al. in Gauthier and Aubry 1996; McCracken 2003b). BBS data indicate that the starling decreased at an annual rate of 2.28% in Canada and 2.31% in Ontario from 1970 to 2021. The trends 2011-21 were annual decreases of 0.947% in Canada and 3.36% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings are capable of strong flight as soon as they leave the nest. After leaving the nest, they usually go to a perch 20-30 m from the nest and remain together, with the adults tending them for 3-4 days or even less if they are starting a second brood. Fledglings are capable of foraging by themselves at this time and become independent, joining postbreeding flocks. Many Ithaca fledglings remained within 32 km of their natal site but others wandered considerably. Fledglings were documented wandering 247 km and 320-547 km. Some remained as residents in the area that they wandered to; others migrated south (Cabe 2020).

Flocks form shortly after breeding and flocking is an important behaviour year-round. Fledglings may form flocks as soon as 4 days after leaving the nest. Flocks of juveniles tend to remain discrete from those of adults during the postbreeding period, although juveniles may occasionally return to the natal area to forage or visit the feeding areas of adults feeding late broods. Flocks of juveniles tend to occur in different habitats than those of adults. Juveniles move out of urban-suburban areas

into rural areas to sites where they are more proficient at capturing prey. They occur mostly in unmanaged grassland where vegetation is taller, such as pastures and meadows, and in soybean and wheat fields. The use of soybean fields and grasslands by juveniles in New Jersey was significantly correlated with insect density. Foraging areas used by juveniles were relatively poor compared with those used by adults, but usage of these areas may reduce competition with adults and juveniles may be more adept at capturing insects in longer grass and obtaining waste grain than probing for insects in short grass. Flocks of adults were most common on lawns and at feeders and sources of garbage. The aggressiveness of adults prevented juveniles from accessing the latter 2 food sources. Adults continued to feed on soil invertebrates throughout the summer in managed grasslands. Starlings exhibit fidelity to the same daily foraging areas, which may be 2-4 km². Individuals return to the same area each day over periods of weeks or even months or the entire year for resident birds. Although birds may change their roosting areas, most remain faithful to their feeding area. A few birds change daily foraging areas, and changes may be associated with a change in roosts. In New Jersey, only 5 of 63 adults (7.9%) switched foraging areas over a 5-month period. In 2 areas in New Jersey, home ranges around individuals' feeding sites averaged 33 and 49 km². Home ranges around all sites (including roosts) in these same areas were 30 and 525 km² from June to November. Of 15 adults, 13 commuted to the same foraging areas from 1-5 different roosts over 3-4 months. The distance to the roost increases in late summer and autumn to 4-12 km from about 2 km most of the remainder of the year; commutes as far as 38-50 km have been documented (Caccamise 1991; Dunnet 1955; Fischl and Caccamise 1985, 1987; Henty 1989; Kalmbach and Gabrielson 1921; Kessel 1975; Maccarone 1987a; Morrison and Caccamise 1985, 1990; Suthers 1978; Yapp 1989).

Roosts are important to the starling year-round. During the nesting period, males and females may roost alone in nest cavities or pairs may roost together. Of 50 pairs of birds found roosting together in New York, 49 were of a male and a female and one was of 2 males. Unmated males may roost in nest cavities and defend them from other species. Almost immediately after fledging, young form communal postbreeding roosts and these may be used by adults as well. Early roosts are small and numerous, but as the season progresses, roosts coalesce into fewer but larger roosts. Mid-June roosts tend to be near the daily foraging areas and consist of 500 or fewer birds. By mid- to late August, birds travel further to larger roosts that may support more than 100,000 birds. These roosts are occupied until mid-November when birds either migrate or switch to winter roosts. Large premigratory roosts are usually near a rich food supply, such as a large grain field. Birds feed as they make the commute to and from their daily foraging areas. The starling may roost in a variety of habitats during the postbreeding season and may do damage when roosts are in warehouses, airplane hangars, electrical substations, on bridges, on ledges of buildings, or in coniferous trees. Most roosts are in deciduous trees along highways, in parks, and particularly in residential areas. It prefers densely leaved trees such as Norway maples and sycamores. In summer, it selects areas where trees grow close together, are heavily leaved, and form a dense canopy. Where trees in such areas have been trimmed or topped, roosting starlings have been eliminated entirely. From August to December, 50,000 roosted in Niagara Region in an area of open water and common reed. The Hamilton Skyway Bridge is another traditional roost, with a high count of 70,000 on 3 November. In Presqu'ile, the maximum summer roost was 3,600 on 21 July. This was likely one of the smaller early

season roosts before roosts become scarcer and larger. The primary function of large roosts appears to be their proximity to a rich feeding area along with sources of food between them and the daily feeding areas. Communal roosting may also decrease the incidence of predation. Starlings follow the same established route each morning and evening. Routes are not in a straight line, avoiding crossing even the smallest of hills and often following a watercourse or valley. In Pennsylvania, there were 3 periods of communal roosts prior to winter: an early summer roost in cattails mixed with shrubby growth from mid-May to mid-June; summer roosts in residential areas from mid-June to September; and the autumn roost from late September through October. Individuals may switch roosts 1-5 times during the postbreeding period while maintaining the same feeding area. In New Jersey, all 36 birds that switched roosts moved more than 2 km from the previous night's roost. Although individual roosts may be used for only 2-4 months of the year, the same sites seem to be selected each year, especially for the larger premigratory roosts. Long-term roosts tend to be in sites that the birds cannot destroy, such as cliffs, or that will regenerate each year. Starling roosts are frequently occupied by other bird species. The most common species sharing starling roosts are the Common Grackle, Red-winged Blackbird, and Brown-headed Cowbird although the American Robin may also be common at times. Other species that occur less frequently are House Sparrow, Rusty Blackbird, and swallows (Bent 1950; Black and Roy 2010; Caccamise 1991; Campbell et al. 1997; Curry 2006; Feare 1984; Fischl and Caccamise 1987; Jumber 1956; Kalmbach and Gabrielson 1921; Kessel 1957; LaForest 1993; Morrison and Caccamise 1985, 1990; Suthers 1978; Weatherhead et al. 1980).

MIGRATION

Some members of each sex and age class may migrate, but most starlings south of latitude 40ºN are permanent residents. Many juveniles wander great distances south of their natal area during the summer and winter. Those that do not breed until their second year may behave much like first-year birds in their wanderings and migration. Migration strategies are irregular, with some individuals migrating some years and not in others. Some nestlings from a nest may migrate; others from the same nest may not migrate. Siblings that migrate may winter far apart. Two Michigan nest mates wintered in Wisconsin and Missouri. As of the early 1950s, 22% of recoveries of birds banded in Ontario were out of the province. Birds banded in Tennessee, Arkansas, and Louisiana migrate northeast and enter southern Ontario from southeastern Michigan. Some birds banded in New York and Washington DC enter Ontario east of Lake Ontario; some Missouri birds have been found in Leeds County. Many follow the southern shores of Lake Erie and Lake Ontario to the St. Lawrence River to Ottawa and Montreal. Birds travel along the northern shores of these lakes in autumn. The extension of the breeding range of the starling was largely due to the migrations and wanderings of yearlings and nonbreeding birds. The more migratory populations of starlings occur in the central and south Midwestern states rather than the Great Lakes region, the northeast, and the Atlantic seaboard. The starling also may be more migratory at the edge of its range (Kessel 1953a). Burtt and Giltz (1977) prepared a vector diagram for all North American recoveries of the starling. Birds from southwestern and central Ontario travelled in a south-southwest to north-northeast direction. Those from north of Lake Superior travelled southwest to west-southwest. Sixty-five percent of birds moved southward in autumn. Dolbeer (1982) summarized banding results from the Great Lakes area. Maximum distances from the nesting area occurred in January (534 km) and February (375 km). Hatch-year birds migrated an average of 249 km further than adults. The mean dispersal distance

from southwestern Ontario was 289 km with recoveries in Ohio, Illinois, Kentucky, and Arkansas. Ontario birds winter primarily in the province and Great Lakes states, but others move to the mid-Atlantic states and as far south as the Gulf Coast (Brewer et al. 2018).

Most migration occurs during the day. Starlings are highly social during migration and migrate in flocks that may number from several birds to 100,000. Flocks routinely fly at heights in excess of 1,000 m, but may fly much lower in high winds or head winds. When flying lower, the starling frequently uses river valleys, lake plains, and coastal plains as flyways. Adults tend to migrate to a specific area; juveniles apparently migrate in a specific direction without reference to any particular area. Juveniles appear to migrate for some specified time after which they depend on external cues to locate suitable winter habitat and cease migration (Cabe 2020; Kessel 1953a).

Spring migration is from mid-February to early April. At Guelph, some starlings arrived in late February but the major influx was in mid-March. In the St. Lawrence valley of eastern Ontario, some arrived in March but most did not appear until April. The peak of arrival at North Bay is in early April. Males may migrate earlier in spring than females (Collins and de Vos 1966; Curry 2006; Kessel 1953a, 1957; Mills 1981; Weatherhead et al. 1980). Autumn migration may extend from late September throughout October and into November; the peak is in August in North Bay. In Parry Sound and Muskoka districts, most birds congregate in flocks in August, and these remain intact into October. The autumn peak at Presqu'ile is in October. At Hawk Cliff in Elgin County, thousands fly westward daily along the Lake Erie shore in October and early November (Kessel 1953a; LaForest 1993; Lancaster et al. 2004; Mills 1981).

During spring migration in New Jersey, feedlots and agricultural crops were the habitats most preferred by the starling, but it also showed some preference for pastures and urban-suburban areas. Near Saskatoon, spring migrants congregate in stubble fields and pastures to feed on waste grain and insects. It begins to organize roosts early in March when spring migrants arrive and maximum numbers occur in late March when migration is almost complete. Spring roosts break up in early May with a shift to several smaller roosts coincident with the start of the breeding season (Fischl and Caccamise 1985; Jumber 1956; Leighton et al. 2002). During autumn migration, birds move to fields of swathed grain or stubble and large flocks may occur in corn fields (Fischl and Caccamise 1985; Leighton et al. 2002).

The starling is an abundant migrant in Ontario with higher numbers in autumn than in spring. In the Kingston area, spring flocks typically contain a maximum of 1,000 birds but 5,000-10,000 may occur in autumn. At Presqu'ile, the highest spring count was 1,000; high autumn counts were 1,000 and 2,300 (LaForest 1993; Weir 2008).

WINTER

During winter in Ontario, the starling is found almost exclusively in towns and urban areas. In rural areas, it is restricted to areas with abundant sources of food such as feedlots and landfill sites; it occasionally occurs at feeders. When the ground is snow-free, it may still inhabit agricultural fields. Smith (2003) summarized its winter habitat in southern Ontario based upon results from Winter Bird-Population Studies. Densities per km^2 were 81.9 in cities, 63.8 in urban natural areas smaller than 10 ha, 38.7 in larger urban natural areas, 1.0 in mixed rural (forest, old field, and agriculture), and 0 in

farmland and forest. Densities in cities were significantly higher than in other habitats. In Muskoka and Parry Sound districts, only the largest towns support starlings year-round (Mills 1981). In British Columbia, wintering birds forage in cultivated areas, parks, gardens, vegetated playgrounds, fallow fields, airports, cattle yards, orchards, berry plantations, landfills, sewage lagoons, poultry runs, and natural areas (Campbell et al. 1997). In Illinois, it was most consistently observed in small grain stubble but high densities also occurred in fallow fields and all types of shrubbery (Graber and Graber 1963). In New Jersey rural areas, it preferred feedlots and agricultural crops in winter, especially corn and soybeans (Fischl and Caccamise 1985).

Roosts continue to be important in winter. The starling may roost in large aggregations or individually or in small numbers in cavities that may be potential nest sites. In Ontario, communal roosts have been documented in a pine plantation in Kingsville, in a cedar swamp in Guelph, and at a St. Catharines apartment complex (Bent 1950; Black and Roy 2010; Curry 2006). In October or November, it abandons deciduous tree roosts and moves to church towers, barns, or other buildings and remains in these areas until the breeding season. Other areas that may be used for communal winter roosts include ledges of city buildings, metal cross-members of bridges, airplane hangars, warehouses, electrical substations, groves of coniferous trees, common reed growths, and thick matted grasses on the ground. In cities where good roost sites are lacking or overcrowded, it may roost in bare deciduous trees well protected by buildings (Campbell et al. 1997; Jumber 1956; Kalmbach and Gabrielson 1921; Whitehead et al. 1995; Yom-tov et al. 1977). Communal roost sites are selected for their warmer microclimate. In Ohio, roosts were established throughout a pine forest in early December. By mid-December, areas along the periphery of the woods had been abandoned in favour of centrally located roosts. Within areas that were used for roosting throughout the winter, the wind velocity was almost always zero. Birds rarely roosted at heights above 3.7 m. Temperatures from the ground to 3.7 m were fairly uniform and consistently higher than at heights of 4.9 and 6.1 m (Kelty and Lustick 1977; Yom-tov et al. 1977). Dominant males occupy the centre of communal roosts where they are most protected from the weather and predators (Dunn and Tessaglia-Hymes 1989). In New Jersey, as many as 25 starlings roosted in an old silver maple along an urban street, with as many as 4 birds per cavity. Individuals tended to nest in the same cavities, with most retaining possession of the cavity until they died, the tree fell, or they were driven out by another starling (Suthers 1978). It may roost overnight in boxes designed specifically for them, and has been known to roost in Purple Martin houses (Stewart 1977) and American Kestrel nesting boxes (Davis et al. 2017). In December, some birds begin roosting in boxes instead of returning to the communal roosts. By mid-December, small numbers of both sexes may be found roosting in boxes. Many flock-roosting birds do not visit nest cavities in winter; others alternate between roosting in boxes and at a communal roost. During the 3 months of winter that roosting in boxes occurs, a bird may change its roosting site and switch partners several times. Birds may move their roosting sites 800 m or more, but are usually faithful to a localized area that decreases in size as spring approaches. Sometimes a bird will roost in the same box all winter but 1 bird was recovered 4.0 km away from the box it had roosted in 2 days previously. Use of cavities for winter roosting is part of the nest-site selection process for resident birds. A high proportion of birds that use nest boxes for winter roosting have previously nested in the general area (Kessel 1953a, 1957; Lombardo et al. 1989b).

In winter, the starling may select warm perches on cold days. It frequently uses chimneys as perches where it sits on the lee side to obtain maximum warmth. Chimneys may be abandoned if high wind or rain result in a greater heat loss than in more sheltered areas. It may also perch on light fixtures, incinerators, and manure piles (Brewer 1963b; Campbell et al. 1997; Leighton et al. 2002; Suthers 1978).

The winter diet of the starling varies depending upon whether there is snow on the ground. In New Jersey, grasses, soybean fields, and corn fields accounted for 35% of the study area and were used by 55% of foraging starlings when the ground was clear. Only 17% used these fields after snow coverage. The few flocks that fed in grassy areas during snow days were on the leeward side of buildings and hedgerows. It had a difficult time finding food once the ground was covered with snow. The most apparent change was a 2-fold increase in the proportion of flocks using human-generated foods from feedlots, dumpsters, and landfills. These areas may be defended by birds in winter (Maccarone 1987b). Hamilton (1949) compared the winter diet of the starling in New York when the ground was bare and snow-covered. The percent occurrence of food items when the ground was bare was 45% fruits and berries, 42% sumac, 7% garbage, 19% grains, 20% green vegetation, 18% insects, 4% millipedes, and 3% snails. Percent occurrences when the ground was snow-covered were 49% fruits and berries, 27% sumac, 19% garbage, 4% grains, 6% green vegetation, 1% insects, and 0% millipedes and snails. Fruits and berries that were consumed included sumac, viburnum, grape, Virginia creeper, poison ivy, hawthorn, and frozen apples; these were available regardless of snow depth. Garbage was also available during periods of deep snow. Most insects, grains, and green vegetation were less available when the ground was snow-covered. When snow was present, it was more dependent on fruits, especially those of staghorn sumac, bittersweet, grapes, and several viburnums, particularly nannyberry. In Saskatoon, it feeds on waste grain, garbage, crabapples, and mountain-ash berries in winter (Leighton et al. 2002). It may feed on waste grain in winter but cannot subsist on this diet and loses weight, even in captivity. It requires invertebrates in the diet to sustain itself (Feare and McGinnity 1986).

The starling is a widespread visitor to winter bird feeders. The number of feeders visited more than doubles from autumn to mid-winter and remains high. The number of birds present at a given time declines as winter progresses. Favourite foods are suet and bird puddings, but it readily eats mixed seeds, cracked corn, hulled peanuts and peanut hearts, pet food, peanut butter mixes, baked goods, and water. Infrequent choices include millet, canary seed, sunflowers, whole corn, milo, wheat, peanuts in the shell, fresh or dried fruit, meat scraps, sugar water, popped corn, and oats (Dunn and Tessaglia-Hymes 1999).

Cold weather may commonly kill roosting birds. Approximately 4.0% of birds at an Illinois roost died after an overnight storm. In 1927, about 500 dead starlings were found at a Massachusetts roost after a storm. At a Kentucky roost, 84% of starlings died after 2 nights when the temperature dropped to −17.2°C and −24.4°C. These birds were roosting in trees, but only 0.4% of those roosting in a nearby barn died. Densities of starlings per km² before and after a severe storm in Illinois were 5.2 and 0 in bottomland forest, 24.0 and 0 in upland forest, and 1,249.4 and 1,605.2 in urban residential, respectively. No dead starlings were observed. They appeared to shift from forested to urban habitat in response to the storm (Graber and Graber 1963; Kalmbach and Gabrielson 1921;

Odum and Pitelka 1939; Stewart 1978). Starlings bathing in a Minnesota bird bath died when the ambient temperature was –30ºC with a windchill of about –45ºC (Longley 1944).

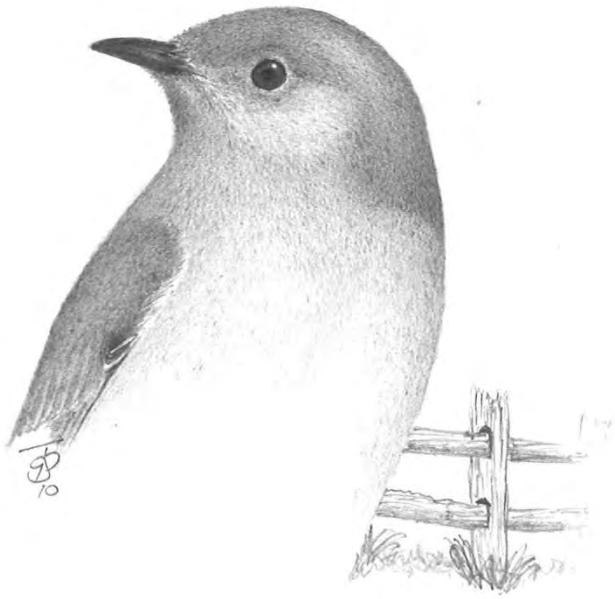
The starling is locally abundant in winter in southern Ontario where it occurs mainly in towns and larger urban centres. It winters north to Kenora and Cochrane and occasionally to Moosonee (James 1991), but it is much less common and more local in the north. The starling was the most abundant bird observed on the Niagara Christmas Bird Count (CBC) and tens of thousands roosted at a St. Catharines apartment during January and February (Black and Roy 2010). The roost at Guelph supported an estimated 100,000 birds. The highest count on the Hamilton CBC was 73,000 in 1980 (Curry 2006).

Numbers of starlings recorded on Ontario CBCs originally increased, but appear to have been declining since the early 1980s. Numbers were relatively stable from 1929 to 1966, after which they averaged about 3 times higher. That was largely because of expanded numbers on the Hamilton count due to birds using the Burlington Skyway bridge as a roost. In 1924, a single bird was observed on the Hamilton CBC; 1,714 were seen in 1928. The average number surveyed there was 3,400 1956-66 compared with 27,000 1967-77. After the high of 73,000 in 1980, numbers dropped steadily. The average for the 10 years ending in 2005 was 18,344 (Curry 2006; Freedman and Riley 1980). CBC data for Ontario indicate that the starling increased at an annual rate of 1.61% 1970-2021 but decreased at an annual rate of 3.91% 2009-21 (National Audubon Society 2022).

Project FeederWatch counts indicate declines, although the starling is still very common at feeders. The percentage of feeders in Canada that it was observed at was 68% in 1988; 60% in 1993, 1998, and 2003; and 58% in 2008 (Wilcox 2008).

Eastern Bluebird

Sialia sialis

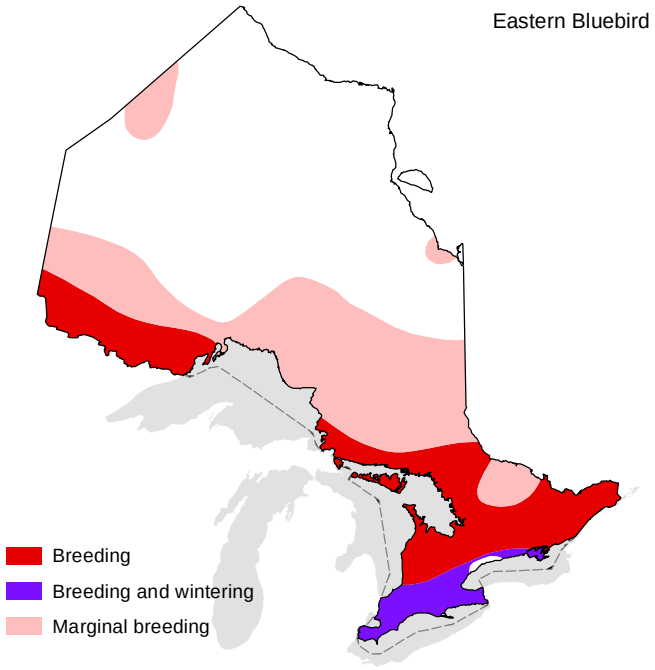


BREEDING SEASON

Habitat Requirements

The Eastern Bluebird is an open-country bird that requires scattered trees or shrubs for foraging. It avoids areas of extensive forest, grasslands with no woody vegetation, and urban areas. It readily nests in boxes constructed for it, so placement of boxes has influenced habitat selection. In Ontario, it has nested in farmland, including orchards, quarries, fencerows, pastures, fields, and willow swales (71.3% of nests); woodlands, including swamps, burns, clear-cuts, and slashes (11.8%); and beaver ponds and marsh edges (1.5%). Single nests were in a sand dune area and in a Cliff Swallow nest attached to a rural school (Peck and James 1987).

The 3 most important habitat characteristics for the bluebird in Ontario are a proper physical setting, a suitable nesting cavity, and foraging perches. It shows a strong preference for old-field habitat with patches of bare soil and standing trees. It shifted from presettlement habitats of natural burns, forest clearings, and stream openings to pastures, fields, orchards, roadsides, and gardens. The most favoured habitat is overgrown upland pasture, although it may inhabit second-growth brushy fields. The physical setting must include nearby foraging areas and shelter. It rarely uses habitats with few or no perches (Risley 1981). James and Peck (1995a) rarely observed it in jack pine stands near Gogama and only in recent clear-cuts or burns where it nested in old woodpecker holes



in snags. Where snags were left after cutting, it remained for several years as long as there was open ground where it could forage.

Ideal habitat is open with scattered trees and sparse ground cover. Natural savannahs or other habitats with savannah-like structure may provide excellent habitat provided that the grass-herbaceous layer is not too tall or dense (Askins et al. 2007; Fitch 1958; Gowaty and Plissner 2020; Pogue and Carter 1995). Large areas of Illinois were devoid of bluebirds, especially in intensively farmed areas. Flat, treeless areas were unsuitable even if nest boxes were provided. Large blocks of forest were poor habitat, although forest edges supported low populations. The earliest successional stages of forest were unsuitable. Nesting habitat usually included woody vegetation in and adjacent to open fields, especially grasslands. Ideal habitat was edge shrubs, forests, pastures, fallow fields, and roadsides (Graber and Graber 1963; Graber et al. 1971). Also in Illinois, all nest boxes placed short distances from woodlots and wooded ravines were occupied but those in open prairie were not (Musselman 1935). The Eastern Bluebird frequently nested in apple orchards and in towns and villages prior to the arrival of the House Sparrow. This species and the European Starling drove bluebirds further from dwellings. Usage of orchards declined due to pruning of dead limbs, filling cavities, and replacing old apple trees with younger ones. The bluebird still nested in rural orchards, along country roads, and in open groves or burned or cut-over woodlands where there were numerous dead trees and stumps to provide suitable nesting cavities (Bent 1949). In Virginia, 7 of 10 clear-cuts supported nesting bluebirds. The cuts were 1-5 years old and sparsely to moderately stocked with regenerating hardwoods 1-2 m tall. One nest was in a 12-year-old cut densely stocked with 4-5-m tall oak and hickory. The 3 clear-cuts that were devoid of nesting bluebirds were 10-15 years old and densely stocked with 3-6-m tall hardwoods (Conner and Adkisson 1974). In Quebec, it inhabits clear-cuts (especially those with retained stumps and snags), burns, and open peatlands near James Bay. Abandoned orchards provide suitable habitat in the south (Banville and Robert in Gauthier and Aubry 1999). Golf courses may be used by bluebirds, and golf course habitat has been reported to be both poor (Stanback and Seifert 2005) and good habitat (Cornell et al. 2011; LeClerc et al. 2005). On Wisconsin golf courses, short-grass areas supported significantly lower biomasses of insects and spiders than tallgrass areas, but bluebirds were more successful at capturing prey in short-grass areas. There were no significant differences in fledging success rates between the 2 habitats. Short mowed areas on golf courses could provide valuable habitat (Ambardar et al. 2018). It has been reported nesting in several types of forest. It was the only cavity-nesting bird species to not nest in bottomland forests in Missouri (Brawn et al. 1984), but Samson (1979) reported it nesting

in lowland hardwoods in northeastern North America. It has nested in or at edges of northern hardwoods, pitch pine stands following fire, oak stands, and aspen-birch (Capen 1979; Evans and Conner 1979). Taylor and Taylor (1979) characterized the Eastern Bluebird as a species of upland openings and edges. Zeleny (1976) stated that it prefers open areas with scattered trees, especially if the trees have a few low dead branches that can be used as perches. These include open fields with fences or wires for perching, pastures, open wastelands, large lawns, country cemeteries, golf courses, and abandoned orchards. It selects areas where the ground is not heavily covered with vegetation or where grass or other vegetation is kept short by mowing or grazing. Gowaty and Plissner (2020) summarized its preferred habitat as open areas with little to no understorey and with sparse ground cover. Modern breeding habitats included orchards, clear-cuts, burned areas, railway lines, and both upland and swampy habitat, including those close to major urban centres.

In 400-m landscapes with less than 30% tree cover in North Dakota, bluebird populations remained stable as tree cover within 100 m increased, but decreased in response to increasing tree cover in wooded landscapes. It preferred areas with 20-46% forest cover (Cunningham and Johnson 2016, 2019). In North Carolina, it was negatively correlated with the amount of tree canopy within 200 m, with greater tree canopy associated with less shrubby cover. It was negatively associated with elevation at the 200-m scale, indicating that it requires some disturbance, which is less frequent at higher elevations. It was negatively correlated with the amount of development within 1,000 m. Exurban development did not create habitat for it (Gilbert and Ferguson 2019).

Some studies used nest boxes to determine microhabitat preferences of Eastern Bluebirds. Near Kingston, 69% of bluebirds nested less than 30 m from forest edge (range 10-53 m). Mean distance from forest edge was not significantly different between the bluebird (25.8 m) and the Northern House Wren (13.9 m), but it was for the bluebird and Tree Swallow (41.3 m; Rendell and Robertson 1990). In Manitoba, bluebirds used sites with the greatest availability of grass and wooded pasture, with a large component of shrub pasture, but devoid of long grass and fallow lands. Occupied sites differed significantly in the percentage of wooded pasture, long grass, and fallow lands. Habitat at used sites was 14.3% forest, 29.4% wooded pasture, 8.2% shrub pasture, 34.5% grass pasture, 12.3% long grass, and 1.3% fallow fields. Habitat at unused sites was 12.8% forest, 11.9% wooded pasture, 5.1% shrub pasture, 26.5% grass pasture, 32.2% long grass, and 11.4% fallow fields. Parameters of used and unused boxes were: trail age, 11.8 and 9.9 years; distance to the nearest tree or shrub taller than 2 m, 27.0 and 59.1 m; distance to the nearest road, 61.4 and 25.3 m; and distance to nearest building, 1,269.2 and 979.4 m, respectively. Distance from the nearest building best separated habitat selection by the Eastern Bluebird and House Sparrow. Distance to the nearest tree, fallow fields, and entrance-hole diameter best separated the bluebird and Northern House Wren. Nest sites were associated with livestock more than expected. Areas where utility lines were present were used less often than expected. Most utility lines were 6 m from the ground and probably too high for effective foraging. Entrance holes to nests were oriented randomly (Munro and Rounds 1985). In Ohio, there was a significant relationship between nest-box usage and distance to the nearest tree. Used boxes were a mean of 4.80 m from the nearest tree compared with 3.04 m for unused boxes. The mean distance to a large tree from boxes that fledged at least 1 young was 6.55 m compared with 2.67 m for unsuccessful nests (Horn et al. 1996). In Maryland, preferred boxes were close (about

6 m) to small shrubs with surrounding low grass and nearby perches. Boxes facing northeast to south were preferred (Gowaty and Plissner 2020). In Wisconsin, selected boxes were in open areas with less than 5% tree cover within 11 m, less than 10% cover within 30 m, and were more than 35 m from the nearest forest edge and more than 200 m from the nearest permanent water (Gowaty and Plissner 2020). In Vermont, used nest boxes had fewer small woody stems under and around the box and were further from high perches. Bluebird nesting sites were in larger openings than those of Tree Swallows and were further from high perches and provided a longer view from the box entrance than those of the Northern House Wren. More bluebirds nested 10 m or more from a tall perch than expected by chance. Only 1 nest box further than 10 m from a tall perch was used by a wren. Sites with 25 or fewer small stems were used by bluebirds nearly twice as often as sites having more stems. Bluebird and swallow nest sites were not sufficiently different to provide useful habitat guidelines (Parren 1991). In Manitoba, tall, weedy growth at the base of the nest site discouraged nesting by the bluebird (Miller 1970).

Roosts are an important habitat component for the Eastern Bluebird. During the breeding season, adults sleep in nesting cavities or on protected limbs of trees, occasionally communally. During inclement weather, 20 or more birds have roosted together in cavities or nest boxes, or on branches in sheltered areas (Bent 1949; Gowaty and Plissner 2020).

Ontario nests were in nest boxes (81.1% of nests); in cavities in fence posts (7.6%); in natural and woodpecker cavities in stumps, in dead and occasionally living trees, and in trunk and branch stubs (7.4%); in cavities in utility poles (1.1%); and in unspecified cavities (0.3%). One nest was in an old Cliff Swallow nest and another was in a hollow of a well pump with a missing cap. Heights of 97 nests in natural cavities were 0.6-18 m, with most 1.4-3.7 m up (Peck and James 1987).

Throughout its range, the Eastern Bluebird changed its nest-site selection. Prior to 1900, it nested mostly in natural cavities and woodpecker holes in trees. After the extensive forests were cleared for agriculture, it adapted to nesting in cavities in wooden fence posts and occasionally in utility poles, and these were the dominant nest sites from 1900 to 1950. Its decline in the mid-1990s was attributed in part to replacement of wooden posts with steel posts. Removal of dead limbs and decadent trees in orchards contributed to loss of natural cavities during this period. Starting circa 1950, most bluebirds nested in boxes especially designed for them. Although it still nests occasionally in woodpecker and natural cavities, it appears to prefer nest boxes if given a choice (Bent 1949; Graber et al. 1971; Hersey 1933; Pinkowski 1976a; Risley 1994; Zeleny 1976). Nests outside of cavities are rare, but Bent (1949) reported South Carolina nests that were saddled on a 3-cm oak limb 3.7-4.6 m from the ground and 4.6 m from the trunk of the tree. Other unusual nest sites were in a drain pipe where the pipes were stacked on top of each other; in empty tin cans or jars; in Cliff Swallow nests, even within active colonies; in a railway signal ball that was raised and lowered about 50 times a day; in the hollow iron coupling of a railway car sitting on a siding; in a cavity in a steep earthen bank similar to that used by the Northern Rough-winged Swallow; in a cannon barrel; in a pile of concrete blocks at a construction site; in mailboxes; in tin newspaper cylinders; in a cavity of a limestone rock; and in a house under construction (Bent 1949; Laskey 1971; Matthey 1987).

Some studies described Eastern Bluebird nests in natural cavities and fence posts after nest boxes became preferred for nesting. Pinkowski (1976a) described 98 nests in trees in Michigan. Most

(88.8%) were in dead trees and 9.2% were in dead limbs of live trees. The other 2 nests were in a Hairy Woodpecker cavity in a white birch and in a decayed portion of an oak that was alive although the heartwood had deteriorated. All 9 nests in dead limbs of live trees were at 1 site and constituted 27.3% of nests found there; 0 of 65 nests at another site were in similar situations. Significantly more nests (86.2%) were in the main trunk of trees at 1 site compared with 63.6% at the other. The differences between sites may have been due to different tree growth (open- versus forest-grown) or to presence of different species of trees. Nest-tree species were used proportional to their availability except for elms which were used more than expected. Abandoned woodpecker nests accounted for 77.6% of the cavities that were used; 17.3% were in cavities produced by natural decay; 5% were in cavities created by fire. Significantly more cavities faced southeastward than any other direction, providing protection from the prevailing wind and exposure to the morning sun. Mean cavity height was 3.6 m. Bluebirds used old nest cavities of the Red-headed Woodpecker, Downy Woodpecker, Hairy Woodpecker, and Northern Flicker. Significantly more flicker nests were unused than those of the Downy Woodpecker and significantly more natural cavities than woodpecker cavities were not used. In Virginia clear-cuts, all nests were in dead snags averaging 23.6 cm diameter at breast height (DBH) and 133.9 m from mature woodlands. Nest cavities averaged 3.3 m from the ground. Many nests were in old flicker nests (Conner and Adkisson 1974). In Illinois, nests in natural cavities were 0.45-3.4 m from the ground; most recent records were less than 2.1 m up (Graber et al. 1971). In Missouri, Brawn et al. (1984) described 4 natural bluebird nests. The average DBH of nest trees was 38.9 cm, tree diameter at the nest was 18.3 cm, the cavity entrance averaged 4.7 m from the ground, average tree height was 8.7 m, basal area averaged 6.3 m^3 per ha, there were 62 stems per ha, the distance to the nearest opening in the canopy was 0 m, canopy height was 0 m, and the average tree decay class was 2.9 where 1 is the least decayed and 5 the most decayed. It nested in the youngest stands of all primary and secondary cavity nesters and in the smallest trees with the exception of the Downy Woodpecker.

Pierson and Scanlon (1986) examined 35 Eastern Bluebird nests in fence-post cavities in Virginia. Ninety-one percent of nest cavities were excavated by woodpeckers. The remainder were created by decay and had entrances at the top of posts. Mean nest cavity height from ground was 133.6 cm (range 78.9-181.3 cm). Hsu and Humpert (1988) checked for use of cavities in fence posts along interstate highways in Ohio by nesting bluebirds. In the first year, 6 of 296 cavities (2%) were used compared with 14 of 374 (3.7%) in the second year. Highest use of cavities occurred when mouse nests were removed prior to the breeding season.

In Ontario, bluebirds preferred boxes with a 4.4-cm diameter entrance hole over those with a 3.5-cm entrance. They preferred box floors measuring 10 x 10 cm over those measuring 15.3 x 15.3 cm, although differences were not significant (Lumsden 1986). Preferences for cavity features vary geographically and are influenced by competition. The cavity entrance size used by bluebirds was large enough to admit starlings, but no starlings used the boxes. This was probably because the interior of the boxes was painted white and the starling prefers black interiors (Lumsden 1989). Pitts (1977) demonstrated that bluebirds preferred boxes with white interiors over those with black interiors, although some boxes with black interiors were used. In Mississippi, bluebirds regularly used 3.5-L wooden boxes but avoided large wooden boxes with a volume of 16.5 L and a 7.6-cm entrance

hole (Twedt and Henne-Kerr 2001). The average diameter of nest-box entrance used by Manitoba bluebirds was 3.93 cm compared with 4.16 cm for unused boxes (Munro and Rounds 1985). When given a choice and there are no competing species, bluebirds prefer nest boxes with a slot entrance rather than a circular entrance (Davis et al. 1986; McComb et al. 1987). In Kentucky, bluebirds preferred boxes with a 3.8-cm wide opening at the top of the front of the box. Next favoured were regular boxes with 3.8-cm diameter holes. Boxes with a slot in the top were seldom used and produced no young. The circular entrance excluded starlings but the slot entrance did not. Bluebirds used boxes with entrances as narrow as 2.9 cm (McComb et al. 1987). In North Carolina, 90.3% of bluebirds nested in woodcrete boxes when given a choice between a clean wooden and woodcrete box (Stanback and Rockwell 2003). Although most nest boxes constructed for the Eastern Bluebird are wooden, it has nested in cardboard half-gallon cartons (Twedt and Henne-Kerr 2001; Woodward and Woodward 1979a), boxes made of tar paper (Low 1933), woodcrete boxes (a mix of sawdust and concrete; Stanback and Rockwell 2003), and polyvinyl chloride tubes (Tyson et al. 2011).

In Kentucky, Davis et al. (1994) put up pairs of boxes with 1 being clean and the other a nest that had fledged young. Thirty-eight new nests were established in boxes with old nests compared with only 3 in clean boxes. In North Carolina, 71% of bluebirds chose an unused box over a box that contained a successful nest for their second brood, but 75% renested in a cleaned used box versus an unused box. Used nests may carry a high burden of parasites within the breeding season, but these parasites disappear over winter. Bluebirds appeared to avoid parasites rather than choose known successful nests (Stanback and Devan 2001). Also in North Carolina, 73% of bluebirds chose a used woodcrete box to a wooden clean box for their second brood, but when given a choice between a clean and used woodcrete box, 71% chose the clean box. Nest-site fidelity was dependent on the quality of the alternate nest site (Stanback and Rockwell 2003). In South Carolina, there was no significant difference between numbers of birds that used a box for a second brood whether the old nest was cleaned out (62%) or left in the nest box (57%). Overall, 68% of males and 60% of females remained to nest at their original box. Leaving old nests in boxes had little effect on nest-site suitability or quality (Gowaty and Plissner 1997).

The Eastern Bluebird is territorial; males and females fight among themselves over other mates and nest sites. In addition to other bluebirds, it attacks Great Crested Flycatchers, Blue Jays, Tree Swallows, American Robins, Northern Mockingbirds, European Starlings, Brown-headed Cowbirds, and House Sparrows. Many of these are potential nest-site competitors, predators, or parasites. Territory size decreases as the nesting season advances and adults are indifferent to trespassers after the young of the last brood fledge. When a territory becomes vacant, the pair in the next territory may extend their hunting range and move into the acquired land for the next breeding cycle while still retaining their original territory. In Illinois, a single territory was 1.4 ha; 3 Arkansas territories measured 0.8-1.2 ha. In Kansas, outlying areas constituting a large part of each territory were seldom used. Activity was concentrated in a smaller central core. Over 3 years, the territory size and more intensively used core area were 2.2 and 0.8 ha, 3.5 and 0.6 ha, and 2.8 and 0.6 ha. In Michigan, home range or territory sizes were 1.1-8.4 ha. Average territory size was 2.1 ha in New York and South Carolina. Territories in burned or harvested areas are smaller than those in old fields, pastures, and orchards. Territory size can be substantially reduced by increasing the number of available nest

cavities. In South Carolina, males had breeding season home ranges averaging 19.2 ha compared with 13.7 ha for females. Four males had home ranges averaging 30.8 ha immediately after breeding (Fitch 1958; Gowaty and Plissner 2020; Graber et al. 1971; Thomas 1946a). When the bluebird nested predominantly in natural cavities, woodpecker holes, and fence-post cavities, nests were seldom closer than 100 m to each other and, in some cases, rarely closer than 400 m. In the 1940s, 2 Arkansas nests were only 8 m apart, but the territories spread away from the dividing line, each encompassing 0.8 ha, and there was no territorial overlap (Brodrick 1938; Graber et al. 1971; Musselman 1935; Thomas 1946a; Zeleny 1976). Now that artificially high nesting densities occur due to provision of nest boxes, it has been suggested that the bluebird may nest semicolonially. Nests have been reported as close together as 30 m in Ontario (Risley 1981). Gowaty and Plissner (2020) considered it a semicolonial nester, tending to settle where other bluebirds had already settled. In their South Carolina study area, the closest nests were 9 m apart. When an excess of nest boxes was present, bluebirds preferred neighbours to be closer (36 m) rather than more distant; some birds still nested solitarily.

Natal philopatry rates are lower in northern migratory populations than in southern resident populations. In resident populations, families often spend the winter together and arrive at the natal area as a unit. Near Chesley, 1 of 309 nestlings (0.3%) returned to nest (Krug 1941). In a Michigan area where some birds were resident and others were migratory, 34 of 592 fledglings (5.7%) returned to the natal area. Taking mortality into account, about 21% of surviving yearlings returned (Pinkowski 1979). In Massachusetts, 3 of 38 nestlings (7.9%) returned to breed in the natal area (Low 1933). In Minnesota, 11% of young returned (Gowaty and Plissner 2020). In Arkansas, 4 nestlings wintered in the natal area and remained to breed (Thomas 1946a). In Tennessee, 6.5% of females that were banded as nestlings returned. One female nested for the first time 8 km from her natal nest (Laskey 1940, 1943). In South Carolina, where the Eastern Bluebird is a resident, the overall return rate of young was 13.3% (11.9% of females and 14.6% of males). In total, 0.58% of nestlings nested in their natal box, 1.7% in or next to their natal territory, and 3.7% within their natal subpopulation. Four females and 2 males emigrated from their natal area to nest in another area 6 km away. The mean distance dispersed by males between natal and breeding territories (1.08 km) was significantly less than for females (1.39 km). Median dispersal distances were 0.57 km for males and 0.90 km for females. Maximum local dispersal distances were 8.69 km for females and 8.17 km for males. Males moved an average of 2.3 territories compared with 2.9 for females, and this difference was significant. One male banded as a nestling was recovered the following breeding season almost 800 km from his natal territory. Yearling females have been reported breeding for the first time more than 500 km from their natal sites (Gowaty and Plissner 2020; Plissner and Gowaty 1996). In Alabama, recoveries of birds banded as nestlings indicated that resident birds either remained in the area or radiated out into surrounding areas no more than 1.9 km from the natal nest box (Holliman 1997).

There are 2 temporal types of adult site fidelity: fidelity between years and within breeding seasons. Return rates of adults to nesting areas in successive years vary depending upon whether birds are resident or migratory, and breeding success the previous year may affect return rates. Near Chesley, of 69 adults, 3 females (4.3%) returned to the same nest box the following year. A female that nested in a fence post nested in a box 2 km away 2 years later (Krug 1941). In Wisconsin where

all birds were migratory, 16.0% of 2,527 adults returned the first year after banding, 3.7% returned for a second year, 1.4% for a third year, 0.4% for a fourth year, and 0% for a fifth year or more. Return rates were similar for males (15.5%) and females (16.4%). Return rates varied annually and ranged from 2.6% to 37.5%. After the coldest winter, only 4.6% of birds returned to breed and all were males. The return rate after the severe winter of 1976 (15.6%) was similar to that of the second warmest winter of 1982 (15.8%). The largest decline in return rates was associated with a slightly warmer than normal winter. Return rates were affected by winter mortality in severe winters. Winters following summer droughts may result in poor over-winter survival because of decreased numbers of insects. During breeding seasons with high populations, returning birds may be forced out of the study area due to higher competition, thus decreasing the apparent return rate (Bauldrey et al. 1996). In Michigan, all birds that returned to nest a second consecutive year had nested successfully the previous year (Pinkowski 1977a). Return rates were also related to nest success in a resident population in South Carolina. If nests were successful, 56% of individuals stayed to nest the following year compared with 15.4% of unsuccessful breeders. Overall, 39% of females and 44% of males returned to breed the following year (Gowaty and Plissner 1997, 2020). In Michigan, 62.9% of 89 returning adults were birds that remained in the area for the entire previous breeding season, rather than those that were there for only the spring, midseason, or late breeding season. Of returning birds, 77.1% of adult males and 54.5% of adult females spent the entire breeding season on site (Pinkowski 1979). In Minnesota, 26% of adults returned to breed at their previous year's nest site (Gowaty and Plissner 2020). In a resident population in Arkansas, 60% of males and 61.5% of females remained or returned to nest in the same territory. One female returned for the third year; another returned for the third and fourth years (Thomas 1946a). In Tennessee, return rates were 40-53.8% for females, with 61.5-85.7% using the same nest box in subsequent years. Some females used the same nest box in 3 consecutive years and one used the same box in 4 years, as did 1 male (Laskey 1939, 1940). Both sexes occasionally move further than 100 km from their previous year's nest site (Gowaty and Plissner 2020). In Maryland, the average return rate for 84 birds over 3 years was 61.2%. Of these, 77.1% returned to the same nest box (88.2% of males and 66.7% of females). Return rates to a specific box were highly correlated with pair reunion (Coss et al. 2019).

The Eastern Bluebird raises more than 1 brood per season in much of its range. There are reports of it using the same nest site all season and also of it switching sites within a season. Some nest boxes may have 3-4 nests per season in them, but not necessarily by the same birds (Graber et al. 1971; Laskey 1939, 1940; Low 1933; Thomas 1946a). In Michigan, site fidelity within breeding seasons was highly dependent on nesting success. Following an unsuccessful spring nest, at least 1 member of every pair left the study area, and both adults left on 16 occasions. Of failed spring nesters, 65.6% of females left compared with 39.3% of males. No females remained after failure if the male left. A few males moved 3-5 km after nest failure. One female nested 19 km from a failed nest and the remainder were not found, suggesting that failed breeding females may move considerable distances between subsequent within-season nests. When a pair remained together and renested in the study area, 81.0% of replacement nests were in a different location and the same nest site was used 19% of the time. There was much movement of birds in and out of the study area within breeding seasons. About 33% of bluebirds remained the entire breeding season and were responsible for a high percentage of nests and an even greater number of successful nests than

those that nested only in spring, mid-season, or at the end of the season. Adult males were more frequent in the spring-only group than the season-end group (6:1); the reverse was true for yearling males (1:4). Significantly more birds that arrived after the start of a season were new to the area (88.2%) than was the case for birds at the start of the season (74.8%; Pinkowski 1977a, 1979). Gowaty and Plissner (2020) reported that 69% of females failing in their first nesting attempt moved for their second attempt compared with 39% of successful females. At Chesley, many females raised both broods in the same box but different boxes were usually used (Krug 1941).

Limiting Factors

Eggs have been reported in Ontario nests from mid-April to early September, but mostly from 21 May to 21 June (Peck and James 1987). In Algonquin Park, nestlings are present from mid-May to late June, and fledglings have been observed from mid-July until mid-August (Tozer 2012).

The time required to build a nest ranges from 1 to 14 days, with most nests built in 3 or 4 days. For subsequent broods, the nest is often built in a day. First nests of the season take the longest to build and construction is halted during cold or wet weather. Egg laying may commence almost immediately after the nest is complete, or there may be a delay as long as 3 weeks. One egg is typically laid a day, but a day is skipped in 5-10% of clutches. This usually occurs in early spring when short-term shortages of insects may occur. Incubation usually begins with the laying of the last egg, but occasionally with the penultimate egg. The incubation period at 41 Ontario nests was 10-15 days, mostly 13 or 14 days. The short incubation period of 10 days plus 2 reports of hatching taking place over 24 hours suggest that incubation occasionally began before the clutch was complete. Other Ontario nests took 17, 19, and 21 days to hatch, suggesting a delay in the onset of incubation after laying the last egg. In Michigan, some females laid 1 egg and then waited 2-10 days before resuming a normal laying sequence. In Arkansas, incubation started with the fourth or fifth egg in some 6-egg clutches. Of 1,121 nests reported to the Cornell nest records scheme, the incubation period ranged from 11 to 19 days with more than 80% taking 12-15 days to hatch. Incubation periods are longer in spring and at high altitudes, reflecting the effects of cooler air temperatures. The incubation period decreased with increasing clutch size. Early in the season, most eggs hatch in a 1-day period, but hatching of the entire brood may take 2-3 days late in the season. The age at fledging ranges from 14 to 22 days, mostly 16-19 days. In Michigan, fledging took significantly longer (mean 19.39 days) in spring than summer nests (mean 18.63 days). The time for a full nesting cycle from initiation of nest building to fledging ranges from 35-47 days, but 37-40 days is typical. Nest initiation in spring is usually fairly synchronous but timing may vary annually depending on weather conditions. Yearling birds may not establish territories and initiate nesting until about a month after adult birds. In Ontario, the interval between fledging of the first brood and initiation of the next clutch was 6-23 days, but was mostly around 2 weeks. Elsewhere, the interval was 2-41 days. In Michigan, the average interval between completion of 1 nesting and initiation of another was 19.5 days for successful nests and 13.0 days for unsuccessful nests (Bent 1949; Brodrick 1938; Butcher 1988; Gowaty and Plissner 2020; Graber et al. 1971; Hartshorne 1962; Herbert 1988; Laskey 1939, 1940, 1943; Low 1933; Peck and James 1987; Pinkowski 1975b, 1977a, 1979; Risley 1981; Thomas 1946a; White and Woolfenden 1973; Zeleny 1976).

In Ontario, the Eastern Bluebird frequently raises 2 broods and there are 4 confirmed records of 3 broods (Peck and James 1987). Throughout its range, it raises 2 broods in most locations. In the central portion of its range, 3 broods are commonly reared and there are rare cases of females successfully raising 4 or 5 broods per year. In Arkansas, 3 pairs successfully raised 4 broods in a season. These pairs laid their first and last eggs on 18 March and 18 September. One male successfully raised 4 broods in a season, but with 2 different females. In Michigan, all birds raised 2 broods per season at 1 study area. All birds were single-brooded at another area a short distance away. These differences may have been due to low availability of nest sites at 1 area. Adults raise more young per season than yearlings because they attempt more broods (Bent 1949; Brodrick 1938; Gowaty and Bridges 1991; Gowaty and Plissner 2020; Graber et al. 1971; Harrod et al. 2021; Laskey 1943; Pinkowski 1976a, 1977a, 1979; Plissner and Gowaty 1988, 1996; Stanback and Dervan 2001; Thomas 1946a; Tucker 1990; White and Woolfenden 1973). The bluebird is a persistent renester if it is unsuccessful at nesting. In Ontario, clutches of 2-8 eggs have been reported, with most containing 4 or 5 eggs. Second and third clutches were smaller; in 44 of these, 25 contained 4 or fewer eggs. All August and September clutches contained 3 or 4 eggs (Peck and James 1987). Risley (1981) reported the average clutch size of 344 southern Ontario nests to be 4.45, with 5-egg clutches most frequent. The average clutch size for Ontario and Quebec combined was 4.18 eggs (Peakall 1970). Outside Ontario, clutches of 2-9 eggs have been reported with most containing 4 or 5 eggs with a normal range of 3-6 eggs. One 9-egg clutch was known to have been laid by 2 females. Seven eggs may be the largest clutch size laid by a single female. Clutch size declines with the season. In Illinois, first nests averaged 4.9-5.1 eggs compared with 4.2-4.4 for second nests. In Tennessee, average clutch size was 5.00 eggs for first nests, 4.65 for second nests, and 3.69 for third nests. In Michigan, average clutch size was 4.7 in early spring, 4.53 in late spring, 4.17 in early summer, and 3.25 in late summer. In Michigan, there was no significant difference in clutch size of yearling and adult females. Similar results were obtained in Arkansas in 1 year, but in another year yearlings laid larger clutches than older females (Bent 1949; Gowaty and Plissner 2020; Graber et al. 1971; Hartshorne 1962; Herbert 1988; Laskey 1939, 1940; Musselman 1935; Peakall 1970; Pinkowski 1977a, 1979; Robinson et al. 2010; Thomas 1946a; White and Woolfenden 1973; Zeleny 1976).

Both sexes are capable of breeding when they are 1 year old, and breeding occurs every year thereafter. In Michigan, some yearling males do not nest due to factors such as nest-site and territory availability, but it is likely that all would nest under ideal conditions. Three returning males did not breed as yearlings but 91.2% of returning yearlings bred (Gowaty and Plissner 2020; Laskey 1943; Pinkowski 1977a, 1979).

Most birds are apparently monogamous, although there are rare cases of polygyny and polyandry. In South Carolina, more than 95.5% of nesting attempts were monogamous; 5 of 177 (3%) were polygynous. In Wisconsin, a male simultaneously overlapped his second and third broods with 2 females using nest boxes more than 200 m apart (Khan 2021). Mate fidelity in Michigan was related to nest success; 139 of 140 adults (99.3%) that nested successfully in spring either remained paired, stayed in the same territory, or remained in the company of the juveniles. Adults nesting successfully in spring usually remained paired and attempted summer nests in the same general area. Renesting together occurred by 34.4-60.7% of unsuccessful pairs and by 70.0-84.3% of

successful pairs. If a pair was successful in spring and failed at the summer nest, the pair bond was preserved and the pair renested in a different location (Pinkowski 1977a). In Maryland, divorce rates in a subsequent year were significantly higher after nest failure. Of failed nests, 56% resulted in divorce compared with 23.7% of successful nests. Of pair bonds, 84.7% lasted the entire season, but on 7 occasions pairs divorced after their first nest attempt. Six of 59 pairs (10.2%) remained together for at least 2 years before divorce or disappearance (Coss et al. 2019). Both sexes are capable of raising a brood on their own if their mate is lost. Males may abandon the nest and either leave the territory for a while and return with a new mate, or remain in the territory until a new female arrives. When a replacement mate arrives, it may adopt the existing brood but typically expends less energy in raising the young than the original mate. Replacement females may occasionally kill the nestlings and replace them with their own eggs. In some cases, replacement mates may not help and the original eggs or nestlings may be abandoned. There are some cases when both members of a pair died during a nesting and the brood was raised by a new male and female. This usually happens when the replacement pair is a neighbouring pair that lost its own brood at about the same time the other adults disappeared (Gowaty 1983a, 1983b; Krug 1941; Ligon et al. 2009; MacDougall-Shackleton et al. 1996; Meek and Robertson 1991; Pinkowski 1978a; Plissner and Gowaty 1988; Thomas 1946a; Wetzel and Chandler 2008).

Extra-pair paternity and intraspecific parasitism occur. Near Kingston, 24% of broods contained extra-pair young and approximately 8% of young were extra-pair. Forty-eight of 90 bluebird offspring (53.3%) had DNA banding that was not seen in either parent. Fourteen percent of broods where the male was present contained extra-pair young; overall 7% of nestlings were extra-pair. Females whose mates were removed were 3 times as likely to have extra-pair young. Nest sites were limited in this population and non-territorial floater males often appeared on territories where males were removed. They were usually accepted by artificially widowed females. Near Kingston, 7 nestlings (8.4%) were fathered by extra-pair males and 24% of nests contained at least 1 extra-pair nestling. Two cases of intraspecific brood parasitism accounted for 2.4% of nestlings and 9.5% of nests. In Arkansas, almost 5% of nestlings were not related to their caretakers. In South Carolina, at least 5% of males and 15% of females took care of young that were not their own, and 9% of broods showed evidence of multiple parentage. Also in South Carolina, nestlings unrelated to parents were significantly more common in areas of high-density nesting where neighbours were close together. Extra-pair fertilizations were most likely to be by neighbouring males rather than non-territorial floaters. An estimated 1% of nestlings in this population resulted from nest parasitism and 19.8% from extra-pair copulations (Gowaty 1983a, 1985; Gowaty and Bridges 1991; Gowaty and Karlin 1984; Gowaty and Plissner 2020; Karlin et al. 1990; MacDougall-Shackleton et al. 1996; Meek et al. 1994; Plissner and Gowaty 1996; Tucker 1990). Extra-pair paternity accounted for approximately 20% of nestlings at 1 study area where an exceptionally high density of nest boxes was provided (Gowaty and Plissner 2020).

Rarely there may be helpers at nests. Nesting females usually chase away helpers, but occasionally they are tolerated. Helpers are usually fledglings from a previous nest during the same breeding season. Fledglings may begin this behaviour when they are as young as 37 days. In 1 case, a helper was a yearling male that left his natal territory, raised a brood, and then returned to assist

his parents in raising nestlings. Helping typically consists of removing fecal sacs and feeding nestlings, but these activities may not actually be very helpful (Gowaty and Plissner 2020; Hartshorne 1962; Laskey 1939; Pinkowski 1975b, 1975c, 1976b).

The Eastern Bluebird forages mostly on the ground, but searches for prey from elevated perches. Food is obtained from habitats such as lawns, pastures, and old fields dominated by grasses and forbs with scattered trees. Sparse ground cover is essential for effective foraging, as are suitable perches for searching for prey. Habitat that is otherwise suitable is not used if there are no suitable perches available. Common foraging perches include tree limbs and branches (especially those that are dead or defoliated), fence posts, boulders, and coarse weed stalks such as mullein and evening-primrose. If low perches are not available, it may perch horizontally part way up tree trunks to view the ground. In Ohio, foraging perches were 0.6-8.2 m high and offered unobstructed views of the ground. There was no significant difference in average height of perches selected by males (2.3 m) and females (1.8 m). The most common foraging technique is dropping from a perch to capture prey. In Michigan, this method was used in 78.8% of 2,638 foraging efforts and 87.4% of 508 attempts in Ohio. Flycatching is the next most abundant foraging technique, representing 10.7% of Michigan and 8.8% of Ohio foraging attempts. Flycatching may occasionally become the only foraging technique when aerial insects are highly visible, after a rain, or when swarming ants are abundant. Gleaning and hover-gleaning from foliage was used in 6.8% of foraging attempts in Michigan and in 3.7% in Ohio. These techniques are often used in areas of tall vegetation and become more common as the season advances and vegetation grows. In Michigan, 2.6% of foraging bouts were by hopping and 1.1% were by dropping from a perch to glean. It uses 3 foraging techniques when obtaining fruit: hovering in the air, perching on a limb and plucking berries, and perching on a fruit head, such as sumac, and plucking fruit directly beneath its feet. Flycatching is more common during favourable weather (14.7%) than inclement weather (1.2%), but the reverse is true for gleaning (20.2% during inclement weather and 7.9% during favourable weather). Ten spring foraging ranges in Michigan were 4.5-38.9 ha, but the size of the area containing the perches was fairly constant at 3.9-8.4 ha, suggesting that perch distribution may affect territory size. For 1 Ohio pair, food captured for young was obtained an average of 141 m from the nest. In Michigan, males obtained food for nestlings closer to the nest (average of 113.6 m) than females (152.4 m), but in some areas they foraged at the same distances (Goldman 1975; Gowaty and Plissner 2020; Graber et al. 1971; Pinkowski 1977b, 1978b; Risley 1981). The bluebird tends to select prey items that are larger than those generally available. In Ohio, 38% of potential prey was 3.3 mm in length; prey this size represented 19% of food. Rates for different size categories were: 6.5 mm, 47% availability compared with 27% of food; 13 mm, 19% availability compared with 31% of food; 26 mm, 1% availability compared with 10% of food; 39 mm, less than 1% availability compared with 10% of food; and 52 mm, 1% availability compared with 5% of food. Young received most of the large prey items. Adults ate 40% of the smaller items and fed 79% of the larger items to the young (Goldman 1975). In Michigan, adults appeared to feed nestlings larger prey items than fledglings (Pinkowski 1978b).

In Tennessee, food items fed to nestlings consisted of 22.4% grasshoppers, 14.7% crickets, 16.3% spiders, 25% caterpillars, 2.4% moths, and 19.2% items too infrequent to be listed individually (including 1 skink) or too small to identify (Gowaty and Plissner 2020). Braman and Pogue (2005)

reported that adults brought a small snake to a nest but it was not eaten. Six pairs in Oklahoma fed skinks to nestlings. Of animal food brought to nestlings in Michigan, 32.4% consisted of caterpillars (adult butterflies and moths comprised 3.6%), 25.6% were orthopterans (12.8% grasshoppers, 9.3% crickets, 3.1% katydids, and 0.4% mantis nymphs), 11.3% spiders including egg sacs (predominantly ground-dwelling species), 11.0% beetles, 5.2% earthworms, 3.9% hymenopterans, 2.3% millipedes, 1.5% leafhoppers, 1.2% snails and snail shells, 0.8% isopods, 0.5% flies, 0.3% scorpionflies, 0.1% dragonflies, 0.1% cicadas, 0.1% bugs, and 0.04% lacewings. Unusual prey included 2 centipedes and 1 fairy shrimp. Spiders and caterpillars were the primary food of recent hatchlings. More grasshoppers, crickets, beetles, and earthworms were provided as the young matured. Seventy-five percent of items fed to 1-day-old nestlings were spiders; larger spiders were fed as the young aged. Three-day olds were fed grasshopper nymphs, but the coarser male grasshoppers were not fed to young until day 7 and the larger females were first fed on day 9. Spiders were provided to nestlings more in May and June (13.1% and 14.3%) than in July and August (7.9% and 4.4%). Ground-dwelling spiders were common in the diet but not as common as spiders dwelling on herbaceous plants. Adult moths were more common in the nestling diet in summer (5.6%) than spring (2.9%). Earthworms comprised 10.8% of the nestling diet in May, 3.3% in June, and were absent in the diet after the first of July. Beetles comprised 17.9% of the diet in May, 8.3% in June, and 0.8% in August. Caterpillars were more common in the diet in May (35.4%) and June (41.8%) than in July (20.8%) and August (28.9%); cutworms were 46.6% of all caterpillars consumed. Bluebirds tended to select ground-dwelling species in spring and those on plants in summer. Fruit was fed to nestlings at only 4 of 45 nests (8.9%) and included mulberries, raspberries, red-osier dogwood, chokecherry, and honeysuckle. Fruit was not fed until late June when it became abundant. At 2 of 4 nests, fruit comprised 37.0% and 33.0% of the nestling diet over 3- and 5-day periods, but was fed to nestlings only once at the other 2 nests. In New York, most of very young nestlings' diet consisted of caterpillars as well as other small, soft invertebrates such as spiders. Later, at least 50% of the food fed to nestlings was orthopterans (grasshoppers, crickets, and katydids). These items were supplemented with berries, moths, beetles, centipedes, millipedes, and preying mantises. One young was fed a spring peeper (Hartshorne 1962). Foods fed to fledglings differed from those fed to nestlings. Caterpillars were more common in the diet of fledglings (44.0% of all food) reflecting peak consumption in June when most young were out of the nest. Earthworms (11.4%) and beetles (7.7%) were more common in fledglings' than nestlings' diet, but the reverse was true for grasshoppers (8.8%), spiders (4.4%), crickets (3.3%), and bugs (3.3%). Fruit (mulberries and cherries) comprised 11.0% of the fledgling diet, but was consumed only in July and August (Pinkowski 1978b).

Beal (1915a) analyzed the contents of 855 bluebird stomachs taken throughout its range in all months of the year. The food consisted of 68% animal matter and 32% vegetable matter. The animal matter consisted of 22.0% orthopterans (mostly in August and September), 20.1% beetles (ground and June beetles and weevils), 18.5% caterpillars, 3.5% ants, 1.6% wasps and bees, 2.8% bugs (predominantly stink bugs), 0.3% flies, 0.3% miscellaneous insects, 4.4% spiders, 1.2% millipedes, and 0.6% miscellaneous animals (isopods, snails, earthworms, lizards, and treefrogs). The vegetation eaten was predominantly fruit. Almost all domestic fruit (raspberries and cherries) was eaten in June and July. Honeysuckles and mulberries became important in the diet in late summer and throughout winter. In spring, cutworms and beetles were important with grasshoppers and crickets

important later in summer. It may glean stoneflies from tree trunks in spring. It may rely on fruit such as staghorn sumac and multiflora rose early in spring before insects become readily available. It has eaten shrews, snakes, salamanders, and western chorus frogs (Gowaty and Plissner 2020; Graber et al. 1971; Pinkowski 1977b; Tekiela 2004; Zeleny 1976). Bluebirds with access to mealworms began laying eggs earlier and had a 5% higher nestling survival rate than birds without supplemental food (Bailey and Bonter 2022).

The Eastern Bluebird is rarely parasitized by the Brown-headed Cowbird. In Ontario, 4 of 5,102 nests were parasitized, less than 0.1% (Peck and James 1998a). Throughout its range, usually less than 1% of nests are parasitized. The rate of parasitism has probably declined recently due to most bluebirds nesting in boxes with entrance holes that are too small to admit cowbirds. Nests in boxes that have lost their tops are vulnerable to parasitism. In Virginia, 6 of 27 nests (16.2%) were parasitized. The nest boxes provided were open cardboard half-gallon cartons that allowed cowbirds access. Cowbirds did not remove any bluebird eggs from these nests. In Illinois, parasitism rates were low, except in 1945 when 7 of 268 nests (2.6%) were parasitized. Parasitized nests were in nest boxes without tops. Parasitized nests were also found in undamaged nest boxes. In natural nests in Kansas, 1 of 4 nests was parasitized. Parasitism rates in Iowa are less than 1%. In South Carolina, 75% of parasitized nests were covered with new nesting material and renesting occurred. When cowbirds fledge, adults feed both cowbird and bluebird fledglings. Often both species are successfully reared from a nest. It is likely that the effects of cowbird parasitism are minor (Gowaty and Plissner 2020; Graber et al. 1971; Lowther 1985, 1991, 1997; Musselman 1935; Rivers et al. 2010; Woodward and Woodward 1979a). Peer et al. (2006) experimentally parasitized bluebird nests with bluebird and cowbird eggs. All parasitic bluebird eggs were accepted, but 65% of cowbird eggs were ejected from the nest box. Butler et al. (2020) demonstrated that bluebirds quickly ejected eggs with a speckled pattern but not those with a solid colour. It is likely that bluebirds eject most cowbird eggs.

Extreme weather during the breeding season is the greatest limiting factor for the Eastern Bluebird. Late winter or early spring snow or sleet storms can result in local, massive mortality. Cold weather after eggs are laid can cause freezing of eggs and desertion. Near Chesley during a cool spell, several birds abandoned their nests. Near the end of May, there were several cool, wet days and this resulted in entire broods dying. Death of young was probably due to the inability of adults to find sufficient food rather than exposure (Krug 1941). The cold spring of 1971 resulted in a 54% decline in the number of nesting attempts on a bluebird trail near Oshawa (Risley 1981, 1994). The ice storm of early April 2003 killed many bluebirds in the Hamilton area (Read 2006) and probably throughout Ontario. In Illinois, 3 severe April freezes over a 7-year period froze many eggs and killed many adult birds. It was estimated that half the bluebird population in west-central Illinois died in spring 1940 due to cold and snow (Graber et al. 1971; Musselman 1939, 1941). Cool or wet spring weather may delay initiation of nesting. This may result in first nests or renesting attempts coinciding with the nesting period of the Northern House Wren, which normally initiates nesting after the first nests of bluebirds are well underway. The delay results in increased competition for nest sites, increased incidence of piercing of bluebird eggs by wrens, and reduced reproductive success (Graber et al. 1971; Musselman 1935, 1939). Hot dry weather late in the summer may reduce nesting

success of second nests. Prolonged periods of temperatures in excess of 30°C may literally cook eggs in nests and result in a high rate of desertion. High temperatures may result in nestlings leaving the nest prematurely; young may also die from heat in the nest (Graber et al. 1971; Musselman 1935; Thomas 1946a; White and Woolfenden 1973).

Nest-site competition is another significant limiting factor for the Eastern Bluebird. Most competition occurs south of the Canadian Shield and near homes and residential areas in the Shield. The 4 main competing species are the Tree Swallow, Northern House Wren, European Starling, and House Sparrow. The Tree Swallow is the most significant nest-site competitor for the Eastern Bluebird. On Ontario bluebird trails, 70-80% of nest boxes are occupied by swallows (Risely 1994). As early as 1938, Tree Swallows were occupying nest boxes designed for bluebirds near Chesley (Krug 1941). Graber et al. (1971) stated that nest boxes situated near water would likely be taken over by Tree Swallows, but swallows now occupy nest boxes in a wide variety of habitats. In Massachusetts, the Tree Swallow was always victorious over the bluebird in disputes over nest boxes (Low 1933). Hersey (1933) reported extreme harassment of nesting bluebirds by Tree Swallows that led to abandonment of nests containing eggs and even nestlings. The swallows prevented bluebirds from feeding young to the point where the bluebirds gave up.

The bluebird may occasionally be successful in outcompeting the Northern House Wren for nest cavities and even evicting them from their nests (Bent 1949; Gowaty and Plissner 2020), but the wren usually prevails. In 1 area in Illinois, the bluebird population decreased as the wren population increased (Graber et al. 1971). Wrens may drive away adult bluebirds, puncture eggs, and fill nest boxes with active and dummy nests. In normal breeding seasons, bluebirds initiate nests prior to the arrival of wrens and nests normally contain nestlings when the wrens arrive. These nests are usually safe from wren competition, but presence of wrens may reduce success of second nests or renests, and bluebirds may be forced to nest in suboptimal areas. In Michigan, 23.3% of nest failures in natural cavities were due to Northern House Wrens. Competition with the Northern House Wren is mostly restricted to areas within 30 m of wooded or shrubby areas. This prevents the Eastern Bluebird from accessing large areas of potentially suitable habitat (Horn et al. 1996; Lumsden 1989; Pinkowski 1977a; Risley 1981; Zeleny 1976).

Declines in bluebird populations in the 1930s in the Oshawa area were attributed to the ingress of the European Starling. By the 1950s, the starling's range included most of rural southern Ontario, and a widespread decline in the bluebird during the same period was partially due to the increase in starlings. Starlings do not evict bluebirds from boxes, but they appropriate most available cavities that are large enough. As starlings increased, they started taking over cavities in wooden fence posts and in orchards that were previously used by bluebirds. The bluebird may initiate nesting earlier than the starling and may be successful in raising the first brood in a natural cavity without interference from starlings. Usage of natural cavities by bluebirds for subsequent broods declines due to competition with starlings. Bluebirds nesting where there are no available nest-boxes may be forced to nest in suboptimal cavities or may not find a nesting cavity (Baillie 1967; Bent 1949; Davis et al. 1986; Krug 1941; Pierson and Scanlon 1986; Pinkowski 1977a; Read 1998, 2006; Risley 1981, 1994; Stewart 1976; Zeleny 1976). Starlings can be effectively eliminated from bluebird boxes

through appropriate design. Cavity entrances smaller than 3.8 cm preclude entrance by starlings (Graber et al. 1971; Lumsden 1986; Risley 1994; Zeleny 1976).

The bluebird cannot compete with the House Sparrow, which evicts bluebirds from nest boxes and may kill nestlings and even adult bluebirds. A noticeable decline in the bluebird was evident in Ontario as early as the 1880s and 1890s due to House Sparrows displacing bluebirds from rural residential areas. Near Vineland, it was noted in the 1930s that interference from the House Sparrow seriously affected bluebird nesting. Nest sites within 400 m of buildings are likely to be used by House Sparrows and be unavailable to bluebirds (Bent 1949; Gowaty 1984; Graber et al. 1971; Herbert 1988; Laskey 1940; Lumsden 1989; McIlwraith 1894; Read 1998; Risley 1981, 1994; Sheppard et al. 1936; Summerour 1988; Zeleny 1976).

Habitat loss and degradation is another significant limiting factor. Much habitat has been lost due to interspecific competition: areas near water and most roadside habitats to the Tree Swallow; areas within 30 m of shrubbery to the House Wren; natural cavities in rural woodlots, hedgerows, and roadsides to the European Starling; and areas within 400 m of residences and barns to the House Sparrow. Habitat losses have occurred due to urbanization and agricultural practices. Fewer fence posts are wooden now, with many having been replaced with metal posts. The amount of total area farmed has declined, and the quality of farmland as habitat has declined. Removal of dead trees, hedgerows, and edge habitats as well as putting fallow fields back into production results in fewer natural cavities and poorer feeding areas. Grazed pasture has the potential to remain good habitat indefinitely provided that grazing is not too intense, but the amount of pasture has declined significantly. Heavier pruning and replacement of old trees in orchards has reduced the number of available nest sites. Natural succession results in habitat becoming unsuitable when vegetation covers patches of bare ground and shrubs become taller than about 1 m (Baillie 1967; Conner and Adkisson 1974; Pierson and Scanlon 1986; Read 1998; Risley 1981, 1994). Forest management practices in the Canadian Shield may be creating habitat for the bluebird.

Pesticides applied to orchards, roadsides, and fields may be a cause of mortality. The bluebird may prey preferentially on pesticide-weakened insects, thereby increasing contaminant burdens in nestlings (Gowaty and Plissner 2020; Risley 1981; Zeleny 1976). DDT and other persistent pesticides were used extensively on fire ants in the southern United States and this may have caused declines (Risley 1994). Read (2006) noted that bluebird numbers began to decline just after 1945 when intensive spraying of DDT began. At that time, apple orchards were sprayed routinely every day with DDT, lead arsenate, or sulphur. Bishop et al. (2000) studied bluebird reproductive success in pesticide-sprayed apple orchards in southern Ontario. Organophosphorus and carbamate insecticides have been sprayed in orchards for decades. There was a significant increase in the number of unhatched eggs as organochlorine levels in eggs increased. Although declines in survival were statistically significant, they were not high, with a maximum decline in survival of 4%. Both carbamate and organochlorines were potentially highly toxic to birds, particularly DDE which may affect egg survival. Oil and sulphur appear to be potentially toxic when birds are exposed. The fungicides used in apple orchards appeared to have low toxicity to birds, but they are applied repeatedly at high rates and often in combination with other chemicals and contribute to the overall toxicity. In Virginia, Bouland et al. (2012) studied clutches of the bluebird nesting in floodplains of

rivers contaminated with mercury and compared them with clutches in uncontaminated floodplains. Blood mercury concentrations of females were 7 times higher in contaminated than uncontaminated sites. Bluebirds in reference areas raised male-biased broods. Those in contaminated areas produced approximately equal numbers of male and female nestlings. Females in poor condition tend to produce female nestlings, which are less fit than male nestlings. In Indiana and most likely elsewhere, PCBs continue to be released into the environment despite their having been banned in the United States in 1977. It is an endocrine-disrupting chemical that results in heart deformities in the bluebird (Gowaty and Plissner 2020). Near lead mines in Missouri, the probability of a female fledging a young decreased from 94% to 84% in areas with elevated soil lead concentrations. Most nest failures were due to predation suggesting that lead may affect birds' behaviour and activity at the nest or affect nest-site quality (Thompson et al. 2024).

In burns in Montana, there were fewer bluebirds and nests per unit area where salvage logging occurred, but the differences between control and logged areas were not significant (Kronland and Restani 2011). In New York, Keller et al. (2003) surveyed bird populations in clear-cuts for several years after harvesting. The bluebird was observed only in 2-year-old cuts.

Bluebird nests are often infested with parasitic blow flies, and this problem may be exacerbated in nest boxes. Wittmann and Beason (1992) found no significant differences in nestling development, weight, fledging, or survival in parasitized or unparasitized nests and concluded that blow fly removal in boxes may not be necessary. Hannam (2006) reported similar results, but found that nestlings in unparasitized nests had a 12.5% higher level of blood hemocrit and a 35% higher concentration of hemoglobin. Nestlings in parasitized nests compensated by taking longer to fledge (19 days) than those in unparasitized nests (17.6 days). The time required for infested fledglings to recover from anemia and the long-term effects of parasitism were unknown. Roby et al. (1992) found that some nestlings died in heavily parasitized nests and that 10-day-old nestlings lost about 28% of their total blood volume daily. Nonetheless, the effects of blow fly parasitism were small and nestlings may recover from anemia prior to or shortly after fledging. Zeleny (1976) concluded that nestlings are generally able to withstand blow fly infestations, but that infestations in excess of 150 larvae per nest may result in death. Risley (1994) reported significant losses of nestlings in Ontario due to blow fly parasitism. In 1980, 23% of broods on a bluebird trail died as a result of blowfly larvae.

Bluebirds are often attracted to smokestacks and chimneys because they may be potential nest sites or roosts. These birds are often asphyxiated by smoke or cannot get out (Gowaty and Plissner 2020).

Anthropogenic noises may affect reproductive success of the bluebird. Low-pitched loud human-generated noises are associated with smaller clutches and fewer fledglings (Gowaty and Plissner 2020; Williams et al. 2021). In Florida, Sieving et al. (2024) studied the effects of chronic highway noise and experimental intermittent playback of construction noise on the bluebird. Nests in quiet areas had higher nest success than any exposed to noise. Nests exposed to chronic road noise and nests in quiet areas that were subjected to 3-4 days of construction noise had the lowest hatching success.

Price (2004) predicted that the breeding range of the Eastern Bluebird could increase in southern Ontario if the average summer temperature increased by 2°C.

Status

The Eastern Bluebird population has fluctuated considerably both in Ontario and throughout its range. It was probably rare to uncommon in Ontario prior to European settlement. Prior to settlement, it was probably restricted to forest fire burns, clearings created by First Nations, prairies, and forest edges. Forest clearing and establishment of stump fences and wooden fence posts created ideal habitat and nest sites. Highest abundance of the bluebird may have occurred in the latter half of the 19th century (Read 1998, 2006). McIlwraith (1894) stated that the bluebird was formerly one of the most abundant breeding birds in the province, but that it was decreasing due to presence of the House Sparrow. Although seldom seen near towns or villages at that time, it was still common in rural areas. Fleming (1907) considered the bluebird abundant in the Toronto area. In the 1930s, it was common to abundant south of the Canadian Shield from Middlesex County east to Ottawa. It was uncommon and occasional in the Shield and central Ontario (Risley 1981). Breeding at that time was documented north to at least the transcontinental railway west to southern Kenora District. There were scattered summer records north to Moose Factory, but it was comparatively rare everywhere north of Lake Nipissing (Baillie and Harrington 1937). Declines in the 1920s in the Oshawa area were attributed to competition with the starling. Gradual declines became apparent in the 1940s and 1950s, and a significant decline of 60-90% occurred in Ontario after the severe winter of 1957-58. This was the first time that populations did not rebound in a few years after a severe winter, probably because starlings had populated rural areas by then. In the Hamilton area, the bluebird remained common as a breeding species throughout the 1940s and early 1950s, but declined dramatically by the end of the 1950s. From 1951-85, there were records of only 1-3 pairs per year, with no records 1951-58, 1960, 1967, and 1968. Populations throughout Ontario remained low in the 1960s and 1970s, although successes were starting to be realized on bluebird trails. The severe winters of 1977-78 and 1978-79 devastated populations and they reached an all-time low in 1978. In 1980, there were only 236 known pairs of bluebirds in the province, although it was thought that the population was more in the order of 1,000 pairs. It was most abundant then along the southern edge of the Shield and on Manitoulin Island. Populations were considered stable or possibly increasing at that time, and the Eastern Bluebird was designated special concern in Canada (Read 1998, 2006; Risley 1981, 1994). During the first atlas, it was more numerous and widespread than previously thought. It was estimated that there were about 2,000 pairs in the province. Numbers appeared to have been increasing since about 1980, largely due to the efforts of bluebird trail operators. In 1998, its status was reassessed as not at risk (Read 1998; Risley 1994). James (1991) considered the bluebird a locally common summer resident in the agricultural south, rare to locally common in the north to Lac Seul and Cochrane, and formerly present and still possible north to Favourable Lake and Moosonee.

The second atlas showed a significant increase in the probability of observation of the Eastern Bluebird for the province as a whole and in all regions that it occurred in, compared with the first atlas. Highest densities occurred south of the Canadian Shield, where it was typically associated with well-managed bluebird trails, and in western Rainy River District where there are extensive pastures

that provide suitable breeding habitat. Distribution was patchy in the Shield indicating a scarcity of suitable habitat, although birds nesting in clear-cuts and burns may have been missed due to lack of coverage (Read in Cadman et al. 2007).

Breeding Bird Survey data for 1970-2021 indicate that the bluebird increased at annual rates of 1.29% in Canada and 0.956% in Ontario. The trends 2011-21 were annual decreases of 2.23% in Canada and 2.53% in Ontario. The long-term results for Ontario were highly reliable; the other results were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young birds that fledge prematurely cannot fly, but are capable of climbing trees to reach cover and shelter. Fledglings remain in or near cover for 7-10 days after leaving the nest and may remain in family groups for 3 weeks. Young are typically fed by the adults until they are 35-40 days old, rarely to age 47 days. Females raising a second brood stop feeding the first fledglings when they are 7-10 days old. Young begin feeding themselves at 22-28 days of age. Those from first nests often leave the natal territory upon independence. Those from later broods often remain on the territory and may stay with their parents all winter. Consequently, natal philopatry may be lower for birds of first broods (Gowaty and Plissner 2020).

Family groups may remain near the nesting area in late summer and early autumn. In Michigan, a group of 12 birds that included a pair, some of their young, some fledglings from the yearlings' nest, and young from a nest that juveniles had helped at, all expelled other bluebirds from the area they occupied (Pinkowski 1976b). Once birds become independent, juveniles form flocks comprised of many families. Flocks range widely, but usually remain in the vicinity of the natal area, although there are reports of juveniles recovered in their natal year 20-300 km from the natal site. Single and multifamily flocks of juveniles may make flights of several kilometres at a time (Gowaty and Plissner 2020).

MIGRATION

Within a given area, some bluebirds migrate whereas others remain all winter. More birds migrate from harsher climates and all birds nesting in central and northern Ontario migrate. Some northern migrants pass over resident populations in the south to winter even further south. Ontario birds have been recovered in winter or late spring in Kentucky, North Carolina, Georgia, and Florida. Individuals may migrate some years and stay over winter in others. In Michigan, birds remained over winter only if they had nested successfully. Food availability influences migration and this may be affected by weather. In the Hamilton area, cool summers result in poor crops of buckthorn and sumac. More bluebirds migrate south then and do so earlier than after summers with ample supplies of fruit. The bluebird is a diurnal migrant with no evidence of nocturnal migration. Movement is in small, loose flocks that travel mostly in the morning (Brewer et al. 2018; Gowaty and Plissner 2020; Pinkowski 1976b, 1977a; Read 2006).

In spring, males usually arrive a few days earlier than females although pairs sometimes arrive together (Banfield and Robert in Gauthier and Aubry 1996; Bent 1949; Gowaty and Plissner 2020). In southern Ontario, bluebirds begin arriving in mid-March and the peak of migration is in mid-April. In the southern Shield, average arrival is mid-April with the earliest arrivals in mid- to late March. In

the southern Shield, family groups begin wandering in August and small flocks may be seen throughout September and into October. In the south, migration begins in mid-September and peaks mid- to late October (Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Risley 1981; Tozer 2012; Weir 2008).

During migration, habitat used by the Eastern Bluebird is similar to that of the breeding season, except for greater use of open-canopy forests. Birds may prefer to move along corridor edges. Roosts continue to be an important habitat component. In Arkansas, migrating birds frequently roosted in trees at the base of a hill. In early spring in Michigan, an adult male and his offspring male roosted together in the same nest box they used as a roost the previous winter. This appears to be the first record of fidelity to a roosting site (Gowaty and Plissner 2020; Pinkowski 1976b; Thomas 1946a).

During spring migration, the bluebird feeds predominantly on residual fruit until insects become available. During autumn migration, fruit dominates the diet. In Ontario, it is likely that buckthorns and sumacs are important in the diet (Read 2006; Risley 1981).

The Eastern Bluebird was formerly an abundant migrant in Ontario and is more common in autumn than spring. Fleming (1907) considered it an abundant migrant in the Toronto area. There are records of many thousands passing over Toronto from west to east each day for a week during spring migration in the early 1900s (Risley 1994). It is now an uncommon migrant (James 1991), although it may occasionally be locally common.

WINTER

The winter distribution of the Eastern Bluebird is strongly correlated with temperature. In the north, its distribution infrequently extends into regions with an average January temperature lower than –7°C. It is highly concentrated in winter in areas that are warm and moist. It is most common where the frost-free period averages about 180 days and there is more than 61 cm of precipitation annually (Root 1988).

In Elgin County, most wintering flocks of bluebirds are found in sheltered places in gullies, predominantly near Lake Erie, particularly where there is lots of sumac, one of the staple foods (Lancaster et al. 2004). In Illinois, it winters along major rivers and in forests and forest edges, shrubby areas, ungrazed grasslands, pastures, and alfalfa fields. In Kansas, preferred winter habitat included open groves of black walnut and honey locust, particularly those on hilltops with shallow soils and short grasses. In Missouri, it was present in moderate density in savannahs, with highest density in woodlands and lowest density in forest. In Arkansas, Kentucky, and Mississippi, there was no difference in its density in fields with or without grassy buffers. Other habitats that may be used in winter include orchards and parklands (Evans et al. 2015; Fitch 1958; Graber and Graber 1963; Graber et al. 1971; Gowaty and Plissner 2020; Kendrick and Thompson 2013).

Roosts are even more important in winter to protect bluebirds from the elements. In Arkansas, 1 roosted in a rotting stump; nest boxes were used for roosting only on the coldest nights. In Tennessee, nest boxes were used only once the temperature dropped below –10°C. Nest boxes containing used nests provide additional protection from cold. Bluebirds have also roosted in old robins' nests (Bent 1949; Gowaty and Plissner 2020; Pinkowski 1977a; Pitts 1979; Thomas 1946a).

Winter flocks of 2-30 bluebirds may defend feeding areas, although defence is less intense than during the breeding season. Family groups and pairs may defend areas around nesting cavities where most birds are year-round residents. Winter home ranges are larger than the defended areas. In South Carolina, where it is resident, home ranges averaged 105.9 ha for males and 120.8 ha for females. Two females had an average home range size of 224 ha from February until April (Gowaty and Plissner 2020).

The winter diet of the bluebird is dominated by fruit, although Pinkowski (1976c) observed several small flocks preying on winter stoneflies emerging from fast-flowing streams. Over 60 species of fruit have been documented in its winter diet, but sumac is one of the staples throughout its range. In Tennessee, analyses of fecal and regurgitated matter indicated that individual birds typically foraged on a single species during each feeding. The diet consisted of 54% sumac, 37% Japanese honeysuckle, 5% holly, and less than 1% each for greenbrier, wild rose, bittersweet, pokeweed, hackberry, and wild grape. In Illinois, mistletoe was most prominent in the winter diet, but grapes, sumacs, hawthorns, and holly were important and Virginia creeper was occasionally consumed. Winter fruits eaten in Georgia included those of black gum, blueberry, black cherry, currants, flowering dogwood, Japanese honeysuckle, pokeweed, red cedar, smooth sumac, and several species that do not occur in Ontario (Bent 1949; Gowaty and Plissner 2020; Graber et al. 1971; Petrides 1942; Pitts 1979).

The Eastern Bluebird is a rare visitor to winter feeders in Ontario, but may visit almost 25% of feeders further south. It is less frequent at urban feeders than elsewhere. Even where it visits feeders, it usually is not present week to week. Flock sizes decline from January on, but the number of feeders visited increases at the same time, probably reflecting the beginning of spring migration. Dried fruit is the most favoured food at feeders followed by water. It infrequently eats mixed seeds, striped sunflowers, suet, and bird puddings. It may also eat peanut hearts, peanut butter mixes, and peanuts in the shell (Dunn and Tessaglia-Hymes 1999).

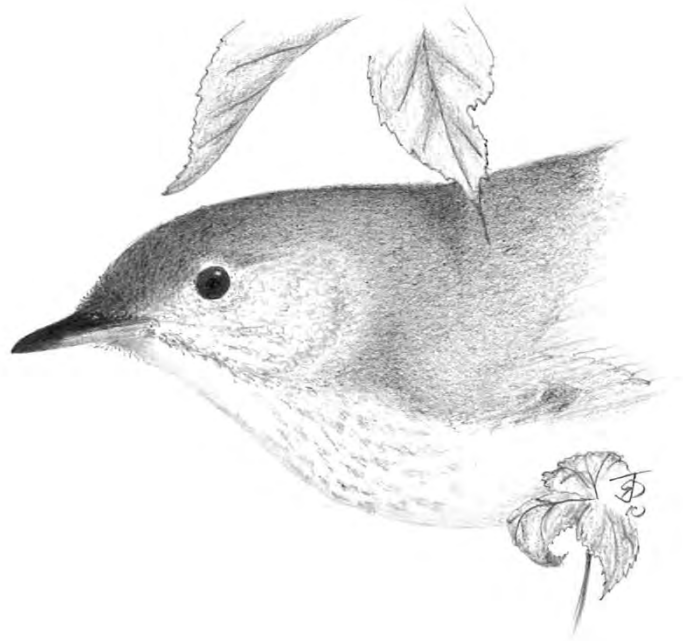
Severe winter weather may now be the greatest limiting factor to the Eastern Bluebird. Severe weather may result in massive mortality and this can affect continental populations if cold, wet weather is widespread in the southern United States. The first reported significant decline was after the winter of 1894-95 when populations declined throughout its range, but full recovery occurred in a few years. In Ontario, populations were significantly depressed after the severe winters of 1894-95, 1911-12, 1957-58, 1976-77, and 1977-78, with a lesser decline after the winter of 1939-40. After the winter of 1957-58, only 3 bluebirds were found in the Kingston region in the summer of 1958. Prior to 1957, populations recovered within 3 or 4 years of a severe winter, but there was limited recovery after bad winters in the 1950s and 1970s. The Michigan breeding population declined by 50% after the winter of 1976-77 and similar declines occurred across North America. Local winter storms may result in declines if food supplies are covered in ice or snow or the weather is extremely cold. There appeared to be massive mortality in Illinois following an intensive winter storm (Bent 1949; Graber and Graber 1963, 1979; Pinkowski 1979; Risley 1981, 1994; Weir 2008; Zeleny 1976).

The Eastern Bluebird is rare and locally uncommon in winter north to Kingston (James 1991). In Elgin County, it was rare in winter in the 1950s. Highest numbers in Canada were reported on Elgin County Christmas Bird Counts (CBC) in 1999, 2000, and 2001 (Lancaster et al. 2004). In the Hamilton

area, the first winter bluebird was not seen until 1954, but small numbers began overwintering regularly in the mid-1980s. Bluebirds were documented on every Hamilton CBC since the mid-1980s except 1993 and 1996 (Curry 2006). The increase in wintering bluebirds may be related to weather conditions and food supplies. From 1947 to 2005, rainfall increased from 340 to 400 mm during the May to September growing season which was beneficial to growth of fruit-bearing trees and shrubs, and therefore bluebirds. Numbers overwintering in the Hamilton area are related to weather conditions with more occurring in warmer winters and winters following hot summers that produce ample supplies of soft mast (Read 2006).

Veery

Catharus fuscescens

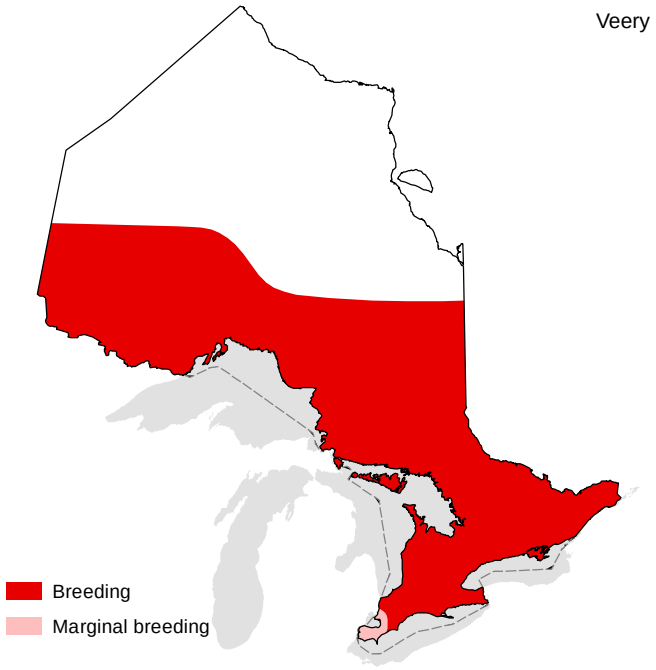


BREEDING SEASON

Habitat Requirements

The Veery usually breeds in woodlands in Ontario, but 4 nests were reported in overgrown fields and one of these was near a woodland edge. Mixed (50.3% of nests) and deciduous (41.5%) woodlands were selected for breeding much more than coniferous (8.1%) forests. Most wooded areas that supported the Veery were open second growth with a heavy understorey or dense ground cover. Several nests were at woodland edges near roads, shorelines, clearings, or fields. Wet habitats were used for nesting much more often than dry sites (Peck and James 1987).

In the Boreal Forest Region of Ontario, abundance of the Veery was significantly correlated with edge. This was a measure of forest-cover configuration and age-class interspersion rather than interfaces between forested and open habitats. It was associated with immature to younger deciduous stands with fairly open conditions (Rempel 2007). In Quetico Park, it was most abundant in early succession forests 1-23 years after a forest fire. It occurred in low numbers in mature stands, but was absent in intermediate-aged and old-growth forests (Apfelbaum and Haney 1985). Welsh (1993) concluded that it was a mid-succession species in northwestern Ontario, reaching highest



density in forests 12-21 years old. Near White River, it was more common in clear-cuts 23-25 years old than clear-cuts 3-20 years old and mature forest, but not significantly (Venier and Pearce 2005).

In jack pine stands near Gogama, the Veery always occurred in forests where there were few or no conifers. It first appeared when forests reached about 10 years of age and persisted in low numbers in more mature forest as long as the undergrowth remained lush. Deciduous trees in stands could be widely spaced provided that taller shrubs were numerous (James and Peck 1995a). In Algonquin Park, Martin (1960) considered the Veery characteristic of deciduous forests, especially those dominated by aspen and white birch. Density declined with intrusion of balsam fir and spruce into aspen-birch stands. It was absent in balsam fir–black spruce, immature white pine, and hemlock stands. In Muskoka District and Haliburton County, it was associated with intermediate canopy volume and slightly less than mean tree density. Singing perches were in deciduous woodlands with a well-developed understorey. Nest sites were associated with intermediate canopy volume and tree density and very high shrub coverage. It would be expected to benefit from tree removal in mature forests if the understorey was not disturbed, resulting in greater shrub density and development of the understorey (Clark et al. 1983). In Parry Sound District, it nested in a moist, open deciduous forest dominated by sugar maple, black ash, and basswood. The forest had a dense understorey of sugar maple and red elderberry. The forest floor was dominated by tree seedlings, spotted jewelweed, raspberries, and spinulose woodfern (Reynolds and Mills 1981).

In Durham Region, the Veery occurred over a wide successional range, but reached its greatest abundance in mid-succession forests. It was most abundant in a young forest with open canopy, poor drainage with standing water, and rank growth of raspberries and tree seedlings. It was also common in a black spruce bog rimmed by deciduous swamp; another open woodland with much of the forest floor under water and a rank growth of ferns and raspberries; mature maple-oak forest adjacent to a floodplain with standing water and dense growth of sensitive and royal ferns; and in a mature sugar maple–beech woodlot with a few springs and gullies and a sparse understorey (Speirs and Orenstein 1975). In the Lake Simcoe watershed, territories had higher mean abundance of black cherry trees, a greater number of logs, and a lower number of trees with a diameter at breast height (DBH) of 23-38 cm than unoccupied areas. It occupied areas characterized by second growth having low, open forest canopies with standing water, little leaf litter, and few mature trees. Second-growth habitat was either regenerating forests, degraded, or floodplain forests. The Veery was found in areas

with high ground coverage by ferns and mosses with large numbers of vines and logs. It was most likely to occupy deciduous forests rather than mixed or coniferous forests and occurred most often in forests with an overstorey of ash and red maple and an abundance of understorey balsam fir. Food sources such as riverbank grape, bunchberry, and black cherry may be important habitat components (Hawey et al. 2020). In the Kingston area, it bred in small numbers in open space within urban areas, and on Amherst and Wolfe islands (Weir 2008).

In the Carolinian Forest Region in Elgin County, the Veery's preferred breeding habitat was larger deciduous or mixed woodlands with patches of cool, damp, dense undergrowth (Lancaster et al. 2004). McIlwraith (1894) stated that some nested in the Hamilton area among the undergrowth in moist, uncleared forests. In the South Walsingham Forest in Norfolk County, its abundance was significantly correlated with shrub density and shrub layers 0-0.3 m, 0.3-1 m, and 1-3 m in height. Its presence was negatively associated with the basal area (BA) of trees smaller than 38 cm DBH and total BA, but there was no relationship with the BA of trees larger than 38 cm DBH. Shrub development was particularly important to the Veery (McCracken et al. 1998).

In addition to forests, the Veery occasionally nests in shrub thicket swamps, in old fields grown up with shrubs and saplings, and in regenerating clear-cuts. These habitats are used only occasionally in Ontario, but are more readily and widely used in the western portion of its range. In Wisconsin, it nested in willow and alder shrub thickets (Hoffman 1989b). In mountainous areas of Wyoming, it was most abundant in lower communities of cottonwood and willows, but was also common in mid-elevation willow shrublands (Finch 1991a). In British Columbia, it nests in aspen and birch forests, in steep hillside gullies filled with shrubs, margins of clearings or abandoned farmland, shrubs along borders of beaver ponds, and other moist woodlands with dense shrubbery (Campbell et al. 1997). In Maine, it was most abundant in alder thicket swamps. Most singing males were in either pure alder or deciduous and mixed forest with red maple and alder (Morse 1971a). In North Dakota, it nested in all forest habitats, but highest densities occurred in willow shrubs (Faanes and Andrew 1983). In New Jersey, it was absent in 10- and 20-year-old successional fields, but present in a 40-year-old field. This field had wooded borders. The Veery increased as shrubs choked out open spaces or as herbaceous cover got shaded out by trees (Suthers 1988).

The Veery nests in a wide range of deciduous and mixed forest types throughout its range, and much less frequently in coniferous forests. It is most likely to occur in swamps and lowland forests, but occasionally nests in forest stands on dry soils. If dry upland forests have damp depressions or seeps, it is often associated with these, or colonizes these areas first in spring. Forest types it has nested in include hemlock bottomland forest, northern hardwoods, lowland hardwoods, aspen-birch, occasionally in pine forests and upland spruce-fir forests, lowland black spruce, lowland tamarack, maple-beech–yellow birch forests, sandy hillsides interspersed with wetlands, mature bottomland forest, white oak, red oak, red maple swamps, black spruce–white cedar swamps, young white pine–alder, dry oak-pine woods, apple orchards (at least formerly), aspen forests, beech-maple-oak forests, and pine-oak barrens with pockets of forest (Back 1979; Beals 1960; Campbell et al. 1977; Capen 1979; Crawford and Titterington 1979; Dawson 1979; Erskine 1977; Gates and Giffen 1991; Golet et al. 2001; Graber et al. 1971; Hoffman 1989a; Holmes and Robinson 1988; Leighton et al. 2002; Martin 1960; Morse 1971a; Mossman et al. 1991; Noon et al. 1979; Samson 1979; Temple et

al. 1979; Tyler in Bent 1949). In the Boreal Forest Region, Erskine (1977) considered the Veery one of the typical species in poplar or birch stands, but also characteristic in swamps and floodplain forests. It is strongly associated with deciduous trees and shrubs, but also nests in mixed and coniferous woods and uses areas dominated by coniferous shrubs. In many areas, mixed and coniferous stands dominate lowland areas and provide suitable habitat. Areas supporting hemlock and balsam fir may be attractive to it. In some areas, its abundance has been correlated with the density of coniferous shrubs. In forests heavily browsed by deer in Michigan, its abundance was somewhat greater in areas with abundant deciduous understorey than in understorey dominated by balsam fir. Nonetheless, presence of balsam fir and some deciduous shrubs shorter than 1 m (presumably protected by snow depth) allowed it to persist in heavily browsed forests. It commonly nested in firs 2-3 m tall indicating that an abundance of taller firs may be important in some stands, although density of balsam fir was not a reliable predictor of its abundance (Dilger 1956; Gates and Giffen 1991; Kearns et al. 2006; Tyler in Bent 1949).

The Veery was restricted to landscapes with 65-75% forest cover in North Dakota and 99-100% forest cover in New York. In North Dakota, the maximum tree coverage present was 75% (Cunningham and Johnson 2019).

Although the Veery nests in a wide variety of forest types and forest ages, it has some specific habitat requirements. The most important appears to be a well-developed understorey of shrubs or lush fern or herbaceous plant coverage. Moisture regime is also important, with wet or damp sites preferred over dry forests. Finally, deciduous shrub and tree cover is important; it generally declines in abundance with increasing conifer coverage, although it may be associated with understorey balsam fir.

The Veery prefers a dense understorey, but may find very high densities of saplings unattractive. In New York, it declined with forest maturation and the associated loss of vertical and horizontal structural diversity. In West Virginia, it occurred in selective cuts but not in mature forest (Litwin and Smith 1992). In Maryland, it was significantly associated with both herbaceous and overall ground cover and with short and tall coniferous shrub coverage (Gates and Giffen 1991). In New Jersey, it occurred in second-growth and climax logged forests but not in wet disturbed forests. Climax forests tended to attract more Wood Thrushes than Veeries as the understorey became increasingly open (Suthers 1988). In eastern northern hardwood communities, it occurred in 18% of mature, undisturbed forests compared with 77% of disturbed and successional habitats. It exhibited a negative trend with forest succession (Noon et al. 1979). Temple et al. (1979) considered it associated with increasing abundance of yellow birch and sugar maple and also with late and mature seral stages of forest. Niemi and Pfannmuller (1979) reported that it was associated with increasing numbers of shrubs but decreasing numbers of saplings. In the mid-Atlantic states, it was positively correlated with foliage density at 0.3-1.0 m and the number of dead standing trees larger than 3 cm DBH. It was negatively associated with the number of trees and mean canopy height (Robbins et al. 1989). In Wisconsin upland forests, it inhabits cool, damp pockets and stream bottoms where there is often a dense understorey; it also nests in the dense understorey of cutovers. In New York, moist disturbed bottomland deciduous and coniferous forests with a lush understorey of ferns and other plants provided optimal conditions. Undisturbed forests probably did not support a dense enough

understorey for the Veery (Dilger 1956). In Connecticut, the amount of herbaceous cover was important. Important plants in territories were either early succession species or those associated with moist soils, and included grey alder, gray birch, black cherry, apple, white elm, and nannyberry (Bertin 1977). On islands in Wisconsin, it occurred in greatest numbers in aspen and red oak forests, especially where the understorey was densest (Beals 1960). In Vermont, it was significantly associated with shrub density, percent coniferous shrubs, and percent ground cover (Noon 1981). In his habitat suitability index (HSI) model, Sousa (1982) considered the structure of the shrub layer to be the key vegetation habitat component for the Veery. It occurred in open and undisturbed areas of deciduous, mixed, and coniferous forests where the density of deciduous shrubs was significantly higher than in the surrounding forest. More than 70% deciduous shrub coverage provided ideal habitat. Areas with less than 20% shrub coverage were probably unsuitable. Shrubs 1.5-3.0 m tall were considered optimal, shrubs less than 0.5 m tall were considered unsuitable, and shrubs or regenerating trees 5 m in height were considered to be half as valuable as shrubs 1.5-3.0 m tall. For ground cover, optimal conditions were more than 90% coverage with herbaceous plants taller than 30 cm. Less than 30% herbaceous cover was considered unsuitable. Herbaceous cover added to the overall quality of habitat, but was only half as important as shrub coverage. In New Hampshire, the shrub and sapling layers became denser over time and all thrush species declined (Holmes and Robinson 1988). Heckscher et al. (2020) stated that shrub cover is the main vegetative consideration in habitat selection by the Veery. In Quebec, Falardeau (in Gauthier and Aubry 1996) considered it characteristic of deciduous woodlands with a fairly open canopy and a dense understorey; it also occurred in mixed-wood forests. In Wisconsin mesic forests, young dense forests of aspens formed after clear-cutting or fire were favourable (Hoffman 1989a). In Delaware, nest sites differed significantly from random sites and were characterized by dense foliage below 1.5 m with sparse vegetation within the 2.5-3.0 layer (Heckscher et al. 2020). In a Connecticut woodlot over a 59-year period, there was a progressive shift to larger trees, a sparser shrub layer, and a less diverse tree canopy. The Veery decreased, probably due to the decrease in shrub cover (Buchanan et al. 2016). Almost all studies concur that dense shrub coverage is the most important habitat variable for the Veery and that lush herbaceous growth may be important but not essential. An exception is in mountainous areas of Wyoming. Bare ground comprised as much as 50% of the surface area in any territory compared with 14.3% at random sites and shrub coverage (34.4%) was always less than at random sites (Finch 1989b).

Although the Veery occasionally nests in dry forests, it reaches its greatest abundance in damp and wet habitats. In many areas, it shows a decided preference for riparian floodplain forests and may be confined to these areas. In eastern Quebec balsam fir–white cedar forests, it was present only in riparian stands and was absent in nonriparian stands of similar composition. When forests covering a wide range of moisture regimes are inhabited, territories along watercourses and in wet areas are occupied first, indicating selection for these areas. In Connecticut, small seeps and springs led birds to establish territories in areas that would probably be unoccupied otherwise. Although presence of water appeared to be important in this study, many territories were far from water in 1 study area and another area supported larger numbers in moist areas away from water. Moisture regime and microclimate variables appeared to be more highly correlated with Veery abundance than vegetation structure (Bertin 1977; Campbell et al. 1997; Dilger 1956; Gates and Giffen 1991;

Heckscher et al. 2020; Holmes and Robinson 1988; LaRue et al. 1995; Leighton et al. 2002; Morse 1971a; Robbins et al. 1989; Sousa 1982).

Other microhabitat preferences have been identified for the Veery. Robbins et al. (1989) found that its presence was associated with the total BA of forest stands. Noon (1981) determined that it was positively associated with BA of coniferous trees, BA of deciduous trees, percent canopy cover, canopy height, density of trees less than 15 cm and more than 22.9 cm DBH, density of trees larger than 38 cm DBH, density of deciduous trees, number of trees per ha, tree size-class diversity, average diameter of trees within a 0.04-ha circle, ratio of total tree BA to average shrub BA, and diameter of the largest tree within a 0.04-ha circle. In New Hampshire and Maine, its presence was significantly correlated with percent ground cover, coniferous trees larger than 10 cm DBH, the number of woody stems per ha, and total foliage volume of coniferous trees 2-10 cm DBH. It was negatively correlated with coniferous trees 2-10 cm DBH, the foliage volume of deciduous trees larger than 10 cm DBH, and the foliage volume of both coniferous and deciduous trees less than 2 cm DBH (DeGraaf et al. 1998). In Delaware, nest sites were characterized by dense foliage below 1.5 m with a sparse overstorey at 2.5-3 m (Heckscher et al. 2020).

The Veery is an area-sensitive species and the minimum size of forest it requires increases as the amount of forest cover in the landscape decreases. In southern Ontario, its probability of detection was positively correlated with the amount of forest 100 m or more from edge, woodlot size, and amount of forest within 2 km, but was negatively associated with the amount of regional forest cover. Woodlot size was the only significant relationship, although the relationship with the amount of forest 100 m from edge was significant at the 10% level (Austen et al. 2001). Also in southern Ontario, the amount of core forest area was the most important predictor of abundance at the scale of 500 m, but was less important at broader scales (Smith et al. 2011). In red maple swamps in Rhode Island, it nested in swamps smaller than 1 ha, but all the swamps were surrounded by upland deciduous forest. Even when the combined area of swamp and upland forest was considered, there was no relationship between its presence and forest size, probably because approximately 60% of the landscape was forested. Its presence was significantly correlated with the amount of deciduous forest within 1 km. Regional forest abundance may be more important in determining its presence and abundance than forest size (Golet et al. 2001). In the mid-Atlantic states, its probability of observation was highest in forests 250 ha in area and was reduced to 50% in 20-ha woodlands. The 3 smallest isolated woodlands that it was detected in were 9.3, 11.3, and 24.1 ha (Robbins et al. 1989). In aspen stands in North Dakota, it was most likely to occur in groves with a greater proportion of trees larger than 23 cm DBH. Probability of detection was 20% in 1-ha stands, 55% in 10-ha stands, and 90% or more in woodlands 100 ha and larger (Grant and Berkey 1999). In northern Illinois where forest cover is only 4-7%, the Veery bred in forest patches ranging from 27 ha to more than 1,000 ha. Only 2 of the 22 forest patches where it nested were smaller than 100 ha; over half were larger than 200 ha (mean 309 ha). Occupied sites had an average of more than 250 ha of additional noncontiguous forest habitat within 2.5 km of the breeding area (Herkert 1995). In southern Wisconsin, the minimum size of forest that had a 50% chance of supporting a breeding population was 24 ha (Mossman and Hoffman 1989). The Veery is area sensitive in Ontario south of the Shield, where it is generally thought to require about 20 ha of forest. It may require much larger forests than

this in extreme southwestern Ontario where there is little forest cover, but may not be area sensitive at all in more heavily forested areas such as the Bruce Peninsula and along the Niagara Escarpment.

Some authors considered the Veery a forest-interior species (Faanes 1987; Freemark and Collins 1992; Golet et al. 2001). In Maryland, Gates and Giffen (1991) considered it an edge species. In eastern northern hardwood communities, Noon et al. (1979) considered the Veery an edge species. In Ontario, it does not appear to be a forest-interior species. It nests throughout forests from the interior to the very edge, and occasionally in unforested shrubby areas. It may tend to nest more in the interior in woodlands that are near the minimum size that it occupies or in landscapes with a low percentage of forest cover, but readily nests near or at forest edge in larger woodlands or when the landscape is heavily forested.

Veery territories frequently overlap with those of other thrush species, including the Wood Thrush, Hermit Thrush, Swainson's Thrush, and American Robin. Agonistic behaviour between these species is rare. Several studies examined microhabitat preferences of the thrushes to determine how they separate themselves without competing for resources.

The greatest overlap in habitat preferences is between the Veery and Wood Thrush and the 2 species commonly have overlapping territories. In mature woodlands in Connecticut, 90% of Wood Thrush territories were overlapped to some extent by Veery territories, and 42% of Veery territories were overlapped by Wood Thrush territories. In this population, moisture was the most important variable for both species. Average microhabitat components in Veery populations were 51.6% shrub coverage, significantly higher than for the Wood Thrush; 15.0 m tree height, significantly lower than for the Wood Thrush; 28.2% early successional stage coverage, significantly higher than for the Wood Thrush; 17.9% late successional stage coverage, significantly higher than for the Wood Thrush; significantly higher moisture regime than for the Wood Thrush; and 6.5% exposed soil, significantly higher than for the Wood Thrush. In Veery territories, there were significantly more striped maple, gray birch, witch-hazel, and Canada mayflower than in Wood Thrush territories, and significantly less red oak, black oak, perfoliate bellwort, and maple-leaved viburnum. The amount of flowering dogwood was almost significantly less in Veery territories. The Veery appeared earlier in succession than the Wood Thrush. When territories in mature woodlands were compared to eliminate the effects of successional stage, no structural or physical parameters differed significantly between Veery and Wood Thrush territories, although shrub coverage was slightly greater in Veery territories (40.2% compared with 33.0%). The amount of shrub coverage was the most important factor separating the 2 species, reflecting the absence of the Wood Thrush in thickets and early successional woodlands. Other significant factors were the presence of striped maple and flowering dogwood (Bertin 1977). Morse (1971a) studied an area in Maine that was originally occupied only by the Veery and Hermit Thrush, but later inhabited by the Wood Thrush. The Veery used moister habitats than the Wood Thrush and was characteristic of damp deciduous forests. The Veery was the only thrush that occupied the wettest habitat, which was alder thicket. As the Wood Thrush became more common, it colonized areas that were more mesic than those used by either the Veery or Hermit Thrush. In 1 case, a Wood Thrush used essentially the same territory that was used by a Veery the previous year; the Veery did not occupy this area when the Wood Thrush was present. The Wood Thrush is larger and may be socially dominant to the Veery. In Vermont, Noon (1981) studied

habitat characteristics of 5 thrush species on a mountain gradient. The Veery overlapped territories with all other thrush species, but there was only about 300 m of elevational overlap in Veery and Wood Thrush territories. The Veery was separated from the Wood Thrush by preferring higher canopy cover, shrub density, and ground cover, and lower density of deciduous trees. The primary difference was shrub density, which consistently separated habitat preferences of the Veery and Wood Thrush. In West Virginia, Dellinger et al. (2007) examined habitat variables around nests of 4 thrush species and found that habitat partitioning occurred at all 3 scales examined: the nest substrate, nest site, and territory scales. Wood Thrush and Veery nest sites had many overlapping variables and were most often misclassified as each other. Both species occurred in forested areas where the ground cover was predominantly leaf litter and woody debris. Veery nests tended to be 1.6 m or lower from the ground; Wood Thrush nests were 1.6 m or higher. Veery nest sites had less woody-debris ground cover, more saplings, and less canopy cover above the nest than Wood Thrush nest sites. The Veery nested at intermediate elevations; the Wood Thrush nested at the lowest elevation. Veery territories were mostly on slopes facing southwest; Wood Thrush territories had a more northeasterly aspect. Both the Veery and Wood Thrush frequently nested in beech, with the Veery usually nesting lower in epicormic branches and the Wood Thrush higher in a main crotch. The Veery was the only species to nest in shrubs such as raspberries, greenbrier, and roses. In New Jersey, climax forests attracted more Wood Thrushes than Veeries as the understorey became increasingly open (Suthers 1988). The primary variables separating the Veery and Wood Thrush appear to be that the Veery prefers areas with denser shrub growth and moister conditions.

The Veery and Hermit Thrush often coexist and may have overlapping territories. In New York, the Veery was positively associated with the Hermit Thrush in the Shield, but not significantly. South of the Shield, Veery presence was significantly negatively correlated with presence of the Hermit Thrush (Dilger 1956). Tyler (in Bent 1949) reported coexisting Veery and Hermit Thrush in Ontario, where the 2 species selected different habitat. The site contained dry, lichen-covered, rocky ridges separated by moist valleys dominated by bracken and other ferns. The Veery was restricted to valleys and the Hermit Thrush occurred only on ridges. On an elevational gradient in Vermont, the Hermit Thrush and Veery did not occur together, but Noon (1981) concluded that Veery habitat might be constrained by the presence of both the Hermit Thrush and Swainson's Thrush. In Maine, the Veery and Hermit Thrush did not occupy any habitat in nearly equal numbers. The only habitats where both occurred regularly were mixed coniferous-deciduous forests and deciduous forests with red maple and alder. Within these habitats, the Veery occurred in the wettest areas, the Hermit Thrush in the driest areas, and the Wood Thrush in areas of intermediate moisture. The Veery selected much wetter areas than the Hermit Thrush. In West Virginia, the Veery placed its nest 2.8 m or further on average from an edge, a greater distance than for the Hermit Thrush. Veery territories were mostly on southwest-facing slopes; those of the Hermit Thrush tended to have a more northeasterly aspect. The Veery was evenly located among slope locations but the Hermit Thrush tended to nest on upper and lower slopes (Dellinger et al. 2007). In Wisconsin, both species occupied disturbed second-growth coniferous forests where over half of each territory was covered with a canopy with a maximum height of approximately 20 m. A well-developed understorey of bracken ferns, shrubs, and tree seedlings grew to a height of 3 m on more than 80% of thrush territories. Both species frequently had adjoining or overlapping territories. Vegetation type and height were important in

partitioning patterns habitat of the 2 species. The Hermit Thrush spent more time in conifers; the Veery concentrated its activities in deciduous species. The Hermit Thrush fed more in conifers and the Veery fed more in shrubs. Both species made little use of aspen relative to its abundance (Paszkowski 1984). Laughlin et al. (2013) studied habitat partitioning by the Veery and Hermit Thrush in Virginia, North Carolina, and Tennessee where the Hermit Thrush has recently colonized. The Veery was a habitat specialist whereas the Hermit Thrush was more of a generalist. Veery territories had a high percentage of cover between 0.5 and 3 m. They had a lower percentage of canopy closure, less leaf litter, and fewer and smaller coniferous trees than Hermit Thrush territories. The microhabitats of the 2 thrushes were significantly different despite the fact that they often nested close together. In Quebec, the Veery nested in damper areas than the Hermit Thrush (Mousley 1916a). The primary habitat features separating the Veery and Hermit Thrush are moisture regime and tree type. The Veery prefers wetter areas dominated by deciduous species; the Hermit Thrush prefers drier areas, often with conifers.

No detailed comparative studies have been undertaken on the habitat preferences of the Veery and Swainson's Thrush. In New York, presence of the Veery was positively associated with presence of Swainson's Thrush in the Shield but the relationship was negative south of the Shield. These relationships were not significant (Dilger 1956). Coexistence of these 2 species in Ontario is predominantly in the southern Shield.

Dellinger et al. (2007) compared nest sites of the Veery and American Robin in West Virginia. Veery nests averaged 2.8 m or further from an edge; robin nests were closer than 2.8 m from edge. Although both species nested in shrubs, the Veery was the only thrush species to nest in very low and weak-stemmed shrubs such as raspberries, greenbrier, and roses.

Males roost in dense vegetation away from the nest at night (Heckscher et al. 2020).

Ontario nests were both on (38.3%) and above (61.7%) the ground. Nests were elevated in or situated at the bases of shrubs, saplings, and trees (61.6% of nests); on, in, or at the bases of stumps (15.3%); among herbaceous plants or clumps of grass (9.5%); on, under, or beside fallen trees, logs, and branches (8.7%); on or under brush or debris (3.3%); and on mossy hummocks (1.7%). For nests in trees and shrubs, deciduous species were preferred (18 species, 58.4% of nests). The other nests were in 6 species of conifers. Nest-tree species in order of preference were balsam fir, maple, alder, spruce, and birch. A small proportion of nests (11) were in crotches of trees and shrubs. Heights of nests above ground ranged from 0.08 to 5.2 m, with most 0.2-0.6 m up (Peck and James 1998). A nest in Parry Sound District was 5.1 m from the ground and positioned against the trunk of a sugar maple. The tree had a dead crown and there was only sparse foliage above the nest (Reynolds and Mills 1981). Tyler (in Bent 1949) reported an Ontario nest that was 0.8 m from the ground in the forks of a fallen limb.

Throughout the Veery's range, it may nest either on the ground or a short distance above it in trees or shrubs, or on stumps. Nests have been found as high as 7.6 m from the ground, but nests higher than 2 m are uncommon; most are lower than 1 m. Most nests are in deciduous trees but balsam fir may be an important nest-tree species. Nests have been reported in the fork of a black cherry tree and in shrubs including raspberries, Japanese honeysuckle, Japanese barberry, mountain

laurel, grape, alder, mountain maple, juniper, greenbrier, and rose. In the mid-Atlantic states, 83% of nests were in multiflora rose, 25% in fallen branches, 8% in Christmas ferns, 5% in spicebush, and 3% in other species; 84% of nests were supported by nonnative species. Of 84 New York nests, 25% were in barberry, 22% in fallen oak limbs, 17% in honeysuckle, 13% in multiflora rose, 5% in open grass tussocks, 3% in witch-hazel, and 15% in others. Based upon availability, most native species were avoided and barberry and rose were preferred. Unusual nests have been reported in tree hollows, in a tin can, and 3 m up on the horizontal limb of an apple tree. There is no evidence that nests are reused, but the same shrubs may be used for nesting in subsequent years (Campbell et al. 1997; Day 1953; Halle 1949; Heckscher et al. 2020; Kearns et al. 2006; LeBlanc 1999; Meyer et al. 2015; Mousley 1916a; Tyler in Bent 1949).

The Veery defends a territory. It can distinguish between the vocalizations of neighbours and strangers and reacts aggressively when strangers intrude (Heckscher et al. 2020). Near Quebec City, territories were evenly distributed with no evidence of clumping or coloniality (Bourque and Desrochers 2006). The size of 61 territories in Algonquin Park averaged 0.27 ha (range 0.04-1.09 ha). Territories extended from the ground upward to the lower tree branches, with an average depth of 7.0 m (Martin 1960). Territory sizes north of Montreal were approximately 0.5 ha in a sugar maple stand and a hemlock stand (Falardeau in Gauthier and Aubry 1996).

No information is available on initial dispersal from the natal site or dispersal from the breeding area (Heckscher et al. 2020), and very little is known about natal philopatry and adult site fidelity. In New Hampshire, Day (1953) banded 105 fledglings and 1 adult over a 15-year period and had no returns. In New Jersey, Suthers (1988) banded 142 and had 14 returns (9.9%) including 1 yearling. In Delaware, 1 of 23 nestlings (4.3%) returned; the return rate of adults over a 12-year period was 62% (Heckscher et al. 2011, 2020).

Limiting Factors

Eggs have been found in Ontario nests from the first week of May until the last week of July, mostly in the first 3 weeks of June (Peck and James 1987, 1998a). Pair formation occurs as soon as the female arrives; the female begins building the nest shortly thereafter. Nest building takes 6-10 days depending on weather conditions. Egg laying begins within 4 days of nest completion. A single egg is laid per day and incubation begins with the laying of the last or penultimate egg. At 1 Delaware nest, incubation began with laying of the second of 4 eggs. The incubation period at 10 Ontario nests was 10-14 days, mostly 11-12 days. Elsewhere, the incubation period has been reported as 10-13 days. Young remain in the nest for 10-15 days. Total time from initiation of nest building to independence of young is about 48 days: 6 days for nest building, 4 days for laying, 12 days for incubation, 12 days for the nestling period, and 2 weeks for feeding fledglings (Allen 1939; Campbell et al. 1997; Day 1953; Dilger 1956; Halley and Heckscher 2013; Heckscher et al. 2020; Peck and James 1998a; Tyler in Bent 1949).

It is uncertain if the Veery raises 1 or 2 broods. Allen (1939) stated that 2 broods were raised but provided no substantiating evidence. Heckscher et al. (2020) stated that there were suggestions of double broods, but no confirming data. In Ontario, Peck and James (1987) noted the possibility of double broods but none were positively confirmed. Campbell et al. (1997) concluded that it frequently attempted 2 broods in British Columbia. In 18 years in Delaware, only 3 females were

known to attempt a second brood but all failed. These attempts may have followed the mortality of fledglings. LeBlanc (1999) provided circumstantial evidence of renesting in New York. Ontario egg dates suggest that at least renesting occurs in the province and it is possible that some birds raise 2 broods. Clutches of 1-5 eggs have been reported in Ontario, with most containing 4 eggs (Peck and James 1987). Small clutches may be due in part to cowbird parasitism. Overall, clutches of 1-6 eggs have been reported. The Veery typically lays 4 eggs, sometimes 3, and occasionally 5 (Campbell et al. 1997; Heckscher et al. 2017, 2020; Tyler in Bent 1949).

The Veery first breeds when it is 1 year old and annually thereafter (Heckscher et al. 2020). It was long considered to be strictly monogamous. Multiple modes of parental care were identified in 1 population: multiple male feeders at nests, males attending multiple nests each with a different female, and 2 males that co-attended the same 2 broods. Of 6 genotyped broods, 2 contained a young sired by an unknown male. All females were the genetic mother of their entire broods. In this population, all 37 genotyped adults were related to at least 1 other bird at the cousin level or greater, and 81% were related to at least 1 other bird at the half-sibling level or greater. It appeared that the kin structure was maintained by natal philopatry in both sexes and that the Veery avoids nesting with close genetic kin. At all nests where adult feeders were genotyped, males were unrelated to the female. There was close kinship between 2 male co-feeders at the nests of 2 females and among 3 of 4 females that were mated to the same polygynous male. At 60% of nests of monogamous pairs, the male was detected as a feeder at a second, third, or fourth nest in the same season, each with a different female. One socially monogamous pair remained together in the second year (Halley et al. 2016).

Foraging occurs on the forest floor and at low heights in vegetation. The Veery may forage on the ground by flipping over leaf debris and gleaning in the shrub layer. In Connecticut, 76% of prey items were obtained by ground foraging, 22% by foraging on vegetation, and 2% by flycatching. In New Hampshire, 74.0% of prey attacks were at heights of 0-0.2 m, 24.4% were in the shrub layer 0.3-2 m from the ground, 0.8% were in the sapling layer 2.1-8 m from the ground, 0.2% were in the subcanopy 8.1-14 m from the ground, and none were in the canopy layer. Fifty-six percent of all prey attacks were in the ground/litter layer, 3.3% in herbs and ferns, 35.8% in foliage, 4.1% on bark, and 0.8% in the air. Prey-attacking manoeuvres were 7.4% probing, 40.6% gleaning, 0.7% jumping and hovering, 33.3% hovering, 15.1% diving and gleaning, and 2.9% hawking. It occasionally perched on rocks or logs, especially near streams, and searched the banks and foliage. When prey was spotted, it dove to the ground and snatched the prey (dive-gleaning). While foraging in Wisconsin, it spent 32% of its time in hardwood deciduous trees, 26% in shrubs, 19% in conifers, and 23% in aspens. Fifty-three percent of foraging time was spent at heights of 3 m or less; it foraged equal amounts of time at other heights (6 m, 9 m, 12 m). During migration, foot quivering to flush prey may be a significant foraging technique that may represent as many as 48% of observations. Although almost all foraging occurs in forested habitat (or thicket swamps if these are used for nesting), it may sometimes visit fields in early morning to feed (Dilger 1956; Heckscher et al. 2020; Holmes and Robinson 1988; Holmes and Sturges 1975; Malmborg and Willson 1988; Paszkowski 1984; Sousa 1982; Tyler in Bent 1949).

Several authors studied the foraging techniques of the Veery, other thrushes, and other low-foraging birds to define habitat partitioning among these species. In New York, all thrush species fed on the ground but the Veery and Swainson's Thrush differed in that they fed more often in the foliage and frequently flycatched. The Veery was primarily an arboreal species that foraged in the interior of forests. The differences in feeding niches involved both the height at which foraging occurred and location with respect to forest edge or interior (Dilger 1956). In Wisconsin, the Veery and Hermit Thrush differed significantly in the amount of time spent in 5 height strata: the ground, 0-3 m, 3-6 m, 6-9 m, and above 9 m. The Hermit Thrush spent 3 times as long on the ground as the Veery and concentrated its activities at heights of 3 m or less. The Veery spent its time equally among the 5 strata. The Hermit Thrush did approximately 25% of its foraging on the ground; ground foraging was less than 10% of the Veery's foraging activity. Overall, the Hermit Thrush was more terrestrial and active most commonly in the lowest forest growth. The Veery was more arboreal, ranging throughout the canopy. Shrubs were the most important foraging site for the Veery in the understorey, with 52% of feeding occurring in the 3-m stratum. Saplings and low tree growth were more important at this height for the Hermit Thrush (79% of feedings; Paszkowski 1984). In New Hampshire, Holmes and Robinson (1988) studied the foraging habitat and diet of 7 ground-foraging bird species: Winter Wren, Veery, Swainson's Thrush, Hermit Thrush, Wood Thrush, Ovenbird, and Dark-eyed Junco. Pairwise comparisons of foraging heights indicated that the Veery was significantly different from the other species. It directed 65% or more of its foraging attacks in the leaf litter, similar to the Wood Thrush, Ovenbird, and Dark-eyed Junco, whereas the remaining species foraged on the ground less than 50% of the time. All species differed significantly in their use of prey-attack manoeuvres. The Veery and Swainson's Thrush were the only species that used the dive-glean technique. The *Catharus* thrushes, especially the Veery and Swainson's Thrush, differed from other species in their search behaviour by flying more often. The Veery was a variable-distance searcher rather than a near-surface or manipulative searcher, along with the Hermit Thrush and Swainson's Thrush. These species searched substrates both near and far from a perch and often took flight to capture more distant prey. Each thrush species had a particular way of foraging that differed from the others. The Veery foraged more on the ground and took a larger proportion of flies, especially crane flies which are often on the litter surface. The Hermit Thrush and Swainson's Thrush foraged from the ground to the canopy, but the Swainson's Thrush was more arboreal. The results from Wisconsin and New Hampshire are somewhat conflicting. In Wisconsin, the Veery was more arboreal than the Hermit Thrush but the reverse was true in New Hampshire. Ground foraging was uncommon in Wisconsin; the high density of shrubs and saplings in the understorey may have inhibited ground foraging (Paszkowski 1984). The species of thrushes present may influence where each individual species forages. There were no Swainson's Thrushes in the Wisconsin study area and it was more arboreal than the Veery in New Hampshire. Presence of the Swainson's Thrush may limit the Veery's use of higher strata. The thrushes partition habitat based on their foraging techniques, but how they do this may vary geographically and be dependent upon which species are present.

Adults initially feed the young hairless caterpillars about 1 cm long, grubs, and small insects. From the fifth day until young leave the nest, they were fed dragonflies, larger insects than during the first 4 days, grubs, caterpillars, and occasionally black swallowtail butterflies (Day 1953). In

Delaware, young were frequently fed crane flies, adult moths, and earthworms (Heckscher et al. 2020).

Early in the breeding season, adult Veeries feed predominantly on insects and other invertebrates but eat increasing amounts of fruit as it becomes available late in the breeding season through to autumn migration. The diet may consist of two-thirds fruit by late summer (Sousa 1982; Tyler in Bent 1949). Beal (1915b) analyzed the contents of 176 stomachs throughout the Veery's breeding range from April through October. The diet consisted of 57.3% animal matter and 42.7% vegetation. Beetles comprised 14.7% of the diet, with no families especially prevalent. Ants comprised 10.4% of the food items and were eaten regularly; other hymenopterans were eaten regularly but accounted for only 3.3% of the diet. Caterpillars were eaten every month and totalled 11.9% of the diet. Grasshoppers were eaten every month except April, with greatest consumption occurring in October (24%), but the annual average was only 4.9%. Bugs (1.3%) and flies (0.9%) were not particularly important in the diet. Isopods, snails, and miscellaneous insects comprised 3.7% of the diet. Spiders (6.3%) were eaten regularly except that none were consumed in October. The vegetation component of the diet was comprised chiefly of fruit, with a few seeds and incidental material. Fruit comprised 35.3% of the diet, of which 12.1% was cultivated and 23.2% was wild. Cultivated fruit included strawberries and raspberries, and it is probable that these were actually taken from wild plants. Besides fruit, the Veery eats a few sumac, grass, and weed seeds. Holmes and Robinson (1988) examined the contents of 18 stomachs from New Hampshire from mid-June to mid-July. They contained 41.5% adult beetles (in order of abundance: soldier, click, scarab, ground, long-horned, and rove beetles, and weevils), 18.8% flies (crane fly adults, larvae of various species, and other adults), 12.9% caterpillars (mostly cutworms and geometer moths), 12.9% hymenopterans (mostly ants), 5.0% spiders, 4.0% bugs, 4.0% molluscs, and 0.9% other. Beetles were the most frequent food item in samples of all 7 ground-foraging species and the same major beetle families (which occur on the forest floor or vegetation) were consumed by all of them. The diet of the Veery differed significantly from the other 6 species except for the Ovenbird. Both fed frequently on spiders and bugs, mostly leafhoppers. The Hermit Thrush ate more beetles, the Swainson's Thrush consumed more ants than other species, the Hermit Thrush and Ovenbird ate large numbers of moth caterpillars, and the Veery, Wood Thrush, and Ovenbird fed more often on flies, particularly crane flies. In New Jersey, 45% of the Veery's diet consisted of fruit. Animal food consisted of 17% beetles, 12% hymenopterans, 10% lepidopterans, 5% grasshoppers and crickets, and 5% spiders. Of 28 stomachs sampled in Louisiana, 12 contained invertebrates only (snails, caterpillars, and centipedes), 11 contained both fruit and invertebrates (snails, caterpillars, and isopods), and 5 contained only fruit (Heckscher et al. 2020). Another study found that the overall diet consisted of 60% invertebrates and 40% fruit. Of the animal foods, the staples were beetles, ants and other hymenopterans, caterpillars (including those of the gypsy moth), grasshoppers, and spiders. Wild fruits consumed included juneberries, strawberries, blackberries, cherries, sumacs, dogwoods, blueberries, wild grape, elderberries, mulberries, spicebush, and honeysuckles. Red elderberry may be favoured because it is found under the canopy in gaps in forests and is one of the earliest woody plants to fruit. It is available during the nesting season and is occasionally fed to fledglings. Where it is available, spicebush fruit may be preferred. In Illinois, 94% of fruit consumed was spicebush and the remainder was wild grape. Foraging occurred more often than expected in forest gaps than

interior. The Veery occasionally eats small vertebrates such as tiny frogs and salamanders (Allen 1939; Dilger 1956; Heckscher et al. 2020; Malmborg and Willson 1988; Stutchbury et al. 2005a; Tyler in Bent 1949). Near Manitouwadge, abundance of the Veery increased significantly overall and in stands 1-21 years old with increasing numbers of spruce budworms (Venier et al. 2009). In Maine, spruce budworm larvae and pupae constituted 46% of the volume of food consumed by 2 birds (Mitchell 1952).

The Veery is a common host of the Brown-headed Cowbird. The rate of parasitism varies geographically and is probably higher where forest habitat is fragmented and less extensive. In Ontario, 82 of 429 nests (18.9%) were parasitized and 17 of 128 southern Quebec nests (13.3%) were parasitized. In south and central Ontario, distance from forest edge did not affect parasitism rates. In New York, 7 of 30 nests (23.3%) were parasitized; 0 of 11 nests were parasitized in Minnesota. In Maryland, 28.2% of 39 nests were parasitized; 0 of 42 nests were parasitized in Delaware. In 2 study areas in British Columbia, parasitism rates were 24.0% and 38.7%. In Alberta and Manitoba parasitism rates may be as high as 87%. The Veery appears to have no defences against the cowbird and readily accepts eggs. Both Veery and Brown-headed Cowbird young may be fledged from nests. In a sample of 11, the Veery fledged more of its own young in unparasitized nests (2.5 young per nest) than in parasitized nests (2.0; Burke and Nol 2000; Campbell et al. 1997; Falardeau in Gauthier and Aubry 1996; Hahn and Hatfield 1995; Hanski et al. 1996; Heckscher et al. 2020; Peck and James 1998a; Tyler in Bent 1949).

South of the Canadian Shield, forest loss and fragmentation may have adverse effects on the Veery. In different-sized forest patches in southern and central Ontario, reproductive success was similar in large forest fragments (average size 849 ha, range 81-2,353 ha, average of 121 ha of forest 100 m or more from edge) and contiguous forest. Success rates in small forest fragments (average size 93 ha, range 11.8-365 ha, average of 7.8 ha of forest 100 m or more from edge) were close to maintenance levels, but were population sinks. Predation rates were highest in small woodlots (64.3%), but only 23.1% in large woodlands and 33.0% in contiguous forest. Parasitism rates by the cowbird were not influenced by forest size and were 0%, 15.4%, and 9% in small, large, and contiguous forests, respectively. There were no significant differences in reproductive success rates between fragmented landscapes and continuous forest (Burke and Nol 2000). In Ontario south of the Shield, the effects of fragmentation on the Veery were scale dependent. The amount of core forest area had a strong positive effect at small scales of 500 m, but a strong negative effect at larger scales. The amount of habitat was more important than fragmentation. The effects of fragmentation were weak at large scales (Smith et al. 2011). Negative effects of fragmentation are more important when the amount of available habitat is low. Nol et al. (2005) found that the probability of the Veery occurring in small forest fragments was associated with distance to the closest large woodland that acted as a source for it. There was a 12-15% reduction in its probability of occurrence with every 1 km increase in distance from a large fragment. The number of large forests within a region did not affect occupancy rates of small woodlots. Occupied small fragments were generally less than 14 km from large fragments and much closer than this on average.

Forest practices may be beneficial or detrimental to the Veery, depending on the technique used and the intensity of the operation. Selective thinning tends to be beneficial because this opens

up the canopy and allows the shrub layer to develop. In Algonquin Park, it was unaffected by typical and intensive group-selection tree harvesting. There were no differences in its abundance in uncut stands and in recent and old single-tree selection cuts (Jobes et al. 2004; Tozer et al. 2010). In the Sault Ste. Marie area, it increased in all forests where selection thinning occurred, but not until 6-7 years after harvest. It was associated with hardwood regeneration (mostly sugar maple) rather than small shrubs (Holmes and Pitt 2007). In the Carolinian Forest Region of Ontario, it exhibited a preference for recent cuts over old cuts, and heavy cuts (diameter limit) were most preferred (Holmes et al. 2004). In the Boreal Forest Region of Ontario, there was no difference in its abundance in early successional or mid-successional clear-cuts compared with similarly aged burns, and it was equally abundant in early succession, mid-succession, and mature forests (Zimmerling et al. 2017). In some areas, the Veery may have experienced a northward range expansion due to deciduous growth once large tracts of coniferous forest were logged (Falardeau in Gauthier and Aubry 1996; Webb et al. 1977). In Pennsylvania, 2 types of improvement cuts were made in forests. In the first, all dead, dying, diseased, suppressed, and low-quality trees were removed. The second treatment was the same except that snags were retained. The Veery was much more abundant in stands where snags were retained. These plots had significantly more low-growing vegetation and shrubs than sites where snags were removed (Stribling et al. 1990). In Quebec, the Veery did not appear to be particularly affected by clear-cutting of areas 1-8 ha in size, but after larger areas were clear-cut it was absent for about 6 years (Falardeau in Gauthier and Aubry 1996). In New York, Webb et al. (1977) did not observe the Veery in unharvested forest stands, but it was present in selectively harvested stands and increased in abundance with the intensity of harvest. Logging changed unacceptable mature stands into acceptable second-growth stands. In New York, it colonized clear-cuts soon after cutting, particularly in those exhibiting rapid regeneration and early canopy closure. It was the dominant species by the eighth year after harvest (Keller et al. 2003). In Minnesota, Manolis et al. (2002) examined edge effects near regenerating clear-cuts for several species, including the Veery. For all species, distance to the nearest clear-cut edge was the best predictor of nest failure. There was strong evidence of a negative edge effect on ground nests extending 100 m or more from clear-cut edges in a forest-dominated landscape. Also in Minnesota, it was more abundant in riparian buffers that were clear-cut than those that were uncut (Hanowski et al. 2005). In Nova Scotia, it was absent in clear-cuts until about 5 years after cutting, with highest densities occurring in stands 8-30 years old (Morgan and Freedman 1986). In Vermont, it tended to avoid small (0.7-1.6 ha) cut patches in hardwood forest (Lent and Capen 1995).

High densities of white-tailed deer can be detrimental to the Veery. Extreme browsing reduces the density of shrubs or saplings in the understorey and makes habitat less favourable (Kearns et al. 2006).

In New York, Veery nests were built in areas with significantly higher eastern chipmunk density than random sites. Its preference for situating its nests in dense shrub patches may make it more vulnerable to predation by chipmunks (Emmering et al. 2018).

In North Carolina, Veery abundance was significantly negatively correlated with temperature, suggesting that it may be vulnerable to climate change in that area. It was negatively correlated with the number of houses and buildings within 200 m of the centre of the breeding patch, but not

significantly. Its abundance was significantly negatively correlated with temperature and number of buildings combined (Lumpkin and Pearson 2013).

In Pennsylvania over a 15-year period, hemlock basal area declined from 56% of the total to 46% as a result of mortality from the hemlock woolly adelgid. There was an increase in deciduous undergrowth as a result of openings in the canopy. The Veery responded positively to the decline in hemlock, probably because of the increase in deciduous shrubs and saplings (Toenies et al. 2018).

In New York, there was no difference in daily nest survival rates in nonnative and native species. Veeries facultatively used nonnative shrubs as nest sites (Meyer et al. 2015). Similar results were documented in Pennsylvania. Almost 60% of 289 nests were in nonnative shrubs, particularly Japanese barberry and multiflora rose. Nest survival, clutch size, and number of young fledged did not differ between nests in native and nonnative shrubs (Goguen and Murray 2025).

Status

The Veery has always been common in Ontario and was probably more common south of the Shield prior to European settlement. McIlwraith (1894) considered it the most common thrush in Ontario next to the robin. Baillie and Harrington (1937) reported that it bred from the southern boundary of the province north to at least southern Sudbury District and Ottawa, and also in southern Thunder Bay and Kenora districts. They considered it common, especially in the southern portion of its range. Mills (1981) reported that it was one of the most common birds of mixed and deciduous forests in Muskoka and Parry Sound districts. It was third in abundance in the South Walsingham Forest where it represented 7.45% of all records (McCracken et al. 1998). It was very common in the Kingston area in the 19th century and there was little change in its status except for some habitat loss due to expanding urban areas (Weir 2008). In Elgin County, where forest habitat is more fragmented, the Veery was common in 1891, but not as common as the Wood Thrush. It was still fairly common in 1954, but by 2000 it was uncommon, breeding in small numbers (Lancaster et al. 2004). During the first atlas, the Veery occurred in high densities and was common both in the north and south. It bred further north than previously recorded, to Timmins, Kirkland Lake, Matchewan, Virginiatown, Schreiber, and northeast of Lake Nipigon. These records probably represented a recent range extension. It was virtually absent from the agricultural areas of Essex County, the fruit lands of Niagara below the Escarpment, and the urban area of Toronto (Sadler in Cadman et al. 1987). James (1991) considered the Veery common in the south, becoming uncommon in the north to Sioux Lookout and Cochrane.

The second atlas indicated that there had been no change in the breeding distribution of the Veery since the first atlas. It disappeared from some more intensively farmed areas in the southwest, notably in western Chatham-Kent and Lambton counties. There was no overall difference in its probability of observation between the 2 atlases. Significant declines south of the Canadian Shield were offset by a significant increase in the Boreal Forest Region. It was most abundant in the Shield in the Great Lakes–St. Lawrence Forest Region, particularly from the Sudbury area south to the edge of the Shield. Within this area, the Veery was found in 95% of squares during both atlases. Its abundance was considerably lower in the Algonquin Highlands, possibly due to the controlled selective cutting in Algonquin Park which may create less suitable habitat for the Veery than is found in adjacent areas (Friesen in Cadman et al. 2007).

Breeding Bird Survey data indicate that the Veery decreased at annual rates of 0.577% in Canada and 0.987% in Ontario 1970-2021. The trends 2011-21 were annual decreases of 0.266% in Canada and 1.04% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young are led to dense habitat as soon as they leave the nest. The brood is split for the first 2 weeks after fledging, with the female caring for the larger number in odd-numbered broods. In an 18-year study, there was only 1 observed case of both adults caring for an individual fledgling. Fledglings begin to hunt insects and find fruit on their own after about 2 weeks and parental care ceases 14-17 days after fledging (Heckscher et al. 2020).

During the postbreeding period in West Virginia clear-cuts, presence of adults was positively associated with arthropod biomass and the total amount of fruit available. Abundance of juveniles was positively associated with the amount of ripe fruit and negatively associated with the vertical complexity of the vegetation (McDermott and Wood 2010). In Michigan, 83% of juveniles were captured in riparian areas that were dominated by shrubs (alders and honeysuckles) and trembling aspen compared with 17% in upland trembling and large-toothed aspen stands. Capture rates of adults and juveniles combined were 1.8 per 100 net-hours in upland habitat and 4.9 in riparian habitat (Akresh et al. 2009). In Minnesota, Streby et al. (2011b) captured 23 Veeries in regenerating clear-cuts during the breeding season and 216 adults and 95 fledglings during the postbreeding season. In Virginia and West Virginia, Marshall et al. (2003) captured 13 adults, 4 juveniles, and no family groups in the centre of clear-cuts. In Pennsylvania, Stoleson (2013) captured 8 adults and 7 juveniles in clear-cuts and 3 adults and 3 juveniles in adjacent mature forest with a dense understorey during the postfledging period.

Hobson and Kardynal (2015) demonstrated that Veeries breeding in the Okanagan Valley of British Columbia undertook long (mean 263 km) postbreeding flights from their territories prior to autumn migration. Timing of the movement overlapped with the moulting period suggesting that this may be a moult migration. Suitable breeding habitat is limited in that region and birds may have to move to find suitable moulting habitat.

MIGRATION

The Veery is a nocturnal, long-distance migrant with the entire population migrating between the North American breeding grounds and the South American wintering grounds. Birds undertook nocturnal migratory flights about 1 night in 6, typically after the temperature rose to 22°C and when it was calm or there were only light surface winds. Thirty of 40 birds migrated solely; of the remaining 10 observations, 8 birds flocked with other Veeries (Cochran et al. 1967; Heckscher et al. 2020).

Males usually arrive on the breeding grounds 5 days before females (Dilger 1956; Heckscher et al. 2020). In southern Ontario, the Veery arrives in very late April or early May, with the peak in mid-May. Arrival in the southern Shield is usually in mid-May. Adults and juveniles migrate at the same time in autumn. In the southern Shield, it begins to move south in August. Most leave the province by early September with stragglers until late September or early October. Birds may rarely persist into November or even December (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Sandilands and Dance 1984; Tozer 2012; Weir 2008).

Spring migration is rapid with birds frequently arriving directly at breeding territories, so migration habitat does not differ from breeding habitat. In autumn, the Veery occurs primarily along forest edges and in the understorey of second-growth deciduous and mixed forests, much the same habitat that is used during the breeding season. During the day during migration, activity may be limited to 0.04-0.2 ha territories (Campbell et al. 1997; Heckscher et al. 2020).

During spring migration in Pennsylvania, there were no significant differences in numbers of the Veery in forest and shrub habitats. It was only 1 of 3 species out of 30 species that showed no habitat preference (Smith and Hatch 2008).

The Veery is vulnerable to being killed by collisions with TV towers, office buildings, and airport ceilometre beams (Graber et al. 1971; Heckscher et al. 2020). Weir (2008) reported that 55 had been killed at the Lennox generating station in the Kingston area.

In Pennsylvania, an outbreak of the viburnum leaf beetle resulted in almost complete mortality of the southern arrowwood, previously the third most abundant shrub species. Prior to the infestation, spring migrant Veeries gained significant mass after sunrise, but no weight gains occurred after the infestation (Smith and Hatch 2017).

The Veery is a common migrant in Ontario (James 1991), although it may be uncommon to rare in certain areas such as Elgin County (Lancaster et al. 2004).

Banding trends at Long Point Bird Observatory showed a significant decline of 3.3% annually 1961-88. Trends within this longer period were –6.3% 1961-70, + 1.4% 1970-79, and –4.2% 1979-88 (Hussell et al. 1992).

Gray-cheeked Thrush

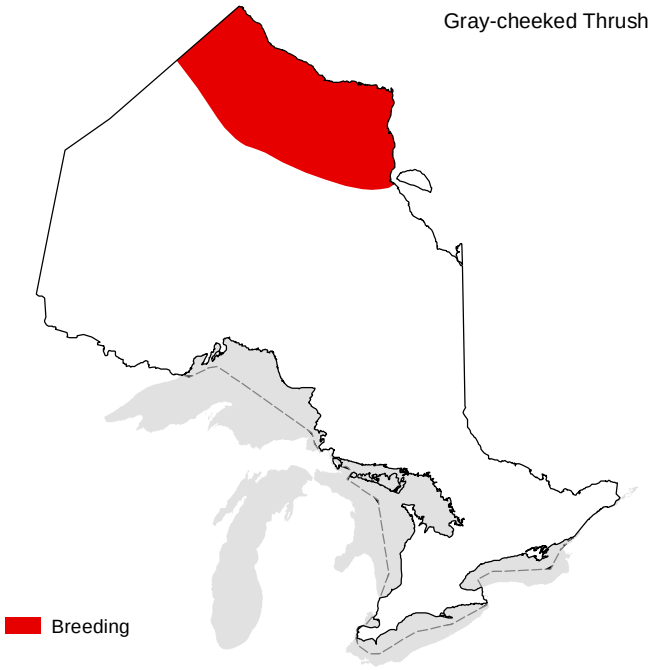
Catharus minimus

BREEDING SEASON

Habitat Requirements

In Ontario, the Gray-cheeked Thrush nests in the northern portion of the Hudson Bay Lowland and the Tundra Region. It occurs in riparian willow-poplar-alder thickets, along edges of extensive burns with dense spruce-willow-birch-alder regeneration, and in open, stunted spruce woodlands with an understorey of willow and birch occasionally interspersed with wet willow and alder thickets. It may also nest occur along rivers and streams bordered by open spruce woodlands and mature aspen stands (Friesen in Cadman et al. 2007). Austen et al. (1994) stated that the Gray-cheeked Thrush nested in dense spruce woods near the treeline.

During the breeding season in Quebec, the Gray-cheeked Thrush occurs in coniferous woods and denser stands near the tree limit. The dominant species in these stands are black and white spruce and, to a lesser extent, tamarack. It prefers a fairly thick, mossy ground cover and rather moist subsoil. In the Quebec boreal forest, it occurs along rivers and streams, lakes, and ponds in clumps of alders or willows. It may also inhabit muskeg, spruce and fir stands, and areas of regeneration after fire (Ouellet in Gauthier and Aubry 1996). In Labrador and northern Quebec, it may occur in tall shrubby enclaves in taiga or above the treeline. At Hamilton Inlet, Labrador, it nested in undergrowth surrounding houses (Bent 1949; Whitaker et al. 2020). In Newfoundland, it has an



affinity for coniferous scrub, but also nests in mature balsam fir forests and clear-cuts (Thompson et al. 1999; Whitaker et al. 2015). British Columbia nesting habitat includes stands of white spruce with a dense undergrowth of blueberries and willow. It also nests in thickets of stunted subalpine fir and spruce interspersed with willows and the neighbouring subalpine parkland coniferous forest, where there is thick growth of blueberries, willows, and other shrubs. It has only been reported nesting in British Columbia between altitudes 840 and 870 m and has the narrowest range of habitat requirements of all thrushes (Campbell et al. 1997). The Gray-cheeked Thrush occurs in open, wet shrubby habitats throughout the Yukon. It is characteristically at or near the treeline in mountainous areas, usually along creeks, gullies, or wet draws with abundant shrubs, and along creeks and rivers that support abundant tall shrubs. It typically occurs in habitats with tall shrubs such as willows or dwarf birch, with or without scattered coniferous trees. It may occur among willows on lakeshores, in burned areas, and in taiga areas such as open black spruce forest with tall shrubs (Sinclair et al. 2003). In the Boreal Forest Region, Erskine (1977) considered it characteristic of both the tundra and alpine ecotones with boreal forest, typically in open black spruce forests. In the Hudson Bay Lowland area of Manitoba, McLaren and McLaren (1981) found the Gray-cheeked Thrush in coniferous forest with a shrub understorey, in coniferous shrubs and heath, and in deciduous and mixed shrubs. It was absent in deciduous forest, coniferous forest without a shrub layer, mixed forest, and tundra. In Alaska, it breeds in tundra where trees are absent, but only where there are clumps of willows or alders. It favours a closed canopy of medium-height shrubs combined with dense woody undergrowth in a layer of dwarf shrubs shorter than 0.4 m tall. Habitats in Alaska include riparian alder and willow thickets, shrubbery in open woodlands, open spruce forests near the treeline, bogs, edges of coastal tundra, alder patches in tundra and coastal hillsides, shrubbery on glacial moraines, and understorey of floodplain cottonwoods. Forest canopy is tolerated if a shrub layer is present. In central Alaska, it occurred in habitats with a high percentage of low shrub cover but not where the vegetation was less than 1.1 m tall. Mean shrub height was 4.2 m for 42 plots where it was present. Shrub species present in inhabited plots included northern red currant, prickly rose, red raspberry, dwarf birch, and black spruce seedlings. The Gray-cheeked Thrush prefers habitat structure with an open canopy, tall shrubs, and very dense cover (Whitaker et al. 2020).

Whitaker et al. (2015) examined environmental factors that affected the distribution of the Gray-cheeked Thrush in Newfoundland. The most important factor was elevation, with its probability of observation increasing with elevation. It was absent below 375 m elevation. There was also strong

support for an influence of shrubs taller than 6.5 m on its occurrence. At the landscape scale (1,250 m), there was a curvilinear relationship between shrub and thrush abundance. Its occurrence was highest where tall scrub comprised 20-25% of the landscape cover. At the neighbourhood scale (115 m), there was a strong linear increase in its occurrence with increasing cover of tall shrubs. Presence of shrubs shorter than 6.5 m had only moderate effects on its abundance. Its occurrence was stable or slightly increasing with old-growth forest at the landscape scale, increasing up to 35% landscape cover then declining. Presence of old-growth forest or 20-80-year-old second-growth forest at the neighbourhood scale had no influence on abundance. At the neighbourhood scale, it was most likely to be observed where there was 60-70% coverage by clear-cuts, but it was negatively correlated with the amount of clear-cuts within 1,250 m. It was most abundant in areas having 50% cover of partially harvested forest (strip and row) at the neighbourhood scale. In Newfoundland at the 5.5-ha scale, it was associated with 10-30-year-old clear-cuts, conifer forests, and tall scrub. At the 490.8-ha scale, it avoided tall scrub, regenerating stands, and second-growth forest (McDermott et al. 2023). In boreal forest plots in New York, Vermont, Maine, Nova Scotia, and Newfoundland, the Gray-cheeked Thrush was associated mostly with high latitude and high elevation sites with colder temperatures. Sites it inhabited had high coverage by moss and lichen ground cover, low numbers of dead snags, low canopy cover, and low numbers of deciduous trees. Because it is associated with colder temperatures, it could be adversely affected by warming due to climate change (Ralston et al. 2019).

Two nests were reported in Ontario. The first was among stunted willows 20 cm from the ground at the base of a willow. The second nest was in a dense spruce-alder-willow bog with sphagnum moss and a few areas of open water. It was 1.5 m from the ground in a 3.0-m tall spruce (Baillie 1961; Peck and James 1987; Schueler et al. 1974).

Nests are typically close to the ground or on it. All 6 reported British Columbia nests were within a metre of the ground and one was underneath a root. Two of 3 Yukon nests were on the ground; one was 1.2 m above water in a willow overhanging a lake. In Alaska, most nests were in crotches of willow or alder shrubs but some were on horizontal or slanting trunks of fallen trees, atop broken-off stubs or rotting stumps, or on the ground; 2 nests were on a ledge of a building. Nests may be as high as 6 m from the ground in spruce in open woodlands, but mean nest height was 0.8 m with only 2 nests higher than 2.5 m from the ground (Bent 1949; Campbell et al. 1997; Sinclair et al. 2003; Whitaker et al. 2020).

No information is available on territoriality, natal philopatry, or adult nest-site tenacity (Whitaker et al. 2020). Territories appear to be fairly spread out and distant from each other (Ouellet in Gauthier and Aubry 1996). Campbell et al. (1997) reported that territorial songs were given from the highest available perches, but most activity was within dense thickets.

Limiting Factors

Eggs are most likely to be present in Ontario nests throughout June into very early July (Peck and James 1987). A nest at Fort Severn contained 3 eggs on 2 July 1940 (Baillie 1961). The time required to build the nest is unknown. One egg is laid per day. The incubation period is uncertain, but is probably 11-12 days. The nestling period is also unknown, but is probably about 11-13 days. In

Alaska, 4 of 6 nests still contained young at age 11 days; young left the other 2 nests by day 11. Three Alaskan young were still together 320 m from the nest 8 days after fledging.

A single brood is raised annually, although renesting may occur if a clutch is lost. Clutches laid after mid-June in Alaska were probably replacement clutches (Whitaker et al. 2020). Of the 2 Ontario nests, one contained 3 eggs and the other contained 3 young (Baillie 1961; Peck and James 1987; Schueler et al. 1974). The most frequent clutch size is 4 eggs with a range of 3-5 eggs. In Alaska, the mean and modal size of 82 clutches was 4 eggs. Most 5-egg clutches occurred early in the season; most 3-egg clutches were late in the season (Bent 1949; Whitaker et al. 2020).

The Gray-cheeked Thrush is apparently monogamous. The age at first breeding is probably 1 year and breeding occurs annually thereafter (Whitaker et al. 2020).

While foraging, the Gray-cheeked Thrush usually hops over the ground, picking prey from the leaf litter. It may visit fruiting shrubs or pick prey off vegetation a short distance above ground. Foot-quivering was an important foraging method (43% of observations) during autumn migration. This involves rapid movement of the legs and feet against the substrate without any forward locomotion. After foot-quivering, it scans the substrate for prey and pecking was observed 67% of times. During autumn migration in Illinois, it fed 89% of the time on fruit in treefall gaps in forests, significantly more than expected (Malmborg and Willson 1988; Whitaker et al. 2020).

The diet is dominated by invertebrates, especially insects, during spring migration and early in the breeding season. As the breeding season progresses, fruit becomes more important in the diet and, by autumn migration, the Gray-cheeked Thrush feeds chiefly on fruit. In Illinois, the diet of 10 spring migrants consisted of 93% insects; ants constituted almost half the food. Eighteen percent of the diet consisted of beetles, especially ground beetles, the lowest percentage of beetles eaten by thrush species in that state. Other food items included 15% caterpillars, 9% crane flies and their larvae, 5% grasshoppers, 5% molluscs, and 2% millipedes. The amount of molluscs eaten was high compared with other thrushes. During spring migration in Wisconsin, it consumed mostly fly larvae (Bent 1949; Graber et al. 1971). A sample of 111 stomachs of birds collected mostly during migration contained 75% animal matter and 25% vegetable matter. The sample was a mix of Gray-cheeked and Bicknell's thrushes stomachs. Animal food in order of importance included 33% beetles (weevils and ground, scarab, and click beetles), 16% ants, 9% caterpillars, 6% bees and wasps, 6% spiders, 2% grasshoppers, and 3% other groups. The remaining food was predominantly fruit (Beal 1915b). One bird collected in Alaska during the breeding season had eaten 3 blow flies, 2 dung flies, 4 ground beetles, 1 rove beetle, and 1 weevil (Whitaker et al. 2020). During the breeding season, the Gray-cheeked Thrush may also feed on crayfish, isopods, and earthworms (Bent 1949). During autumn migration, it often feeds on owlet moth caterpillars, but much of the diet is fruit; in Illinois, 92% of foraging bouts were on fruit. Fruit commonly consumed includes wild grape, Virginia creeper, greenbrier, Canada moonseed, spicebush, raspberries, black cherry, flowering dogwood, elderberry, spikenard, nightshade, barberry, poison ivy, and pokeweed (Bent 1949; Graber et al. 1971; Malmborg and Willson 1988).

There appear to be no breeding season limiting factors for the Gray-cheeked Thrush in Ontario. The ranges of this thrush and the Brown-headed Cowbird do not overlap, so brood parasitism has

not been reported. The Gray-cheeked Thrush is more likely to be affected by habitat alteration during the nonbreeding season than on the breeding grounds (Whitaker et al. 2020).

The Newfoundland population of the Gray-cheeked Thrush has declined precipitously due to introduction of red squirrels to the island. High nest-predation rates appear to have restricted it to high-elevation sites where the red squirrel is scarce or absent (Whitaker 2017). In the remainder of Canada, the ranges of the Gray-cheeked Thrush and red squirrel overlap extensively. It is uncertain if depredation of nests by squirrels is an issue in areas other than Newfoundland.

In northeastern Quebec and Labrador, the Gray-cheeked Thrush was associated with cool, drier stands. Its potential response to climate change in that region is uncertain (DesGranges and LeBlanc 2012).

Status

The breeding status of the Gray-cheeked Thrush in Ontario is not fully understood, but it is uncommon at best. McIlwraith (1894) thought that it occurred only as a migrant in Ontario. The first confirmation of breeding was a collection of a female and 2 young just out of the nest on 13 July 1900 in the Hudson Bay Lowland (Manning 1952). Clifford Hope found the first nest at Fort Severn on 2 July 1940 and collected a juvenile male on 15 July from a brood of fledged young. He was there 15 June to 23 July of that year and his highest daily count was 15 on 20 June (Baillie 1961). Schueler et al. (1974) found a female with a brood patch at Hawley Lake and the second nest for the province at Aquatuk Lake on 6 July 1964. It was uncommon in suitable habitat at Winisk and common at Hawley Lake. None were seen on a field expedition to the Sutton Ridges in 1980 or at Kerine Lake, 80 km southeast of Winisk in 1981. Peck and James (1987) concluded that it probably bred mainly in the northwest within a short distance of the Hudson Bay coast, regularly at least as far east as Fort Severn, and with perhaps fewer and more isolated populations east to Winisk and the Sutton Ridges. No abundance estimates were available from the first atlas. The full extent of its range was uncertain, but it was concluded that it could occur in much of the Hudson Bay Lowland. It appeared to be only sparsely distributed in the northernmost areas of the province (Sadler in Cadman et al. 1987). James (1991) considered the Gray-cheeked Thrush locally rare and a likely irregular summer resident near Hudson Bay and possibly throughout the northern Hudson Bay Lowland. Wilson and McRae (1993) observed single birds at Shagamu on 5, 6, and 8 June and concluded that Gray-cheeked Thrushes were breeding there.

The second atlas provided little additional information on the distribution and abundance of the Gray-cheeked Thrush; it was documented in only 8 squares. Distribution data from the 2 atlases suggest that it breeds throughout the Hudson Bay Lowland south to about 53°N in the vicinity of the Attawapiskat River. It may have been overlooked due to the species' weak song that is delivered only at dawn and dusk, but it is unlikely that it could have been consistently missed if it were present (Friesen in Cadman et al. 2007).

Breeding Bird Survey (BBS) data for Canada indicate that the Gray-cheeked Thrush declined at an annual rate of 0.991% from 1970 to 2021 but increased at an annual rate of 1.36% 2011-21. The long-term results were of medium reliability; the short-term results were of low reliability. There are no BBS data for Ontario (A.C. Smith et al. 2023).

MIGRATION

The Gray-cheeked Thrush is a nocturnal long-distance migrant, typically travelling 200-700 km (mean 300 km) in a night. One bird banded at Mitchell's Bay, Ontario was recovered 3 years 7 months later in Texas (Brewer et al. 2018; Whitaker et al. 2020; Winker et al. 1992). During migration, it often accompanies flocks of Swainson's Thrushes (Bent 1949; Whitaker et al. 2020). In Illinois, 8 Gray-cheeked Thrushes confined their daytime activity during spring migration to an area of 0.04-0.2 ha and migrated solely at night (Cochran et al. 1967).

The Gray-cheeked Thrush is the latest thrush to arrive in spring, arriving around mid-May. Spring migration may extend as late as mid-June. Wilson and McRae (1993) observed autumn migrants at Ekwan on 5 September and at Longridge on 8 September. In Algonquin Park, it occurs from late August to mid-October. In the south, it usually occurs from about mid-September to the first or second week of October. There are a few December records for the province but it is likely that these records are of ill or incapacitated birds (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; McRae 1984; Tozer 2012; Weir 2008).

Most records of the Gray-cheeked Thrush during migration in the Kingston area were from wooded areas with an open understorey and low ground vegetation (Weir 2008). In Quebec, it may be observed in any treed or shrubby area, including city parks and suburban gardens. Whitaker et al. (2020) stated that migrants preferred well-wooded sites with a thick understorey or shrub layer, were scarcer in more open woodlands, and infrequent in areas with sparse or no canopy. During migration in British Columbia, it usually occupies subalpine habitats, but also occurs at forest edges and in river bottomland forests and willow edges in muskeg (Campbell et al. 1997). In the Yukon, it is most often seen at forest edges or openings during migration, but has been seen along narrow roads through dense forests. Occasionally, it visits residential yards with tall shrubs and open forest habitat. It is possible that Yukon migrants may be more common in dense forest, but they are seen less frequently in these habitats (Sinclair et al. 2003).

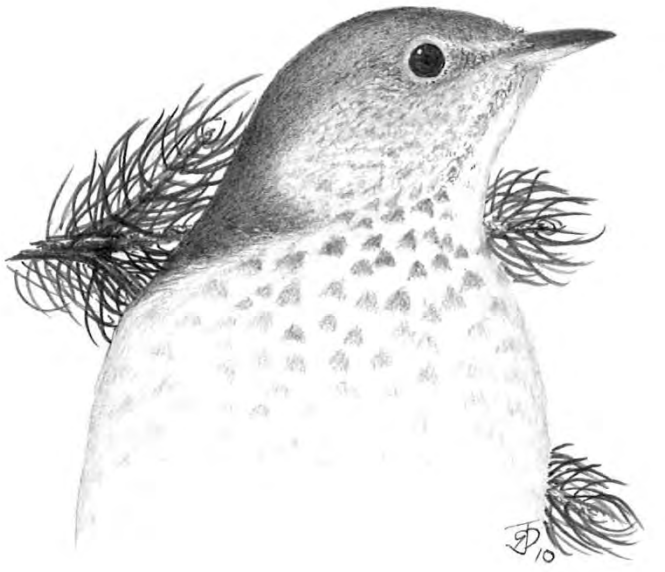
In Algonquin Park, the Gray-cheeked Thrush has eaten wild raisin during autumn migration (Tozer 2012).

The Gray-cheeked Thrush is vulnerable to striking tall structures during migration. In Illinois, it represented about 11% of birds killed at television towers. Some kills occurred at television towers in North Carolina during autumn migration (Graber et al. 1971; Lee 1995; Whitaker et al. 2020).

The Gray-cheeked Thrush is an uncommon migrant in Ontario, but 2,000 occurred on 21 September 1985 at Presqu'ile during a grounding event. It is more common in autumn than spring, due in part to the more prolonged season, but probably mostly because birds that breed west of Ontario migrate through the province in autumn but not in spring (Curry 2006; LaForest 1993; Weir 2008).

Swainson's Thrush

Catharus ustulatus



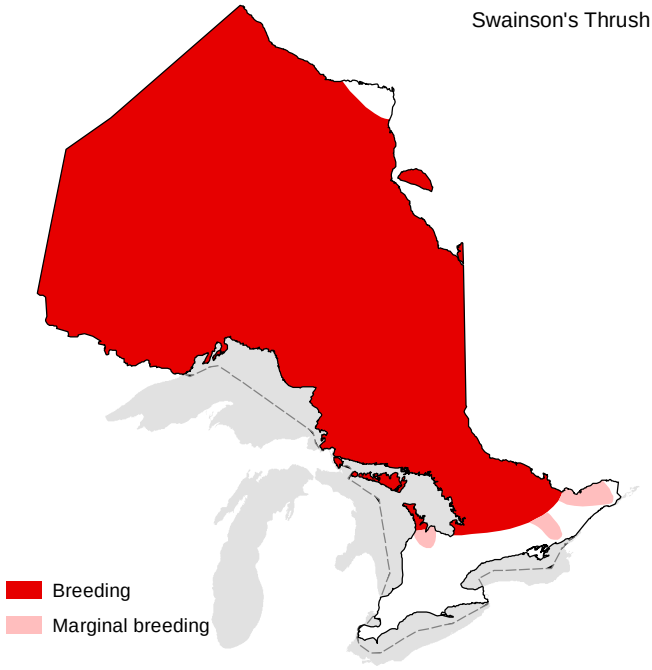
BREEDING SEASON

Habitat Requirements

In Ontario, the Swainson's Thrush has nested in both dry and wet forested areas (85.7% of nests), on rocky outcrops with sparse deciduous growth (5.9%); in sphagnum bogs (4.2%); on blueberry barrens (1.7%); on limestone savannahs (0.8%); in rocky, open burns (0.8%); and in a grassy area of alder growth near a woodland. Forested areas containing nests were coniferous (35.3% of nests), mixed (24.5%), deciduous (22.5%), and unspecified (17.6%). Most forests supporting nests had open canopies; otherwise, nests were often in clearings or near forest edges, shorelines, or roads (Peck and James 1987).

In the Boreal Forest Region of Ontario, the amount of edge at the landscape level (5,000 ha) was a significant predictor of the Swainson's Thrush's abundance. It showed no strong pattern for habitat selection based on other parameters (Rempel 2007). Near Pickle Lake, it was one of the most frequently encountered species, occurring in all forest types including black spruce, black spruce bog, and trembling aspen–white birch mixed forest (James 1980). Near White River, it was significantly more abundant in clear-cuts 23-25 years old than in clear-cuts 3-20 years old or in mature forests (Venier and Pearce 2005). Near Hearst, it was absent in clear-cuts younger than 6

years old. In lowland conifers, it was present in clear-cuts 11-19 years old, but absent in older or younger cuts and in uncut coniferous stands. In mixed-wood stands, it was present in uncut stands and clear-cuts 6-24 years old, reaching highest densities in cuts 17-24 years old (Welsh and Fillman 1980). In the Boreal Forest Region, it was essentially absent from tamarack-cedar, black ash, and balsam poplar stands, but occurred in other forest types. It reached its greatest abundance in balsam fir–white spruce, trembling aspen–white birch, red pine–white pine, and black spruce stands (Welsh 1993).



In Quetico Park in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Swainson's Thrush was most abundant in mature stands followed by early successional stands (1-23 years old). It was not recorded in intermediate-aged (67-73 years) or old-growth stands (175-370 years; Apfelbaum and Haney 1985). Near Gogama, it was most abundant in mixed forests where jack pine predominated, but rare in pure pine stands. It occurred in both these habitats where there were significant amounts of tall shrubbery. It occupied young, dense stands with both coniferous and deciduous growth that was approximately equal in height. It began to inhabit stands once they reached 10 years of age, and was most abundant in 20-year-old stands. Large areas of tall deciduous shrubs were scarce in older pine forests, so it seldom occurred in these areas (James and Peck 1995a). In jack pine woodlands near Parry Sound, it occurred in open stands with less than 25-50% crown closure. All stands were mixed with other species such as trembling aspen, white birch, white pine, silver maple, tamarack, red and white oak, and white spruce (James 1979a). In Muskoka District and Haliburton County, it was associated with high canopy volume and intermediate tree density indicative of undisturbed forest. It was also associated with a high composition of conifers with little understorey (Clark et al. 1983). In Algonquin Park, the Swainson's Thrush was most abundant in black spruce stands followed by hemlock, black spruce–white cedar, and balsam fir–spruce-hardwood stands. It occurred in white birch–aspen-fir-spruce stands where it remained in the shrubs and lower branches of conifers. In black spruce–white cedar stands, it occurred from the ground to a height of 5.5 m, just above the bottom of the canopy (Martin 1960). In Algonquin Park, it typically nests in fringes of coniferous forests around lakes (Tozer et al. 1996). In Muskoka and Parry Sound districts, it preferred mixed forests, often nesting at water's edge (Mills 1981).

The western subspecies of the Swainson's Thrush is a riparian woodland specialist during the breeding season. Eastern and northern populations occupy mixed hardwoods and boreal spruce-fir

forests, respectively (Ruegg 2007). In Colorado montane habitat, it nested in riparian willows and avoided aspen stands (Glass and Floyd 2015). California populations are unique in that they breed primarily in deciduous riparian forests rather than coniferous woodlands (White et al. 2005). Eastern and northern populations nest in habitats similar to those it uses in Ontario. It is most typical of coniferous forests, particularly those dominated by spruce and fir, and is one of the most common and characteristic species of these habitats. The presence of at least some spruce or fir appears essential in most areas. It appears to prefer spruce-dominated forests to those dominated by balsam fir; it may be locally common in hemlock and jack pine stands. It may be a common or even dominant species in poplar and birch stands. It nests in both upland stands and swamps. Although coniferous and mixed stands are more frequently inhabited, it also uses deciduous stands, predominantly those dominated by aspens and birch, but also northern hardwoods dominated by sugar maple and beech, often mixed with hemlock. It may be quite common in regenerating clear-cuts and burns, especially 10-20 years after disturbance. It was common in New Brunswick clear-cuts regenerating with white birch and pin cherry and those that had been replanted with black and white spruce and jack pine. In Quebec, it nests in thickets along forest edges, in clear-cuts with saplings shorter than 2 m and 2-5 m tall, and in young and mature forests. It was not observed in recent burns where saplings were less than 2 m tall. Its abundance was similar in all age classes of habitat. In Wisconsin, it nested in pine, aspen, white birch–red oak, white birch–yellow birch–white cedar, hemlock–yellow birch, and sugar maple–yellow birch stands. In the Yukon, the Swainson's Thrush nests in forests dominated by spruce, trembling aspen, balsam poplar, spruce-cottonwood, and thick growths of spruce, as well as willow and alder thickets. In British Columbia, 39% of nests were in mixed forest, 17% in deciduous stands, 17% in coniferous stands, 12% in rural and suburban areas, and 9% in shrublands. In the Boreal Forest Region, it was in a guild of birds associated with coniferous species, although it did not show a strong preference for any forest type. Occupied sites tended to be dry and nutrient poor. In New York, it nests in large plantations dominated by Norway spruce and white spruce (Back 1979; Beals 1960; Bent 1949; Campbell et al. 1997; Crawford and Titterington 1979; Dawson 1979; Dilger 1956; Eaton 1998; Erskine 1977; Evans Mack and Yong 2020; Falardeau in Gauthier and Aubry 1996; Imbeau et al. 1999; Kirk et al. 1996; Nixon et al. 2001; Noon et al. 1979; Sinclair et al. 2003; Temple et al. 1979; Thompson et al. 1999). In boreal forests in New York, Vermont, Maine, Nova Scotia, and Newfoundland, it had broad habitat preferences and an ability to use multiple boreal forest habitat types. It was associated with high numbers of dead snags, high canopy cover, and high numbers of deciduous trees (Ralston et al. 2019).

Many studies identified microhabitat preferences of the Swainson's Thrush with canopy closure, understorey cover, tree density, and presence of conifers being the most important habitat attributes. In Alaskan taiga, it occurred in forest habitat and not shrub thickets. There were more territories where tree height, canopy cover, and canopy thickness were greater, where the distance between trees was less, and the shrub layer was open. In Oregon, it was positively associated with density of trees 10 cm diameter at breast height (DBH) or larger, reaching peak abundance where this measure was highest. In mixed coniferous forests in Idaho, nests were nearer water in areas with denser shrubs and saplings, where there were more trees 8-23 cm DBH, more trees with a DBH greater than 38 cm, and greater canopy coverage (85%) than random sites. Similar characteristics were noted in Utah: 86% canopy cover and a high density of fir trees in all size classes. In New

Hampshire and Maine, its abundance was positively correlated with the number of deciduous trees 2-10 cm DBH. It was negatively correlated with the total foliage volume of both deciduous and coniferous trees 2-10 cm DBH. It occurs in open jack pine forests in the Boreal Forest Region, but the Hermit Thrush is more common than the Swainson's Thrush in this forest type. Over 30 years in New Hampshire, the Swainson's Thrush disappeared as a breeding species. During this time, the forest changed from having a dense, fairly closed canopy with an open subcanopy and a dense low shrub layer to a more open and patchy canopy with a denser and taller shrub and subcanopy layer, and a more sparse low shrub layer. In subalpine communities in New Hampshire, territories were on mid-slopes, contained wet depressions, had a canopy height of 9.0 m, canopy closure of 64%, 61% conifer foliage volume, 28% conifer volume 0-2 m from the ground, 45% deciduous foliage volume, and average DBH of 12 cm for live trees. The western subspecies may prefer more open canopies (DeGraaf et al. 1998; Evans Mack and Yong 2020; Erskine 1977; Holmes and Sherry 2001; Sabo 1980; White et al. 2005). In Minnesota, it was negatively associated with the amount of black spruce and tamarack within 200 m and 1 km, and the amount of sedge meadow within 500 m. It was associated with white cedar but avoided black spruce and tamarack (Zlonis et al. 2017).

Presence of low shrubs is essential, with the Swainson's Thrush preferring moderate to high density of shrubs. Coniferous shrubs are preferred but in some areas deciduous shrubs are important. In New York, it selected areas with moderate to dense shrub densities, and all territories contained some coniferous shrubs. In California and British Columbia, its abundance was positively correlated with shrub density, particularly species bearing fruit during the breeding season. In Idaho, occupied sites had a higher density of shrubs, saplings, sapling firs, higher sapling species diversity, and greater cover within 1-2 m of the ground than unoccupied sites (Campbell et al. 1997; Evans Mack and Yong 2020; Falardeau in Gauthier and Aubry 1996; Noon 1981; White et al. 2005).

In many areas, the Swainson's Thrush is associated with water or damp areas. Bent (1949) stated that it showed a preference for the lower and damper portions of forests, particularly near woodland streams, but that it often nested in dry woodlands. In Michigan, it preferred damp areas along streams among balsam fir and spruce, especially the lower 0.9-1.5 m where tree branches had died off. In British Columbia, almost 40% of nests were in riparian areas regardless of forest type (Campbell et al. 1997). In British Columbia rainforest, it was more common near rivers than distant from them, but Shirley (2005) did not consider it a riparian specialist and termed it a forest generalist. In subalpine communities in New Hampshire, most territories contained at least a damp depression (Sabo 1980). Nests in Muskoka and Parry Sound were often adjacent to water (Mills 1981).

The Swainson's Thrush is often considered a species that requires mature or old-growth forests, but some studies found equal or higher densities in early successional forests, particularly closed-canopy plantations (Evans Mack and Yong 2020). In white pine stands in the southern Canadian Shield in Ontario, it was more common in old-growth than mature stands, but not significantly. Its abundance was significantly negatively correlated with presence of supercanopy white pines (Kirk et al. 2012). In Saskatchewan, it occurred more frequently in forests older than 50 years. Probability of detection was 20-49% in 50-60-year-old forests, 50-79% in 80-110-year-old forests, and 100% in forests older than 140 years. The percentage of coniferous trees increased with increasing forest age and the amount of shrub and moss cover was highest in the oldest forests. The amount of litter was

significantly higher in the youngest forests (Cumming and Diamond 2002). In Alberta, it was significantly more abundant in old-growth than in mature and young aspen-dominated stands and selected areas with conifers within these stands (Schieck et al. 1995). In Wisconsin, it tended to increase as vegetation matured and reached climax conditions (Beals 1960). In the western Boreal Forest Region, Kirk et al. (1996) considered it an old-forest species. It occurred in 33% of very young stands (0-9 years), 83% of young stands (15-20 years), 100% of mature stands (40 years), and 67% of old stands (80 years). Also in the Boreal Forest Region, Erskine (1977) reported that it was characteristic of mature coniferous stands and scarce or lacking in young coniferous stands. In Pennsylvania, the Swainson's Thrush occurred in 63.6% of old-growth forests, 0.9% of woodlands statewide, and in 1.9% of woodlands on the Appalachian Plateau. Haney (1999) considered it to have old-growth affinity but thought that it should be considered an old-growth associate rather than an old-growth obligate. In the Yukon, it is most common in mature mixed forests but reaches its highest density in old-growth white spruce stands (Sinclair et al. 2003). Bent (1949) concluded that it was less common in mature, dense forests than in the bordering growth of small trees where young balsam firs were growing. It was originally found throughout the West Virginia spruce belt. When most of the mature timber was removed, it adapted well to the brushy second growth, particularly if there was some spruce regeneration. It is possible that the structure of the shrub layer within forests is more important than the age of the forest, although forest age can have a large influence on the density of the shrub layer.

The Swainson's Thrush has been termed both a forest-interior and edge species. Freemark and Collins (1992) considered it a forest-interior species, as did Dilger (1956) in New York and Morse (1972) in Maine. Stanwood (1913) stated that Maine birds were just as common in narrow strips of forests abutted by hayfields as in larger woodlots that provided forest interior habitat. In California, its density at forest edge was twice that at 400 m from edge (Brand and George 2001). In Newfoundland balsam fir stands, it was significantly more abundant in forest interior than in riparian and nonriparian forested edges. Although it occurred in intact forests 20-50 m from edge in riparian habitat, it was absent in similarly sized buffer strips adjacent to clear-cuts (Whitaker and Montevecchi 1997, 1999). In balsam fir–white cedar stands in eastern Quebec, there was no significant difference in its density in riparian and nonriparian stands (LaRue et al 1995). In coniferous forests in British Columbia, it was significantly more abundant in riparian habitat during the breeding season and autumn migration, but not during spring migration. It was observed mostly in the willow and alder understorey in riparian areas and may have been responding to the deciduous shrub layer rather than the proximity of water or edge (Wiebe and Martin 1998). In British Columbia, it frequently builds its nest at the edge of forests (Campbell et al. 1997), and the same is true in Ontario (Peck and James 1987). In Ontario, the Swainson's Thrush does not appear to be a forest-interior species. Where it nests within forests may be influenced by which other thrush species are present and by shrub density.

There is evidence to both suggest that the Swainson's Thrush is and is not area sensitive. In riparian cedar-hemlock forests in northern Idaho, it was considered area sensitive, but it was not along the Pacific coast. It was not detected in aspen woodlands smaller than 10 ha in an agricultural matrix. In Saskatchewan, it was more common in contiguous forests, with 46 records in contiguous

forest and only 2 in forest fragments. In Quebec, there were no significant differences in its distribution relative to the amount of forest cover, edge, or interior habitat within 100-ha landscapes. Its abundance in the northern Rocky Mountains was not associated with the patch size of forests within landscapes, but stands in more fragmented landscapes had fewer nests and lower success rates than stands in more contiguous landscapes. In Maine, the Swainson's Thrush occurred on islands as small as 0.49 ha, and it was regular on islands 1.5 ha and larger (Drolet et al. 1999; Evans Mack and Yong 2020; Hobson and Bayne 2000; Morse 1972).

Where the Swainson's Thrush overlaps with other closely related thrushes, they may inhabit mutually exclusive ranges partitioned by elevation, foraging tactics, and differential use of habitat structure. Of thrushes in the same genus, it is most adapted to an above-ground foraging niche, possibly due to competitive pressures (Evans Mack and Yong 2020). In Ontario, thrush species typically occur together where there are no significant elevational gradients, so other types of habitat partitioning are required. The greatest overlap in habitat with the Swainson's Thrush occurs with the Hermit Thrush, but overlaps also occur with the Veery and Gray-cheeked Thrush.

In New York, there was a high association between the breeding habitat of Swainson's and Hermit thrushes. Habitat partitioning was achieved by the Swainson's Thrush feeding more often in above-ground foliage than the other thrushes (Dilger 1956). Also in New York, Noon (1981) found extensive overlap of territories of Swainson's and Hermit thrushes. The Swainson's Thrush selected habitats with moderate to high shrub densities and this separated it from all other thrushes except the Veery. Swainson's Thrush territories were discriminated from other thrush territories by a higher percentage of coniferous shrubs, with all territories containing some coniferous shrubs. It keyed in on coniferous patches created by disturbance in the largely deciduous forest. In Maine spruce forests on large islands and on the mainland, the Swainson's Thrush occurred in areas of denser growth than the Hermit Thrush. On small islands where the Hermit Thrush was absent, the Swainson's Thrush consistently used mixed forests of mountain and striped maple, yellow birch, white spruce, and balsam fir, but these habitats were not used when the Hermit Thrush was present. This strongly suggests that the Swainson's Thrush is excluded from these habitats by the Hermit Thrush (Morse 1972). Both Dilger (1956) and Morse (1972) considered the Swainson's Thrush to occur predominantly in forest interior. Morse (1972) concluded that the Hermit Thrush was chiefly an edge species, thereby resulting in some habitat partitioning. In the Boreal Forest Region, Erskine (1977) concluded that the Hermit Thrush typically replaces the Swainson's Thrush in more open forests such as bogs and disturbed or young successional forests. On Haida Gwaii in British Columbia, ecological segregation between the Swainson's Thrush and other thrush species was achieved by different timing of breeding. The Hermit Thrush arrives there about 6 weeks earlier than the Swainson's Thrush and its young have begun to fledge when the Swainson's Thrush begins to arrive. The differences in nesting phenology result in a reduction of competition for resources (Sealy 1974). The difference in timing of nesting of these 2 species is not as pronounced in Ontario, with the Hermit Thrush initiating egg-laying only 10-14 days before the Swainson's Thrush and the peak periods of nesting of the 2 thrushes overlap considerably (Peck and James 1987).

Erskine (1977) concluded that the Swainson's Thrush may experience competition with the Veery in the Boreal Forest Region because the Swainson's Thrush occurs regularly in deciduous

forests only northwest of the Veery's range. In New York, Swainson's Thrush territories differed from those of the Veery by containing coniferous shrubs (Noon 1981). In New York, there was a positive association between breeding habitat of the Swainson's Thrush and Veery, but it was weak (Dilger 1956). Where it shares habitat with the Veery in British Columbia, the Swainson's Thrush forages higher above the ground and prefers areas with less undergrowth Veery (Campbell et al. 1997).

In Ontario, breeding territories of the Swainson's and Gray-cheeked thrushes may potentially overlap in the Hudson Bay Lowland. Where these species coexisted in Alaskan taiga, the Swainson's Thrush used the ground layer more than the Gray-cheeked Thrush (Evans Mack and Yong 2020).

It appears as though the presence of the Hermit Thrush and Veery may inhibit use of certain types of mixed and deciduous forests by the Swainson's Thrush. When thrush species coexist, habitat partitioning may be achieved through density of the woody understorey, by the amount of coniferous cover in the understorey, and by the height at which different thrush species forage. The Swainson's Thrush may select different foraging strata, depending upon which other thrush species are present.

Ontario nests were mostly in trees and shrubs that were alive, although a few were dead or partially dead. Coniferous trees were chosen more often (70.2% of nests) than deciduous trees and shrubs, and most nest trees were small (DBH 2.5-15 cm). Trees selected most often were spruce (53 nests), balsam fir (21), alder (11), willow (8), and birch (8). Eight nests were in tops of tree stubs, 6 were in fallen trees, and 1 was in an open cavity in the side of a standing tree. Nests were in tree crotches or less often on lateral branches, and were more apt to be near the trunk (29 nests) than away from it (6 nests). Distance from the trunk of 4 nests was 1-1.8 m. One nest was wedged between the trunks of a small balsam fir and a large yellow birch. Nests were placed from the top to the lower part of a tree or shrub without any apparent preference. An unusual nest was on the top of a hummock outside the centre of an alder clump, and was about 0.3 m above the surrounding ground level. Nests were 0.3-9 m above ground, with most 0.9-2.4 m up (Peck and James 1987). A nest in Algonquin Park was on top of a small bracket fungus growing on a sugar maple (Tozer et al. 1996).

Most nests reported outside Ontario were in trees and shrubs. They were most frequently in the understorey, particularly in thickets of deciduous shrubs or conifer saplings and less often below 3 m from the ground on top of a horizontal branch away from the bole of a large diameter tree. In New York, almost all nests were on the lowest living branch of a hemlock in an area of thick hemlock needles several metres from the trunk. This was an adaptation to heavy deer browsing that essentially eliminated hemlock from the understorey; nest placement far from the trunk presumably reduced predation by red squirrels. Tree and shrub species that nests have been reported in include 17% willow, 15% fir, 14% spruce, and 11% blackberry. Other species include alder, aspen, birch, maple, oak, hemlock, gooseberry, rose, sumac, cedar, pine, and lilac. A few British Columbia nests were among tree roots, 1 was on a post, and 6% were in snags. Nests have been reported on driftwood, a rock, and the ground. Heights of 981 British Columbia nests were 0-24 m with 60% between 1.0 and 2.4 m. Higher placement typically occurs in coniferous forests. More than 90% of nests in California and the Pacific Northwest were less than 3 m from the ground, 53% of inland northwestern nests were 3 m or less from the ground, and 70% of northeastern North American

nests were at heights of 1-2.5 m. Mean nest height in Alaskan taiga was 1.8 m. Nests in over-browsed hemlock forest in New York averaged 5.8 m from the ground with a range of 2.3-9.8 m (Bent 1949; Campbell et al. 1997; Eaton 1998; Evans Mack and Yong 2020; Sinclair et al. 2003; Stanwood 1913).

The Swainson's Thrush is territorial but boundaries are loosely defined and may not be entirely exclusive. The breeding home range is approximately the same as the territory. In California, adults tolerated each other in close proximity; active nests may be within 4-5 m of each other. In Algonquin Park, average territory size was 0.96 ha (range 0.04-1.09 ha). Territories ranged from the ground to a height of 5.5 m, slightly above the bottom of the canopy. Where it occurred in high densities in Idaho, territories averaged less than 1 ha. Within a breeding season, 75% of observations of birds were within 125 m of the capture site (maximum distance 350 m) and 80% of adults were captured within 100 m of the nest. In subalpine communities in New Hampshire, average territory size was 2.1 ha (Evans Mack and Yong 2020; Martin 1960; Sabo 1980; White et al. 2005).

In California, 37 of 200 hatch-year birds (18.5%) banded over 11 years returned to nest in at least 1 subsequent year. This is a different subspecies and habitat for it is limited, thus increasing the probability of young returning to the same area (Gardali et al. 2003).

Adults of both sexes often return to previous breeding sites. In Idaho, 42% of males and 31% of females returned. The distance between the original and subsequent capture sites was less than 150 m and less than 1 territory width. More than 50% of birds were present at least 2 years after the original capture and 6 were present at least 3 years. Two females returned to the same plot 5 consecutive years (Evans Mack and Yong 2020).

Limiting Factors

Eggs have been found in Ontario nests from the end of May until the end of July, with most present in the last half of June and first week of July (Peck and James 1987). In Algonquin Park, nest construction occurs from late May to mid-July, eggs are present from late May to late July, nestlings occur from mid-June to early August, and dependent fledglings occur from late June to mid-August (Tozer 2012)

A new nest is built every season and for renesting attempts. The time that it takes to build a nest does not appear to have been quantified. Egg laying commenced within 5 days of nest completion at Idaho nests. One egg is laid per day. Incubation begins by noon of the day that the last egg is laid, but timing of initiation of incubation may be variable because eggs often hatch at irregular intervals. The incubation period of 4 Ontario clutches was 12-13 days. Overall, the incubation period is 10-14 days. Young leave the nest when they are 10-14 days old, but usually at age 12-14 days if they are undisturbed (Campbell et al. 1997; Evans Mack and Yong 2020; Stanwood 1913; White et al. 2005).

Egg dates suggest that only a single brood is raised in Ontario. Throughout its range, it appears as though the Swainson's Thrush is single-brooded, but double broods have been confirmed in British Columbia. There is no evidence of second broods in Quebec; second broods were suspected but unconfirmed in Maine. Renesting may occur if a clutch is lost early in the season. Clutches of 2-4 eggs have been reported in Ontario, with most containing 3 or 4 eggs. Overall, clutches of 1-5 eggs have been reported. Five-egg clutches are rare, with 3 and 4 eggs most frequent and almost equal in occurrence. Mean clutch sizes were 3.53 eggs in the northeast, 3.48 in the inland of the

northwest, and 3.69 in the Pacific Northwest (Bent 1949; Campbell et al. 1997; Evans Mack and Yong 2020; Falardeau in Gauthier and Aubry 1996; Peck and James 1987; Stanwood 1913).

The Swainson's Thrush probably first breeds when it is 1 year old and annually thereafter. The mating system is presumed to be monogamous (Evans Mack and Yong 2020).

Closely related thrushes partition habitat using different foraging techniques. Dilger (1956) found that the Swainson's Thrush fed more often in foliage than other thrushes and engaged in frequent flycatching. Only the Veery and Swainson's Thrush flycatch and the Swainson's Thrush does so much more frequently. The Swainson's Thrush may forage in treetops during migration and during the breeding season. It is the most highly adapted of the thrushes for arboreal foraging based on its leg morphology, wider and shorter bill, and long wings. Foraging heights of the Swainson's Thrush averaged 1.4 m in subalpine habitats and 2.7 m in hardwoods suggesting an opportunistic shift to a lower and denser understorey in subalpine habitats. Foraging heights vary depending upon what other thrush species are present because vertical habitat partitioning of species occurs (Evans Mack and Yong 2020). In subalpine habitats in New Hampshire, foraging techniques consisted of 0.4% aerial flycatching, 21.6% leaf gleaning, 6.7% leaf hawking, 6.7% leaf hovering, 1.4% twig pecking, 7.1% twig gleaning, 4.6% twig hawking and hovering, 0.7% branch pecking, 1.1% branch gleaning, 18.8% litter pecking, 27.9% litter gleaning, and 3.9% fallen log manoeuvres. Foraging locations were 17.6% distant from the trunk, 20.0% near the trunk, 12.4% in coniferous tree foliage, 25.2% in deciduous tree foliage, 14.9% in herbaceous foliage, 48.6% on the forest floor, 22.3% in the understorey (0.1-2 m), 19.9% in the midcanopy (5-8 m), and 0% in the upper canopy (above 8 m; Sabo 1980). Adults may feed nestlings after dusk and into the night, particularly at high latitudes where provisioning occurred all night. Night provisioning did not occur until day length exceeded 19.3 hours, suggesting that some ambient light is required for foraging. Adults that fed young at night were compensating for a lower delivery rate during the day. Nests provisioned during the night were not more successful or productive (Ball et al. 2011).

Nestlings in Maine were fed cherry sphinx caterpillars, rosy maple moth caterpillars and adults, numerous unidentified caterpillars, earthworms, spruce budworm moths, glowworm beetles, crane flies, flying ants, grasshoppers, cutworms, geometer moths and caterpillars, ground beetles, ants, spiders, bees, and wild fruit. Young snapped at insects, including mosquitoes, when they flew near the nest (Stanwood 1913). The diet of 25 nestlings of the western subspecies consisted of 92.6% animal matter and 7.4% vegetable matter. Caterpillars were found in all but 7 stomachs and comprised almost 27% of the diet. Other food items included 22% beetles (7.7% ground beetles), 13.8% bugs, 12% hymenopterans (mostly ants), 12% spiders (predominantly harvestmen), and 6% miscellaneous insects. The vegetation consumed was chiefly blackberries and raspberries (Beal 1915b).

During spring migration and early in the breeding season, the Swainson's Thrush is largely insectivorous, but fruit becomes increasingly important in the diet as the breeding season progresses. By autumn migration wild fruits are more prevalent in the diet than invertebrates. During spring migration in Illinois, 6 Swainson's Thrushes ate 98% insects, the highest percentage of any thrush species. Dominant prey included 31% hymenopterans (mostly ants), 30% beetles, and 22% caterpillars (Graber et al. 1971). Beal (1915b) analyzed 560 stomachs collected in all seasons. The diet

consisted of 63.5% animal matter and 36.5% vegetation. Animal food included 21.5% hymenopterans (15.2% ants and 6.3% bees and wasps), 16.3% beetles (mostly ground beetles and weevils), 11.1% bugs (stink and shield bugs, treehoppers, leafhoppers, and cicadas), 10.3% caterpillars, 6.2% flies (mostly crane flies and march flies including larvae and adults), 3.8% scale insects, 2.4% orthopterans (primarily crickets eaten mostly in August and September), 2.2% spiders plus a few millipedes, 0.5% miscellaneous insects, and 0.3% snails, isopods, and earthworms. Domestic fruit constituted 12.6% of the diet, including cherries, blackberries, and raspberries. Only the western subspecies ate domesticated fruit; the eastern subspecies ate wild fruit. Fruits eaten included those of red and white cedar, false solomon's-seal, greenbrier, hackberry, pale smartweed, pokeweed, mountain-ash, juneberry, blackberries and raspberries, roses, black cherry, chokecherry, domestic cherry, domestic plum, sumacs, holly, grape, spikenard, flowering dogwood, gray dogwood, red-osier dogwood, huckleberry, nightshade, honeysuckles, snowberry, maple-leaved viburnum, and common and red elderberry. Deckel et al. (2025) analyzed the diet of breeding males in the White Mountains of New Hampshire. The diet consisted of 33.4% flies, 23.2% spiders, 15.2% beetles, 12.5% hymenopterans, 7.4% true bugs, 5.8% lepidopterans, and 2.5% millipedes. At higher elevations, they ate more isopods and ghost spiders, suggesting that they may be eating lower-quality food than birds at low elevations. In Illinois, autumn migrants ate 60% fruit, especially grapes plus cherries, elderberries, and blackberries. It frequently ate elderberries but preferred pokeweed if it was available. It also ate Virginia creeper fruit (Graber et al. 1971). Tietz and Johnson (2007) analysed fecal matter of autumn migrants in California. Food items in order of frequency were 87% arthropods, 70% huckleberries, 43% wax myrtle bracteoles, 7% blackberries, and 4% heaths. Over 2 years in Maine, spruce budworm larvae and pupae constituted 30.3% and 42.0% of the invertebrates it consumed (Mitchell 1952). In New Hampshire and Maine, it showed no significant response to spruce budworms, with an average of 0.9 present per stomach (Crawford and Jennings 1989). Venier et al. (2009) found no significant relationship between thrush and budworm abundance near Manitouwadge. In New Brunswick, Morris et al. (1958) observed a direct but weak relationship between the abundance of the Swainson's Thrush and budworm numbers. In California, it foraged on saddled prominent caterpillars and spruce budworm moths and was more abundant when these species were present. Use of mixed hardwoods later in the season occurred in areas of irruptive caterpillar abundance. The amount of fruit present was important in determining abundance of juveniles later in the breeding season. Fruit that was consumed included red elderberry, dogwood, honeysuckle, and blackberries. Fruit eaten was 4.2-17.6 mm in diameter and 0.1-2.4 g (White et al. 2005). In British Columbia rainforests, it frequently feeds on fruits of raspberries and devil's club (Shirley 2005).

The Swainson's Thrush is rarely parasitized by the Brown-headed Cowbird. In Ontario, 1 of 174 nests (0.6%) was parasitized (Peck and James 1998). Bent (1949) was aware of only 5 cases of parasitism. None of 526 nests reported to the Western Foundation of Vertebrate Zoology from 1867 to 1970 and 1 of 110 Idaho nests (0.9%) were parasitized. The highest rates of parasitism were 8%, reported from British Columbia and 2 areas in California (Campbell et al. 1997; Evans Mack and Yong 2020).

The Swainson's Thrush experiences a very high rate of nest predation and subsequent low reproductive success, and this may be its greatest limiting factor. In Idaho, 63% of failed nests were depredated as were 62% of nests reported to the Cornell Nest Records Scheme. The red squirrel appears to be the most significant predator (Evans Mack and Yong 2020). Creation of forest edge and the Swainson's Thrush's propensity to nest near forest edge may contribute to high predation rates. In Alaska, there was a slightly lower rate of daily survival in narrow (less than 250 m) than wide (more than 350 m) forested corridors (97.8% versus 98.6%), although results were not significant. Predation was the primary cause of nest failure, mainly due to red squirrels (D.M. Sperry et al. 2008). In California, Brand and George (2001) concluded that the Swainson's Thrush may be caught in an ecological trap because it may suffer higher levels of predation near the edges that it prefers for nesting. In urbanizing areas near Seattle, it was most abundant in forested portions of cities and in specific forest patches where American Crows, squirrels, and chipmunks were uncommon, indicating that it tended to avoid areas with high densities of predators (Marzluff et al. 2007).

Because the Swainson's Thrush typically nests in the shrub layer, habitat changes to this layer such as clearing of shrubs around cottages may have detrimental effects (Clark et al. 1983). In a forest over-browsed by deer in New York, it was forced to nest in the lower limbs of large hemlocks, thus making nests more susceptible to predation by red squirrels (Eaton 1998). Over a 30-year period in a New Hampshire forest, it declined as the original dense, low shrub layer grew into a dense, tall subcanopy layer with sparse coverage by low shrubs (Holmes and Sherry 2001).

The effects of forestry on the Swainson's Thrush vary depending upon the prescription used. Studies related to forestry impacts have focused on its abundance but effects on survival and nest success have not been studied (Evans Mack and Yong 2020). Selective thinning may have little impact (Webb et al. 1977) and may be beneficial by opening the canopy, thereby promoting shrub growth. Clear-cutting results in an initial loss of habitat, but areas may support substantial numbers of Swainson's Thrushes 10-20 years after treatment. It may then decline during the pole- and timber-size stages of forest maturation, and once again become common in mature stands. In the Boreal Forest Region of Ontario, its abundance did not change when 30% or 50% of trees were removed, but decreased when 70% of trees were removed. It experienced a 25% decrease in abundance when 65% of trees were removed, a 50% decrease when 70% of trees were removed, and a 75% decrease when 75% of trees were removed (Vanderwel et al. 2007, 2009). Single-tree selection in Algonquin Park had no effect on its abundance (Jobes et al. 2004). In the Ontario Canadian Shield, there was no difference in its abundance in early and mid-successional clear-cuts compared with similarly aged stands after fire. It was significantly less abundant in early and mid-successional stands than in mature stands (Zimmerling et al. 2017). In British Columbia where forests were thinned or thinned and treated with herbicides, the Swainson's Thrush consistently selected patches for breeding that had either escaped or recovered from silvicultural treatments (Easton and Martin 2002). In Alberta, it declined significantly when 50-100% of trees in mixed forests were removed (Harrison et al. 2005). On treatment plots in New Brunswick northern hardwoods, an average of 41.9% of the basal area was removed and the canopy closure was reduced by about 20%. In the first 3 years postharvest, density of the Swainson's Thrush tended to be higher in controls. The opposite was true 5 years postharvest (Háche et al. 2013). In Maine clear-cuts, it was absent in the earliest seral stages: dense

slash and abundant open ground, and dense raspberries and regenerating hardwoods less than 2 m tall. It first reappeared when hardwood regeneration was more than 2 m tall and there was a well-developed, slow-growing coniferous stratum. Highest abundance occurred when hardwood regeneration was taller than 4.5 m with trees with DBH of 10-15 cm. It also occurred at lower density in the final seral stage which was a dense softwood overstorey with an open forest floor (Titterington et al. 1979). In Alberta, residual tree blocks were left in uniform patterns in all clear-cuts and non-merchantable timber was retained. It declined significantly in the cut areas. Tittler et al. (2001) estimated that more than 40% of trees and more than 46% of tree basal area would have to be retained in cut areas to maintain it. Logging of boreal mixed-wood forests may be contributing to its decline; maintenance of old-growth reserves may be critical to its conservation. In Saskatchewan boreal forests, it was significantly more abundant in tracts older than rotation age. Cumming and Diamond (2002) concluded that it was likely to suffer reduction in population density if stands older than rotation age were lost entirely from the landscape. In a netting survey in Newfoundland, 48% of Swainson's Thrushes were captured in areas that had been clear-cut; there was no difference in survival rates in cut and uncut areas. Whitaker et al. (2008) suggested that it may be resilient to a moderate level of clear-cutting.

In Alberta, the Swainson's Thrush was significantly more abundant at pipelines than in adjacent forest interior, significantly less abundant at well pads than in adjacent forest interior, and there was no difference in its abundance at seismic lines and in adjacent forest interior (Bayne et al. 2016). There was no difference in its abundance near noisy compressor stations and quiet well pads. It did not appear to be affected by chronic noise (Bayne et al. 2008).

In Quebec, DesGranges and Morneau (2010) concluded that the Swainson's Thrush was associated with boreal forest and cooler and wetter summers. They considered it sensitive to climate change.

Status

The Swainson's Thrush has always been a common breeder in Ontario. Baillie and Harrington (1937) stated that it occurred commonly from southern Georgian Bay and Hastings County to the southern edge of James Bay. It bred at that time west to southern Kenora District and to Lake of the Woods and on Manitoulin Island. It was the most common thrush along the northeastern shore of Lake Superior (Baillie and Hope 1943). In white pine forests in the Shield portion of the Great Lakes–St. Lawrence Forest Region, it was the fourth most abundant species and represented 5.4% of all birds documented (Kirk et al. 2012). The first atlas documented breeding throughout the Hudson Bay Lowland to the north coast, except in the northeastern corner of the province. It was widespread on Manitoulin Island and the Bruce Peninsula, with only scattered records elsewhere south of the Canadian Shield (Sadler in Cadman et al. 1987). James (1991) considered it a common summer resident throughout the province south to the Bruce Peninsula and central Peterborough County and occasional and rare to Wellington and southern Frontenac counties.

The second atlas revealed that there were no changes in the distribution of the Swainson's Thrush between atlases. Overall, there was a nonsignificant increase in its probability of observation, with a significant increase in the Boreal Forest Region. Greatest abundance occurred in the Boreal Forest Region and southern portion of the Hudson Bay Lowland (Friesen in Cadman et al. 2007).

Breeding Bird Survey data indicate that the Swainson's Thrush increased at an annual rate of 0.0964% in Canada and decreased at an annual rate of 0.31% in Ontario 1970-2021. The trends 2011-21 were an annual increase of 0.78% in Canada and an annual decrease of 1.67% in Ontario. The trends for Ontario were highly reliable; the Canadian trends were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

White et al. (2005) and White and Faaborg (2008) studied habitat use by fledglings in California. Their results may not be representative of populations in other areas because this is an endemic subspecies that nests in different habitats than eastern birds. Seventy percent of juveniles stayed an average of 54 days postfledging in their natal watershed until transmitter batteries failed. The other 30% remained an average of 41 days before dispersing. During the first 2 weeks postfledging, 27% of adults led their broods to upland mixed hardwoods or coastal shrubs at least once. Broods were found in upland vegetation communities 38% of the time. Independent juveniles used upland areas an average of 56% of the time and 74% of individuals used uplands at least once. Juveniles were attracted to sites with abundant fruit. They used sites with less tree cover than random sites whereas a high percentage of canopy cover was important in adult nest-site selection. The habitat used by fledglings was not used by adults for nesting. Immediately after fledging, juveniles used thicket areas near the nest. Adults of 21 broods remained on the territory during the postfledging period and adults of 9 broods moved. There was no difference in mobility between late and early nesters. Mobility was low for both groups for the first few days postfledging, with mobility increasing for drifting broods 3-7 days after fledging and again 8-12 days postfledging. Drifting adults led young hundreds of metres from the nest, but the maximum distance moved in a day was only 40 m. Brood-rearing areas used by drifting adults were fruiting-shrub thickets with abundant fruit, or, in 1 case, where there were abundant moths. After independence, all juveniles established at least 1 dispersal area and some established 3 or 4. The home range for most juveniles consisted of disjunct dispersal areas. The median home range of juveniles was 2.0 ha (range 0.2-9.0, mean 2.58 ha) and the median core area was 0.41 ha (range 0.05-1.6 ha, mean 0.49 ha). Time spent in different dispersal areas was 3-39 days, with most time spent in the first dispersal area. Mean length of time spent in the first dispersal area was 22.7 days compared with 9.6 days in the second area. Juveniles did not move far within dispersal areas, often remaining in the same shrub thicket, but they made long-distance movements between dispersal areas. The mean initial dispersal distance was 242 m (range 28-1,040) and the mean subsequent dispersal distance was 598 m (range 154-2,624 m). Adults were faithful to brood-rearing areas, leading young to the same areas in subsequent years. Brood-rearing areas may have an important role in territory or nest-site selection. Juveniles became independent at 15 days postfledging in stationary broods and at 20 days in drifting broods.

In Quebec, Major and Desrochers (2012) captured Swainson's Thrushes in clear-cuts during the postfledging period. It was more abundant in control plots than in those where fruit had been removed, and this difference approached significance. Fruit availability may be an important factor in attracting it to clear-cuts. In Pennsylvania, Stoleson (2013) captured 11 adults and 1 juvenile in clear-cuts and 11 adults and 2 juveniles in mature forest habitat with dense understorey. The capture rate was slightly higher in forests than clear-cuts, indicating that it may be a habitat generalist during

the postfledging period. In Minnesota, Streby et al. (2011b) captured only a single Swainson's Thrush in regenerating clear-cuts during the breeding season, but caught 31 adults and 1 fledgling during the postbreeding period.

Whittaker and Marzluff (2009) studied movement patterns of fledgling, juvenile, and postbreeding adult Swainson's Thrushes in Washington. Of 4 species studied, areas used by Swainson's Thrushes had the lowest proportions of heavy to medium urban (10%) and light urban cover (19%) and the lowest road density. There was no significant difference in its usage of forested and urban habitats.

MIGRATION

The Swainson's Thrush is predominantly a nocturnal migrant, but some early morning daylight flights may occur. Fat birds may continue migrating in the morning. Lean birds tend to remain in 1 location for the day. In Illinois, no daytime movements were observed during spring migration and all remained within an area of 0.04-0.2 ha. Two birds banded during autumn migration in Ontario were later recovered in Nebraska and Alaska. A bird banded at Long Point in autumn 2001 and another banded the following autumn were recovered in Peru, a flight distance of 6,100 km. A bird banded in spring at Long Point was recaptured the following morning at Prince Edward Point, a distance of 300 km (Brewer et al. 2018; Cochran et al. 1967; Evans Mack and Yong 2020; Graber et al. 1971; Mackenzie and McCracken 2002; Weir 2008).

Mills et al. (2011) radio-tagged 28 Swainson's Thrushes at Long Point during autumn migration. The mean duration of stopover was 3.4 days (range 0.3-11.4 days). The mean duration of time from capture to landscape-scale movement was 3.0 days and the mean duration from time of capture to final detection was 6.4 days. Nocturnal local movement occurred late in stopover, 0-5 nights prior to final departure. Multiple nocturnal movements occurred locally prior to final departure. On most successive days, birds were found within a few hundred metres of their previous location, but some undertook movements exceeding 1 km. Most local nocturnal flights were from the tip of Long Point where the habitat is less suitable for migrants than at the 2 other banding stations.

In spring, males migrate before females but there are insufficient data to determine autumn migration schedules. In Illinois, males arrived an average of 4.5 days earlier than females. In southern Ontario, birds arrive in late April and migration continues until late May, with the peak in mid-May. In central and northern Ontario, it arrives in mid-May with migration continuing until early June. At Long Point, the midpoint of spring migration is 21 May (Black and Roy 2010; Bowlin 2007; Curry 2006; Evans Mack and Yong 2020; Kendeigh 1947; Lancaster et al. 2004; Mills 1981, 2005b; Tozer 2012; Weir 2008).

The Swainson's Thrush may start to leave northern breeding grounds in early to mid-July, but some remain near the nesting areas until August or September. Some leave the breeding areas prior to starting to moult or when they are in the early stages of moult. Others move at least 250 km from the breeding area before undertaking the moult. Few birds are likely to move during the middle of the moult. Near Montreal, birds that moulted there remained an average of 47 days compared with 7 days for those that had moulted on the breeding grounds. Birds have been captured at banding stations at Long Point, Prince Edward Point, and New York from late July to mid-September (Cherry

1985; Evans Mack and Yong 2020; Morales et al. 2022). At Long Point in 1990, there was no difference in the timing of autumn migration of adults and juveniles, but the median passage period of adults was significantly earlier than that of juveniles in 1991. There were no differences in timing of the 2 age classes at 2 other eastern banding stations during this period (Woodrey and Chandler 1997). In the southern Shield, birds are moving southward by August and are seen into the second week of September, with late records to mid-October. Birds may arrive in southern Ontario in July, but mid- to late August is more typical. The peak of autumn migration is in September and October, with late birds occurring until mid-October (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981, 2005b; Mills et al. 2011; Tozer 2012; Weir 2008). McNicholl (1985, 1991) examined winter records of the Swainson's Thrush in Ontario, most of which were actually late autumn records from December. December records may be of birds that were injured or sick during autumn migration or those responding to unseasonably warm weather. A bird observed in High Park, Toronto on 3 March 1984 may represent a true winter record.

Mills (2005b) examined the timing of spring and autumn migration at Long Point in relation to global warming 1975-2000. In spring, there was a trend toward earlier migration based on the first arrival date, but this trend was not significant. Results were similar when quartile means were examined. The Swainson's Thrush also exhibited a nonsignificant trend toward later autumn departure.

During migration, the Swainson's Thrush uses a wider variety of habitats than during the breeding season. These may include several forest types and shrubby areas. Within forested areas, presence of some shrub cover appears important, but it will use woodlands without a shrub layer. Presence of fruit may be important in determining usage of an area. In addition to wooded areas in forested or agricultural landscapes, it may inhabit urban areas such as parks, university campuses, and gardens. Other habitats it may use include brushy fields, shrubby fencerows, orchards, cattail marshes, and shrubbery near farm houses and cottages. Riparian shrubby and wooded areas as well as moist woods with shrub cover may be favoured. In Ohio urban landscapes, spring migrants occurred significantly more often in upland forests than riparian forests. In British Columbia, it is common along shorelines with dense thickets of fruit-bearing shrubs, around lakes and beaver ponds, at edges of forest openings, in fields, at sewage lagoons, at muskeg edges, in coniferous forests and subalpine fir, in deciduous woodlands with scattered conifers, and in swales and gullies in grassland slopes that support thickets of hawthorn, chokecherry, and juneberry. In Minnesota, spring migrants were found approximately equally in floodplains, swamps, willows, and uplands. In autumn, it demonstrated a switch from upland habitat toward wetter sites such as floodplains and willows (Bent 1949; Campbell et al. 1997; Craves 2009; Evans Mack and Yong 2020; Graber et al. 1971; Leighton et al. 2002; McIlwraith 1894; Rodewald and Matthews 2005; Winker et al. 1992).

Juvenile autumn migrants in California showed no consistent selection of forest types within the study area or within their home ranges. They selected microhabitats with abundant huckleberries, but the widespread and variable distribution of this species may have precluded selection for or against any particular forest type. On average, Swainson's Thrushes showed no selection or avoidance of coniferous forest. Some individuals strongly selected conifers and others strongly avoided them. A mixture of habitats may be important to fulfill the stopover requirements

of different birds (Tietz and Johnson 2007). It was more abundant on a treed island in the Gulf of Maine during spring migration than on an adjacent island dominated by shrubs (Suomala et al. 2010).

In Michigan, Oguchi et al. (2018) examined use of nonnative and native shrublands by the Swainson's Thrush during autumn migration. Nonnative shrublands were dominated by autumn olive, 3 nonnative honeysuckles, and multiflora rose. Gray dogwood, winterberry holly, and spicebush dominated native shrublands. Over 2 years, it was significantly more likely to be captured in native shrubs, with 21% and 29% more captures than in nonnative shrubs. Recaptured birds were more likely to be recaptured in native than nonnative shrublands. Differences were nonsignificant in 1 year and significant in the other. No thrushes moved back and forth between shrubland habitats. The number of days spent in different habitats included 2.4 days in nonnative shrublands, 2.9 days in native shrublands, 0 day in open habitat, 1.0 day in marshland, and 0.9 day in woodland. Selection of native shrubland over other habitats was highly significant; use of nonnative shrublands was 44% less than expected. Ninety-nine percent of fecal matter contained fruit. Significantly more spicebush was consumed in native than nonnative shrublands and significantly more common buckthorn and autumn olive was consumed in nonnative than native shrublands. Native shrublands were more important for the Swainson's Thrush during autumn migration than nonnative shrublands because it preferentially selected spicebush fruits.

Migration stopover sites for Swainson's Thrush need not be large provided the habitat is suitable. In California, birds used a highly fragmented narrow strip of vegetation along a creek. Stopover sites in Minnesota were only 1-3 ha. Both sites were used extensively by migrants; many individuals stayed considerable periods and almost all gained weight (Othahal 1991; Winker et al. 1992). Migrating Swainson's Thrushes may require a minimum forest patch size in urban areas during spring in Columbus, Ohio. All thrushes relocated to larger sites (11.9-38.4 ha) remained within the release site until departure; 28% of those released in small patches (0.7 ha and 4.5 ha) moved away from the release site. Those that left the patch where they were released moved 100-1,000 m to small hedgerows where they remained for 1-2 days (Matthews and Rodewald 2010).

In California during autumn migration, the average home range size was 1.9 ha. The home range size of lean birds (2.5 ha) was twice that of fat birds (1.2 ha). The smaller home range of fat birds suggests that they did not have to search for food as much as lean birds (Tietz and Johnson 2007). In Michigan, the 50% kernel foraging range averaged 5.4 ha (range 1.1-11.2 ha); the 99% kernel range was 34.1 ha (range 6.4-71.0 ha; Oguchi et al. 2018).

The Swainson's Thrush may exhibit site fidelity to migration stopover sites. Two banded in Nashville, Tennessee on 15 May 1932 were recaptured on 18 September 1932; 1 returned 30 May 1933 and was captured again on 24 September 1933 (Bent 1949).

Craves (2009) concluded that there may be limitations to the quality of urban migration stopover areas. These include frequent human disturbance, competition for fruit by urban-adapted species, domination by nonnative fruiting plants, and depletion of high-quality fruits early in the autumn migration season leaving thrushes to rely heavily on low-lipid nonnative fruits. Fruits of nonnative shrub species such as autumn olive, common buckthorn, and honeysuckles have higher

sugar and water content but lower energy content compared with native species such as spicebush, gray dogwood, and Virginia creeper (Oguchi et al. 2017).

Oguchi et al. (2018) reported that the Swainson's Thrush consumed fruits of common buckthorn, guelder-rose, nightshade, autumn olive, multiflora rose, nonnative honeysuckles, spicebush, winterberry holly, common elderberry, nannyberry, and Virginia creeper as well as a few arthropods during autumn migration. It highly selected for spicebush berries.

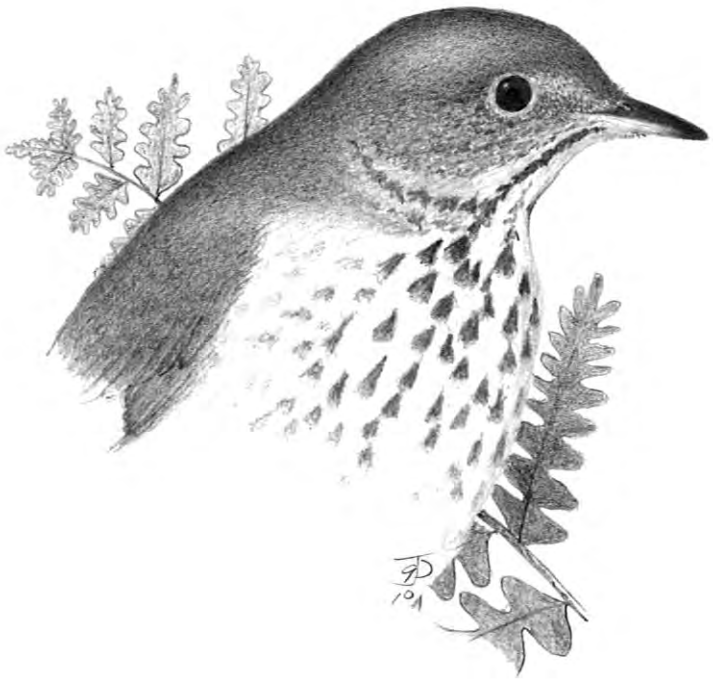
Collisions with television towers, lighthouses, tall chimneys, and tall buildings are the most significant limiting factor during migration. More Swainson's Thrushes are killed than any other species some nights at towers. It was the number 1 species killed at the Long Point lighthouses 1961-2001. It represented 9% of 17,500 casualties. Fifty-seven were killed at the Lennox generating station chimneys (Anonymous 2002; Bent 1949; Evans Mack and Yong 2020; Graber et al. 1971; Leighton et al. 2002; Weir 2008). Throughout the United States, it was particularly vulnerable to striking residences 1-3 stories tall, where it was 34.7 times more likely to suffer a collision than birds on average. It was not among the top 20 species most vulnerable to striking low-rises and high-rises (Loss et al. 2014).

The Swainson's Thrush is a common to locally abundant migrant in much of the province (James 1991), although it is uncommon in Elgin County (Lancaster et al. 2004).

Data from Long Point Bird Observatory indicated a significant decrease of 2.9% per year 1961-88. This included a decrease of 7.8% per year 1961-70, an increase of 1.2% 1970-79, and a decrease of 3.3% 1979-88 (Hussell et al. 1992). More recent data suggest that numbers at Long Point have been stable the past 40 years (Anonymous 2002).

Hermit Thrush

Catharus guttatus

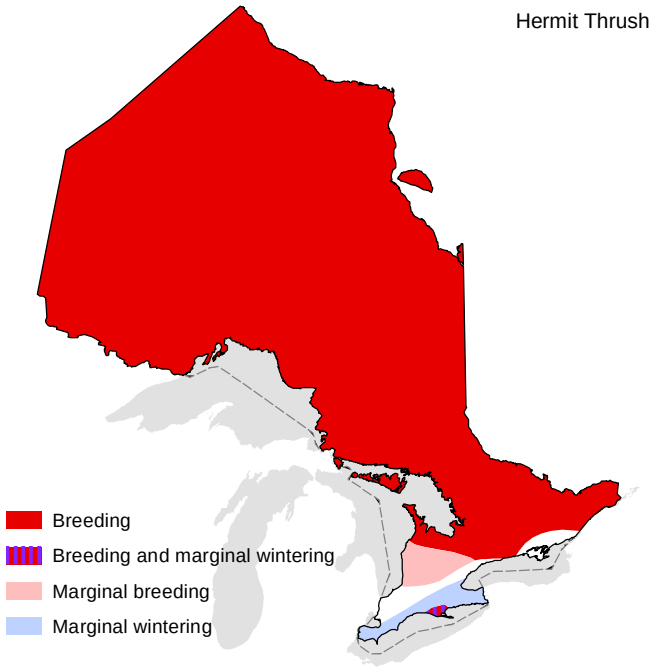


BREEDING SEASON

Habitat Requirements

In Ontario, Hermit Thrush nests have been found in dry and wet forests (85.7%) of nests); on rocky outcrops, usually with sparse deciduous growth (5.9%); in sphagnum bogs (4.2%); on blueberry barrens (1.7%); on a limestone savannah (0.8%); in a rocky, open burn (0.8%); and in a grassy area of alder growth near a forest (0.8%). Of nests where forest type was specified, 42.9% were in coniferous forests, 29.8% were in mixed forests, and 27.4% were in deciduous forests. Canopies of forests selected for nesting were more open than closed. In closed forests, nests were often in clearings or near forest edges, shorelines, and roads (Peck and James 1987).

In the Boreal Forest Region of Ontario, the Hermit Thrush was significantly associated with hardwood forest cover type, but not forest age at the 50-ha scale. At the 5,000-ha scale, it was significantly associated with edge, a measure of forest cover configuration and age-class interspersion. It was associated with open, mixed-wood forest with high edge density (Rempel 2007). From Pickle Lake to Little Sachigo Lake, it occurred in low densities in coniferous forest with understorey, in mixed forest, and in deciduous, coniferous, and mixed shrubs. It was absent in deciduous forest, coniferous forest without understorey, heath, and tundra (McLaren and McLaren 1981). Near Hearst, it bred in 17-24-year-old clear-cuts in coniferous lowland forests and in a 19-year-



old lower-slope mixed forest. It was absent in uncut or clear-cut upland mixed stands or in uncut or young (3-13 years) clear-cuts in lowland coniferous stands (Welsh and Fillmore 1980). In the Clay Belt, it was most abundant in nutrient-poor, wet forest stands (Welsh and Lougheed 1996).

In Quetico Park in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, the Hermit Thrush occurred in early successional and intermediate-aged stands, but not in mature or old-growth stands (Apfelbaum and Haney 1985). In jack pine forests near Gogama, it was one of the most ubiquitous and characteristic species of pine forests and, to a lesser extent, mixed woods. It tended to move into an area once vegetative cover of any type reached a height of 3 m. It preferred more open areas, either between dense patches of trees or shrubs or preferably where dense tree cover rose above low shrubs, leaving open space between low shrubs and lower tree branches. Maximum densities occurred when pines were about 20 years old. Lower numbers in more mature forests were probably because deciduous shrubs were usually numerous, but numbers remained high in maturing pine forests where tall shrubs were less abundant (James and Peck 1995a). In Muskoka District, it nested in a mature hemlock forest (Armstrong and Euler 1983). It was found in open forests in Muskoka and Parry Sound districts and preferred areas where there were natural bedrock openings (Mills 1981). In Algonquin Park, it was characteristic of pioneer deciduous forest and one of the most conspicuous species in white birch–poplar stands (Martin 1960). In Parry Sound District, it occurred in pure and mixed stands of jack pine with less than 25-50% canopy closure (James 1979a). In the Kingston area, it occurred mostly in the Canadian Shield where it was partial to red pine plantations (Weir 2008).

In the Kingston area south of the Shield, high-quality white cedar forests for the Hermit Thrush were associated with the presence of a contiguous and varied forested landscape, pockets of distinct vegetation within the forest community type, vegetative layering, and microhabitat features such as snags, woody debris, and standing water (McLeish and Robertson 1997).

Throughout its range, the Hermit Thrush nests in a variety of forest types and much less frequently in open areas such as bogs, old fields at edges of forests, along edges of forest roads, in open thickets, barrens and rock outcrops, lake shorelines, cemeteries, golf courses, and on hydro rights-of-way through forested habitat. In Quebec black spruce forests, it nested in recent burns and clear-cuts where saplings were less than 2 m and 2-5 m tall, in young forests with saplings 5-11 m tall, and mature forests 120 and 200 years old. It was most abundant in recent burns where shrubs were less than 2 m tall and least abundant in clear-cuts where saplings were 2-5 m tall. Abundance

in young and mature forests was not significantly different from recent burns or clear-cuts (Imbeau et al. 1999). In New York, it occurred most often along interior forest edges such as margins of old burns, fire lanes, power-line cuts, and edges of lakes and burns rather than exterior forest edges. It was tolerant of dry habitats but occurred frequently in damp areas. It occurred more frequently in coniferous and mixed woods than deciduous forests, and was most abundant in coniferous forests in both disturbed and undisturbed areas (Dilger 1956). In mountainous areas of New York, it selected mid-successional forests with high canopy cover of dense stands of intermediate-diameter (15.3-38.0 cm diameter at breast height [DBH]) trees (Noon 1981). In Quebec, it occurred where there was a mean of 56.4% forest cover within a radius of 500 m (Bourque and Desrochers 2006). Dellinger et al. (2020) reported that 93% of nests east of the Rocky Mountains were in forests; 5% were in wet areas, and 2% were in open areas. More nests were in undisturbed (64%) than disturbed (29%) forest. Nest records from disturbed forests included 19% in mixed second growth, 17% near forest roads, 16% in recent clear-cuts, 13% in coniferous second growth, and 35% collectively in old fields, forest edges, hydro rights-of-way, deciduous and open second growth, selectively logged or regenerating forests, blowdowns, and burned areas. In wet habitats, 22 nests were in spruce bogs and 10 were in cedar swamps, mixed swamps, or marshes. Nests in open areas were in open barren lands, upper beaches, golf courses, and cemeteries. The Hermit Thrush also nests in open woodlands with bunchberry or fern thickets, and on borders of pastures skirted by shrubbery and trees. In the Boreal Forest Region, it is regular in black spruce communities along the subarctic border where open stands occur. It is found in most jack pine stands. Jack pine stands are much more open than spruce, balsam fir, or hemlock stands, often with only 20-30% canopy cover. In Vermont, territories encompassed both hardwood forests and clear-cuts (Lent and Capen 1995). In Saskatchewan, it was more common than expected in aspen forests (Hobson and Bayne 2000). In Wisconsin, it was rare in pine and oak barrens but fairly common in areas that were nearly forest (Mossman et al. 1991). Also in Wisconsin, it occasionally occurred in coniferous plantations. It was common in northern mesic forests in sapling-stage deciduous stands and occurred in pole-sized or mixed stands (Hoffman 1989a; Bielefeldt and Rosenfield 1994). In the Boreal Forest Region, it was in a guild of species associated with conifers and occurred in drier, nutrient-poor stands. It had a slight tendency to occur in younger than older stands, but not significantly (Kirk et al. 1996). On islands in Wisconsin, maximum density occurred in a red pine stand but it occurred in small numbers in white birch–red oak, aspens, white birch–yellow birch–white cedar, and sugar maple–yellow birch stands (Beals 1960). High densities of the Hermit Thrush occurred in Wisconsin woodlands where clubmosses were abundant (Loss 2012). In the northeast, it had a major association with mature coniferous upland stands, a moderate association with mature coniferous lowland forests, and a minor association with alder thickets, mature deciduous upland forests, disturbed shrubby areas, young plantations, aspen regeneration, and recent clear-cuts. It was associated with a high density of low shrubs, trees, and saplings (Niemi and Pfannmuller 1979). In the northeast, it occurs in northern hardwoods, lowland hardwoods, aspen-birch stands, upland spruce-fir stands, lowland conifers, and mixed forests. In northern hardwoods, it was found in 13% of mature, undisturbed habitats and 23% of disturbed and successional habitats. In aspen-birch, it occurred predominantly in the seedling-sapling and pole-mature stands. It was absent in 1- and 2-year-old burns and clear-cuts, and in sapling-pole-stage stands. In pine and mixed pine-hardwoods stands, it occurred in all ages of

forests and first appeared in burns 1 year after fire. In lowland conifers, it was present in shrubby areas with scattered conifers, all-aged black spruce stands, and tamarack and white cedar stands. In mixed forests, its abundance was associated with increasing abundance of pines (Back 1979; Capen 1979; Crawford and Titterington 1979; Dawson 1979; Noon et al. 1979; Samson 1979; Temple et al. 1979). In Quebec, it occurs in a variety of forest types but prefers edges of lakes, clearings, burns, and mid-successional areas. It also nests in black spruce plantations (Falardeau in Gauthier and Aubry 1996). In British Columbia, preferred nesting habitat is mixed coniferous forests with a dense shrub understorey. At low elevations, the Hermit Thrush is most abundant where berry-bearing shrubs are abundant. In low areas, it nests in coniferous forests, trembling aspen forests, pine-aspen stands, spruce-tamarack stands, and black spruce muskeg. Away from the coast, it nests in subalpine spruce, alpine fir, and krummholz forests. It inhabits the upper edges of forests where openings and shrub patches, including blueberries, provide late summer and autumn food. It favours moist areas (Campbell et al. 1997). In the Yukon, it occurs in subalpine areas and in trembling aspen forests and burned areas at lower elevations. It uses 2 distinct habitats for nesting: open, mixed forests near the treeline in mountainous areas, especially along creeks, wet draws, and gullies with tall deciduous shrubs; and, at lower elevations, in trembling aspen forests, including burns. In central Yukon, it occurs in deciduous and mixed growth where it favours second growth, especially trembling aspen in burned areas (Sinclair et al. 2003). On Long Island, it frequented the hottest and driest barrens where the ground was carpeted with bearberry and pine-barren sandwort. In northern Michigan, nests were in dry upland covered with second growth after fire a few years previously (Gross in Bent 1949).

In New Jersey, the Hermit Thrush was a primary facultative hemlock species. It occurred within hemlock woods and on dry deciduous ridge tops with dense ground cover. It tolerated a wide range of moisture gradients and occurred in dense young mixed growth along interior edges and within heavy cuts. The relative importance of habitats for it was 40% for hemlock growth, 60% for hardwoods with some pine, and 0% for coniferous plantations. Canopy reduction may temporarily increase understorey habitat for it (Benzinger 1994). In Connecticut, it was strongly associated with intact hemlock stands and exhibited 34% declines in forests with high hemlock mortality (Dellinger et al. 2020). In New Jersey and Pennsylvania, it was adversely affected by hemlock decline due to the hemlock woolly adelgid and decreased in abundance (Toenies et al. 2018).

A forest burn in California was intense and left no cover except for scattered snags and occasional live trees. The Hermit Thrush was absent in the burned area but bred in the adjacent intact forest. It was the only ground-foraging species that was absent in the burn. It was characteristic of only the most shaded and concealed areas of the forest floor (Bock and Lynch 1970).

In balsam fir stands in Newfoundland, Whitaker and Montevecchi (1997) considered the Hermit Thrush a forest-interior species, although there were no significant differences in its abundance in riparian habitat, forest interior, and nonriparian forest edges. In eastern Quebec, it was significantly more abundant in nonriparian than riparian balsam fir–white cedar stands (LaRue et al. 1995).

Some studies indicated that the Hermit Thrush is associated predominantly with older-growth forest; others suggested that it is more common in young forests. In Pennsylvania, it occurred in 100% of old-growth forests, in 27.8% of forests state-wide, and in 49.2% of forests on the

Appalachian Plateau. Haney (1999) considered it to have a positive old-growth affinity but concluded that it was probably an old-growth associate rather than an obligate. In West Virginia, it was most likely to be present in forests older than 120 years and least likely to occur in 0-19-year-old stands (Dimmig et al. 2020). In Newfoundland balsam fir stands, it occurred in forests that were slightly older than average and relatively nutrient-poor. It may be associated with older-growth forests that have larger snags, large conifers, forest gaps, and shrub growth within the gaps (Thompson et al. 1999). In Nova Scotia, it inhabited older stands (Morgan and Freedman 1986). In Alberta trembling aspen forests, it was significantly more abundant in young than mature or old-growth stands. It occurs in poplar–white birch stands but is associated with scattered coniferous trees or clumps of trees, especially white spruce and balsam fir, within these stands. It tends to be associated with rather open canopies and small trees (Schieck et al. 1995). The Hermit Thrush was more common in young or slightly younger than average stands in the Boreal Forest Region. It actively selects young and open jack pine forests in the Boreal Forest Region thereby reducing habitat overlap with the Swainson's Thrush (Erskine 1977; Kirk et al. 1996). In southern Ontario, the Hermit Thrush nests in more mature stands in the Carolinian Forest Region and on the Bruce Peninsula, but also occurs in younger coniferous plantations on the Oak Ridges Moraine.

It is uncertain whether the Hermit Thrush is an area-sensitive species. In Saskatchewan, it was randomly distributed within a fragmented landscape and there was no significant relationship between its abundance, forest size, or amount of forest in the region (Hobson and Bayne 2000). In the Saskatoon area, it was restricted to aspen stands 24 ha and larger (Leighton et al. 2002). In Michigan, its abundance was correlated with forest size (Crozier and Niemi 2003). In Ontario, it appears to be restricted to very large forest tracts in the Carolinian Forest Region. In the remainder of the area south of the Shield, it is becoming increasingly common on the Oak Ridges Moraine where the relatively high proportion of forest cover may be more important than forest size.

Several studies studied habitat partitioning of the Hermit Thrush with the Veery, Wood Thrush, Swainson's Thrush, and American Robin.

In New York, the Hermit Thrush had only a moderate breeding-habitat association with the Veery (Dilger 1956). Along an elevational gradient in New York, it bred at low elevations along with the Veery, but it had the greatest elevational range of the thrushes studied. All thrush species showed significant habitat segregation along at least 1 axis and the Hermit Thrush had an exclusive area of niche space where there was no competition with other thrushes (Noon 1981). In Maine, it mostly occurred in dry to mesic coniferous and deciduous forests, particularly those dominated by pines and oaks. The Hermit Thrush and Veery did not overlap much except in mixed woods with red maple and/or alder. In these areas, the Hermit Thrush occurred in the driest areas and the Veery occurred in the wettest. Although there were few differences in areas used by the Hermit Thrush and Veery, the 2 species seemed to use different parts of these habitats. Some of the driest habitats used by the Hermit Thrush were not occupied by the Veery or Wood Thrush, and the Hermit Thrush enjoyed exclusive use of these areas without competition (Morse 1971a). In Wisconsin, the Hermit Thrush and Veery occurred in forests containing both deciduous and coniferous trees with sapling aspens being most abundant. Over half of both species' territories were covered by an overstorey with a maximum height of about 20 m and there was a well-developed understorey of bracken

ferns, shrubs, and tree saplings to a height of 3 m over more than 80% of territories. There were no significant differences between the 2 species' territories in the distribution of tree species, tree size, or overstorey or understorey structure, and no macrohabitat difference in use of coniferous and deciduous stands. Habitat partitioning between the Hermit Thrush and Veery was achieved by the amount of time spent in different height strata. The Hermit Thrush spent 8% of its time on the ground, 23% under 3 m, 45% at 3-6 m, 18% at 6-9 m, and 5% above 5 m; the Veery spent approximately equal time in each height stratum. The amount of time the Hermit Thrush spent on the ground was approximately 3 times that of the Veery. The Hermit Thrush concentrated its singing in the 6-m stratum; the Veery sang most frequently at heights above 9 m. The Hermit Thrush spent more time in conifers; the Veery concentrated its activities in hardwoods. Both species made little use of aspens in relation to their abundance (Paszkowski 1984). In Virginia, North Carolina, and Tennessee, the Hermit Thrush was a habitat generalist; the Veery was more of a specialist. Hermit Thrushes preferred forests with high percentage canopy closure, a high percentage of leaf litter, and low percentage coverage by woody stems shorter than 3 m. Veeries preferred high percent coverage between 0.5 and 3 m and less canopy closure. Hermit Thrushes preferred more and larger conifers than the Veery. The microhabitats of the 2 thrushes were significantly different despite the fact that they often nested close together (Laughlin et al. 2013). In West Virginia, Hermit Thrush nests were separated from those of the Veery by distance to edge, with the Hermit Thrush nesting closer to roads and skid trails than the Veery. Hermit Thrush nests were at the highest elevations; Veery nests were at intermediate elevations. The Hermit Thrush was completely isolated from other thrushes at the higher extreme of its range. The Hermit Thrush tended to nest on upper and lower slopes; the Veery was evenly distributed but absent from the highest elevations (Dellinger et al. 2020).

Habitat partitioning occurs between the Hermit Thrush and Wood Thrush. There is no evidence of interspecific territoriality between these 2 species but the Wood Thrush appears to be behaviourally dominant to the Hermit Thrush. Initial encounters between these 2 species may be sufficient for the Wood Thrush to establish a territory even though a Hermit Thrush may have previously established a territory (Morse 1971a; Noon 1981). In a New York area with elevational gradients, the Hermit Thrush bred at low elevations with the Wood Thrush but the species were separated along an index of tree spacing. The Hermit Thrush also occupied higher elevations than the Wood Thrush (Noon 1981). In Maine, both the Hermit Thrush and Wood Thrush occupied coniferous and deciduous woodlands, but the Hermit Thrush selected areas that were drier than those inhabited by the Wood Thrush (Morse 1971a). In West Virginia, Hermit Thrush nests were significantly closer to roads and skid trails than those of the Wood Thrush. Hermit Thrush nests were at the highest elevations; the Wood Thrush nested at the lowest elevations (Dellinger et al. 2007).

On Haida Gwaii, British Columbia and Forrester Island, Alaska, ecological segregation of the Hermit and Swainson's thrushes is temporal. The Hermit Thrush returns about 6 weeks before the Swainson's Thrush and their young have begun to fledge by the time the Swainson's Thrush arrives (Sealy 1974). In other areas of British Columbia, these 2 thrushes are separated by habitat and altitudinally. The Hermit Thrush is mostly a species of spruce woods at elevations of about 1,900 m; the Swainson's Thrush is more numerous 300 m lower in willow and poplar thickets (Campbell et al.

1997). In New York, there was a high breeding-habitat association between Hermit and Swainson's thrushes. Dilger (1956) considered the Hermit Thrush a bird of interior edges that foraged mostly on the ground and the Swainson's Thrush a bird of interior that foraged largely in trees. Also in New York, there was extensive overlap of the Hermit and Swainson's thrushes at lower elevations, but the Hermit Thrush ranged higher (Noon 1981). In Maine, Hermit and Swainson's thrushes both nested in spruce forests along the coast. On large islands and the mainland, the Swainson's Thrush preferred denser growth and was more arboreal than the Hermit Thrush. The Hermit Thrush did not nest on islands 4 ha or smaller, but the Swainson's Thrush did. The Hermit Thrush appeared to be socially dominant to the Swainson's Thrush and may have prevented it from breeding in some habitats (Morse 1972). Dellinger et al. (2020) stated that the Hermit Thrush was displaced by the Swainson's Thrush in the Appalachians in West Virginia.

In West Virginia, both the Hermit Thrush and American Robin nested significantly closer to roads and skid trails than other thrushes. Hermit Thrush and robin nest sites differed by their being more medium-sized trees present at Hermit Thrush nests than those of the American Robin. The Hermit Thrush tended to nest on upper and lower slopes; the robin nested on midslopes (Dellinger et al. 2007).

Most Ontario nests were on the ground (87.5%); 7.7% were elevated in deciduous and coniferous shrubs, saplings, and trees; 1.9% were on fallen logs and trees. Single nests were found in a cavity in a 12.7-cm DBH sugar maple, on a tree stub, and on roots. Elevated nests were 0.08-1.8 m from the ground but most were 0.3-0.9 m up. Two nests were in the sides of road cuts 0.8 and 1.3 m from the toe of the bank, one was in a crack in a vertical rock face 1.2 m from the bottom, and one was on the edge of a boulder at 1.8 m. Another nest was in an abandoned mine shaft. Nests on the ground were often in depressions and were among or at the bases of shrubs and vines (44.0% of nests); at the bases of trees and stumps (20.2%); among clumps of ferns, grasses, and other plants (20.2%); sunk in moss and mossy hummocks (13.1%); under tree branches (11.9%); beside a rock (1.2%); under a log (1.2%); and on an upturned root (1.2%; Peck and James 1987). A nest in Hastings County was 4.3 m up in a hemlock and 4.3 m from the trunk on a limb (Peck and James 1998a). In Muskoka and Parry Sound districts, 14 of 15 nests (93.3%) were on the ground; the other was 1.3 m up on a rock face (Mills 1981). In Muskoka District, 1 nest was on an open ledge of a 2.25-m tall rock face in a rectangular-shaped cavity 1.5 m up the cliff. Two old nests were found in the same cliff. The presence of 3 nests within 1 m suggested that rock faces may be fairly typical nesting habitat, or that the same thrush may have returned to the same site for 3-4 breeding seasons (Armstrong and Euler 1983). A nest near Huntsville was on top of an Eastern Phoebe nest that had been active the previous year. The nest was on a nesting tray 2.1 m from the ground under the eaves of a cottage adjacent to a house. The dwellings were in a 0.4-ha opening surrounded by mixed forest (Tozer 1997a). A nest in Peterborough County was in a potted plant on the deck of a cottage. The plant was on a picnic table directly outside a door providing access to the deck, which was 3.6 m above ground. The nest was in a 25-cm plastic flowerpot among planted ornamental flowers and grasses (Lemieux and Sutherland 2007).

Throughout its range, the Hermit Thrush nests predominantly on the ground or in shrubs, saplings, or trees at low heights from the ground. A minority of West Virginian Hermit Thrushes

nested atop boulders or in small trees (Dellinger et al. 2007). In Arizona, all nests were in trees: 93% in trees 1-3 m tall, 5% in maples, and 2% in firs taller than 3 m. Nest orientation was mostly south-southwest. Birds selected trees for nesting that had high cover density. Nests were positioned to take advantage of the afternoon sun. High-quality nest sites may not be as abundant as typically assumed because suitable nest trees must be dense but provide a small opening for a nest with a southwest exposure (Martin and Roper (988). In Quebec, nests were invariably on the ground and usually at the base of a small balsam fir or hemlock whose lowest branches touched the ground and provided cover for the nest. The only exception was one built 1.2 m from the ground at the trunk of a small balsam fir (Mousley 1916a). In British Columbia, 64% of nests were in trees, including snags, or among tree roots. Coniferous trees (42% of nests) were preferred to deciduous (8%). Nests in trees were among branches (71%), either saddled on the branch or in a fork or crotch (45%), against the tree trunk (20%), or near the top of a tree (6%). Six percent of nests were in shrubs. Fifty-seven percent of nests were on or close to the ground at the bases of trees, on banks, in tree or rock crevices, or under fallen logs. Nest height ranged from 0 to 6 m, with 57% between 0.3 and 1.5 m (Campbell et al. 1997). Nests east of the Rocky Mountains were typically on the ground in a natural depression and under a small conifer that provided protection. Eighty-nine percent of nests were covered: 295 under a live tree, shrub, or sapling; and 200 under live nonwoody vegetation such as ferns, grasses, forbs, mosses, and sedges. Of the remaining nests, 8% were in open areas with no vegetative cover (on dead logs or stumps, road-cut banks, in dead leaves, on bare ground) and 2% were in slash, on roadsides and mounds, or at forest edge. The mean height of 621 nests was 0.07 m (range 0-0.3 m; Dellinger et al. 2020). Unusual nest sites include 1.2 m up on bean poles, in old robin and phoebe nests, on a barren ledge of rock in an abandoned quarry, on shelves under the eaves of buildings, in a tin gutter under the eaves of a 2-storey house, on a rafter under the roof of a building, in deciduous tree cavities, in golf-course rough, in a previously used Northern Waterthrush nest, in an abandoned mine shaft, and in short grass under a cemetery grave marker (Dellinger et al. 2020; Gross in Bent 1949; Lemieux and Sutherland 2007).

In Algonquin Park, the average size of 23 territories was 0.78 ha (range 0.06-3.38 ha). In white birch–poplar stands, the Hermit Thrush was active from the ground to 11.6 m, and this was the average depth of territories overall. It was not seen above 12.2 m in white birch–poplar–balsam fir–spruce stands, which represented the top of the coniferous forest canopy. In hemlock stands, it ranged up to 11.6 m which was 2.4 m above the bottom of the canopy but well below the top of the canopy (24.4 m; Martin 1960). The average size of territories in Quebec was 1.0 ha, but was 0.6 ha in a hemlock forest near Mirabel (Falardeau in Gauthier and Aubry 1996). Morse (1977) reported a mean territory size of 2.00 ha in white spruce stands in Maine. In Quebec, the Hermit Thrush clustered territories at all spatial scales (Bourque and Desrochers 2006). In Wisconsin, Loss (2012) found nests as close together as 12 m but in a second year nests were more evenly spaced with a minimum of 46 m between nests.

No information is available on natal philopatry but it is probably low. Almost nothing is known of adult site fidelity during the breeding season. Dellinger et al. (2020) reported that 8 of 18 males (44%) returned to the same territory the following year in Algonquin Park. Schlossberg (2009) summarized return rates of 127 adults from 2 studies and estimated a site-fidelity rate of 35%.

Limiting Factors

Eggs have been found in Ontario nests from mid-May until the third week of August, with most present in June and the first week of July (Peck and James 1987). In Algonquin Park, nests are under construction from mid-May to early July, eggs are present from mid-May to late July, nestlings are present from late May to early August, and dependent fledglings have been observed from late June to mid-August (Tozer 2012).

It takes 7-10 days to build the nest, and eggs are laid at the rate of 1 a day. Incubation begins continuously with laying of the last egg, or a day later. The incubation period of 7 Ontario nests was 11-13 days. Overall, the incubation period has been reported as 10-13 days. Eggs hatch synchronously or a day apart. Young fledge at age 10-15 days, but typically on day 12 (Campbell et al. 1997; Dellinger et al. 2020; Dilger 1956; Gross in Bent 1949; Morton and Pereyra 2010; Peck and James 1998a).

Most Hermit Thrushes raise a single brood but some have been documented raising second broods, and second broods have been suspected in many areas. There are a few cases of nests being reused, including in Ontario, and this is suggestive of second broods. A probable second nesting was reported in Ontario and egg dates strongly suggest 2 broods, but second broods have not been confirmed in the province. In Quebec, egg dates indicate high probability of second broods, but none have been confirmed. In California, 3 of 66 pairs (4.5%) were confirmed attempting second broods after successfully rearing the first. Double broods usually occurred in years when the snow melted early. It has been suggested that it may raise 3 broods in the southern portion of its range, but this has not been confirmed. Renesting is common if the first clutch is lost. In Arizona, all birds that renested moved to another patch of firs for the replacement nest. In Ontario, clutches of 2-5 eggs were reported, with most containing 4 eggs. Elsewhere, clutches of 3-6 eggs have been documented with 4 eggs typical. The average clutch size east of the Rocky Mountains is 3.36 eggs (Armstrong and Euler 1983; Campbell et al. 1997; Dellinger et al. 2020; Falardeau in Gauthier and Aubry 1996; Gross in Bent 1949; Martin and Roper 1988; Peck and James 1998a; Smyth 1947).

The age at first breeding is assumed to be 1 year but this requires confirmation. The Hermit Thrush probably breeds annually thereafter. The mating system is monogamous (Dellinger et al. 2020).

Different foraging techniques and substrates further partition habitat among coexisting thrush species. All thrush species that Dilger (1956) studied in New York occasionally foraged on the ground, but the Hermit Thrush and Wood Thrush did so most frequently. They were primarily ground feeders at forest edges; the Veery and Swainson's thrushes were predominantly arboreal foragers in forest interior. The Hermit Thrush did some flycatching as well as foraging in trees and shrubs for small fruits, especially in autumn and winter. In Wisconsin, the Hermit Thrush and Veery differed significantly in the heights at which they foraged. Foraging methods of both species were dominated by capturing prey on foliage, often while in flight similar to flycatchers. The Hermit Thrush spent only 8% of its time on the ground, but 24% of prey was captured on the ground. Ground foraging accounted for less than 10% of Veery prey captures. Both thrushes fed mostly below 6 m, but the Veery concentrated its activities in the lowest stratum (0-3 m). Shrubs were the most important site for Veery (52% of feeding bouts occurred in the 3-m stratum); saplings and low

tree growth were most important for the Hermit Thrush (79%). The Hermit Thrush fed more in conifers and the Veery fed more in shrubs (Paszkowski 1984). Foot-quivering is another foraging technique of the Hermit Thrush whereby the feet are moved rapidly in the leaf litter to flush potential prey. On the ground, hopping and gleaning is its most frequent foraging technique (Brackbill 1960b; Davis 1996; Thurber 1999).

Nestlings are initially fed small caterpillars, but by age 3 days the diet is supplemented with winged insects, spiders, and ants. By days 7 and 8, large moths, grasshoppers, and beetles were fed to the young. In Pennsylvania, nestlings were fed blueberries and cherries. Young at 1 New York nest were fed geometer moth caterpillars and blueberries. In New York, 1 pair brought Allegheny Mountain dusky and red-backed salamanders to nestlings on about a quarter of trips (Dilger 1956; Gross in Bent 1949; Smyth 1947).

Beal (1915b) analyzed 551 stomachs collected in all months of the year. The diet consisted of 64.5% animal matter and 35.5% vegetation. The animal foods were predominantly insects with some spiders; the vegetable matter was mostly wild fruit. Animal food included 15.1% beetles (ground and scarab beetles and weevils), 12.5% ants (consumed mostly May through September with lesser numbers in July), 5.4% other hymenopterans (bees and wasps), 9.5% caterpillars (eaten every month with peak numbers in June), 3.6% bugs (mostly stink bugs), 3.0% flies (mostly crane and march fly eggs and larvae), 6.3% grasshoppers and crickets, 0.3% miscellaneous insects, 7.5% spiders and centipedes, and 1.3% miscellaneous animals such as isopods, snails, and earthworms. The Hermit Thrush seldom eats domestic fruit, but occasionally consumes strawberries, grapes, currants, apples, and raspberries. Wild fruit constituted 26.2% of the vegetable food; 8.1% was seeds, ground-up vegetation, and seeds of poison ivy and poison sumac. Fruits eaten included those of sumacs, blackberries and raspberries, dogwoods, huckleberries, blueberries, greenbriers, pokeweed, and winterberry holly. It subsists almost entirely on invertebrates in spring and early in the breeding season, with fruit becoming increasingly important in the diet as the breeding season continues until fruit dominates by autumn. Dellinger et al. (2020) stated that it eats insects, other small invertebrates, amphibians, reptiles, fruit, snails, earthworms, centipedes, millipedes, and termites. Fruit consumed includes elderberries, pokeweed, sassafras, dogwoods, hollies, greenbriers, juneberries, sumacs, poison ivy, raspberries and blackberries, alders, spicebush, mulberries, Virginia creeper, privet, and juniper. Leckie (2006) observed a Hermit Thrush eating a DeKay's brownsnake and Dellinger et al. (2020) reported an adult bringing a red-bellied snake to nestlings. It has eaten salamanders in New York, Maine, Michigan, and Rhode Island. Due to their abundance in woodlots, salamanders are potentially a significant component of the diet. When given a choice between holly berries, earthworms, and salamanders, 1 bird selected salamanders (Gross in Bent 1949; Thurber 1999). In late summer and autumn in Illinois, its degree of frugivory differed significantly over 3 years, with 28-100% of birds exhibiting frugivory yearly with an average of 44%. The Hermit Thrush was the least frugivorous of the species studied. It foraged significantly more in forest interior than in gaps created by treefalls. It foraged significantly more for fruits in gaps and for insects in the interior. Areas with clumps of fruit were preferred to those with isolated plants. The type of fruit consumed annually differed significantly. In the first year, 100% of the fruit eaten was Canada moonseed; in the second year, it was 53% grapes, 35% greenbriers, and 12% moonseed; in the third year, it was 39%

grapes, 48% Virginia creeper, 4% greenbriers, and 8% spicebush. The annual differences in diet were not correlated with levels of fruit abundance. All bird species tended to concentrate on 1 or 2 particular fruits each year, but the favoured fruit was seldom the same year to year. The Hermit Thrush was one of the most important species in consuming and dispersing Canada moonseed (Malmborg and Willson 1988). In Maine, it ate few spruce budworms at low budworm densities, but increased its consumption of them as the budworm density increased to a level where the budworm content per stomach reached about 14 larvae or pupae (Crawford and Jennings 1989). Near Manitouwadge, Venier et al. (2009) found no relationship between abundance of the Hermit Thrush and the spruce budworm. Over 2 years in Maine, spruce budworm larvae and pupae constituted 13% and 12% of its invertebrate diet (Mitchell 1952).

The Hermit Thrush is a relatively infrequent host of the Brown-headed Cowbird, although it has been suggested that it is a regular, if not preferred, host choice of the cowbird. The Hermit Thrush tends to nest in habitats that are inhospitable for the cowbird. In Ontario, 11 of 154 nests (7.1%) were parasitized. In New York, 46.2% of 13 nests found at 1 site were parasitized. Hahn and Hatfield (1995) concluded that parasitism rates in 1 region could not be used to predict parasitism rates in other regions. Most Hermit Thrush nests were 1 m or less from the ground, and low-nesting forest birds experienced the highest parasitism rates. Parasitism rates vary in different regions: 2.3% in Minnesota, 5% in Quebec, 21.7% in northern Michigan, and 6% in British Columbia. The average parasitism rate east of the Rocky Mountains is 4.7% compared with 1.5% west of the Rockies. The Hermit Thrush accepts cowbird eggs, and both species may fledge successfully from a parasitized nest. East of the Rockies, parasitized nests had an average of 2.7 Hermit Thrush eggs (range 2-4); unparasitized nests contained an average of 3.4 thrush eggs (range 1-5; Campbell et al. 1997; Dellinger et al. 2020; Gross in Bent 1949; Manolis et al. 2002; Peck and James 1987).

South of the Canadian Shield, habitat loss and fragmentation do not appear to be an issue for the Hermit Thrush. Maturation of coniferous plantations in this area has increased the amount of available habitat.

The effects of forestry practices on the Hermit Thrush vary depending on the type of management undertaken. In the Boreal Forest Region, with particular reference to Ontario, its abundance did not change significantly when 30% or 50% of trees were removed, but decreased when 70% of trees were removed. It experienced a 25% decrease when 35% of trees were removed, a 50% decrease when 50% of trees were removed, and a 75% decrease when 70% of trees were removed (Vanderwel et al. 2007, 2009). In Algonquin Park, there was no significant change in its abundance as a result of single-tree selection harvesting (Jobes et al. 2004). In the Ontario Canadian Shield, there was no difference in its abundance in early successional and mid-successional clear-cuts compared with similarly aged stands after fire. It was equally abundant in mid-successional and mature stands but significantly more abundant in early successional than mature stands (Zimmerling et al. 2017). In New York, there was no trend in its abundance in unlogged forests and those where 25%, 50%, 75%, or 100% of the merchantable timber was removed. It was not affected by logging (Webb et al. 1977). In New Brunswick and Nova Scotia, it was absent in recent clear-cuts, burns, and shelterwood cuts where the basal area was reduced by 55%, and was uncommon in strip-cut areas relative to uncut areas. It returned in low densities after 8 years and became most

abundant after 40 years (Falardeau et al. 1999; Freedman and Johnson 1999; Freedman et al. 1981; Morgan and Freedman 1986). In Newfoundland balsam fir stands, its density was significantly higher in uncut stands than in 40- and 60-year-old second growth (Thompson et al. 1999). In Newfoundland, its overall occurrence tended to be higher in natural than harvested landscapes, especially at higher percentages of forest cover. It was negatively associated with the amount of woodland in harvested landscapes and positively associated with amount of woodland in natural landscapes. In harvested landscapes, the proportion of sites occupied was 30% at 15% forest cover, peaking at 60% for 45% cover, and declining to 20% at 95% cover. In natural landscapes, there was a regular increase with increasing forest cover from 0% occupation at 10% forest cover to 50% at 95% cover. Taylor and Krawchuk (2005) concluded that the Hermit Thrush could fulfill its resource needs in harvested landscapes. Whitaker et al. (2008) studied its annual survival in relation to forest fragmentation by clear-cuts and natural openings in Newfoundland. They concluded that it may be resilient to moderate amounts of clear-cutting. In Newfoundland balsam fir stands, Whitaker and Montevecchi (1999) examined the effectiveness of 20-50-m wide riparian strips between clear-cuts and watercourses and water bodies. There were no significant differences in its abundance within 30 m of water in undisturbed areas, within buffer strips including adjacent clear-cut areas, in undisturbed buffer strips only, and in buffer strips when observations in clear-cuts were excluded. Buffer strips may provide suitable habitat for the Hermit Thrush. In Quebec, it nested in aggregations. Forest fragmentation could be detrimental if the forest became too small to support more than 1 territory (Bourque and Desrochers 2006). In Minnesota, nesting success increased significantly with distance from forest edge (Manolis et al. 2002). In Michigan, it avoided recent clear-cuts in jack pine, but was common in stands cut 5-23 years previously. In Maine, forests were used for nesting 16 years after clear-cutting, and possibly sooner (Dellinger et al. 2020). In Alaska, distance from edge (the coastline) was the most important factor in determining Hermit Thrush nest survival. In narrow corridors (less than 250 m) successful nests averaged 90 m from edge compared with 37 m for depredated nests. In corridors wider than 350 m, successful nests averaged 202 m from edge compared with 107 m for depredated nests (D.M. Sperry et al. 2008). In New Hampshire, it was less abundant near edges of clear-cuts, but its distribution did not differ from that of randomly placed territories. King et al. (1997) concluded that its lower abundance in edge habitats was not necessarily evidence of edge avoidance, but may be due to the absence of suitable habitat beyond clear-cut edges.

Fire may result in short-term avoidance of burned areas, but long-term effects depend upon the severity of the burn and on changes to vegetation. The Hermit Thrush will nest in burned areas and early postfire successional areas. In California, it was absent 8 years after fire. In Labrador, its density peaked 14 years after fire. Presence of residual snags in burned forests may be important in determining if it will still use the area. Snags provide cover, food, and singing perches. In a burned forest in Newfoundland, numbers of breeding pairs were 5.5 where snags were retained and 0 where snags were removed (Dellinger et al. 2020). In Oregon, it declined after fire regardless of the severity of the burn. Populations were still depressed 9 years after the fire (Stephens et al. 2015).

Akresh et al. (2024) determined that the Hermit Thrush had a significant increase in nest success as distance from forest edge increased. Core areas greater than 250 m from edge tended to have higher nest success.

Loss and Blair (2011) studied the effects of introduced earthworms on Hermit Thrushes breeding in northern hardwoods in Wisconsin. Nonnative earthworms consume leaf litter and organic layers below the leaf litter, mix soil horizons, reduce the abundance of mycorrhizal fungi and arthropods, and alter nutrient dynamics. Significantly lower densities of Hermit Thrushes occurred at areas with earthworm invasion (Loss 2012). Nonnative earthworms may be a contributing factor to its decline in some areas.

Gutzwiller and Anderson (1999) researched the effects of human disturbance in a remote area. Intrusions consisted of a person walking around for an hour in a 1-ha plot. The mean abundance of the Hermit Thrush was 57% lower in intruder than control plots. Intrusions resulted in displacements and prevented normal access to habitats and their associated resources. Sensitivity to intrusion can depend significantly on whether previous interactions with humans were positive, neutral, or negative. It is likely that birds nesting in remote areas where humans are seldom encountered will be greater affected by disturbance than those nesting where interactions with humans are frequent.

In Alberta, there were no differences in Hermit Thrush abundance adjacent to noisy compressor stations and quiet well pads. It did not appear to be affected by chronic noise (Bayne et al. 2008). It was significantly less abundant at well pads than in adjacent forest interior. There was no difference in its abundance at seismic lines and pipelines than in forest interior adjacent to these features (Bayne et al. 2016).

Extreme cold and/or heavy snowstorms early in the spring may cover up food and result in significant mortality (Gross in Bent 1949).

Status

Baillie and Harrington (1937) considered the Hermit Thrush a fairly common summer resident of the central and less settled portions of the province, from Halton and Leeds north and west to Lake of the Woods and Thunder Bay and Algoma districts. They thought that it probably bred north to James Bay. The first atlas indicated that the Hermit Thrush was a common and widespread breeder in Ontario. The breeding range was continuous throughout the Canadian Shield and Hudson Bay Lowland, and it was well distributed on Manitoulin Island and the Bruce Peninsula. There were numerous breeding records south of the Canadian Shield in eastern Ontario and east and west of Lake Simcoe and it also bred in the Long Point area. There was a retraction in range south of the Shield from what Baillie and Harrington (1937) reported, with no records from Halton (Knapton in Cadman et al. 1987).

The second atlas indicated that the Hermit Thrush range had not changed significantly except south of the Shield. It was found in virtually every square on Manitoulin Island and the Bruce Peninsula. There were many additional records south of the Shield, particularly on the Oak Ridges Moraine, the Niagara Escarpment, and in eastern Ontario. Maturation of pine plantations on the Oak Ridges Moraine coupled with a general increase in forest cover are probably key in its increased distribution south of the Shield. It remains rare in the portions of southwestern Ontario that support

extensive agriculture from Grey County south to Lake Erie. Its probability of observation increased significantly province-wide and in all regions except the Carolinian Forest Region, where the increase was nonsignificant. It was most abundant in the Boreal Forest Region and Hudson Bay Lowland. High densities also occurred between Lake of the Woods and Thunder Bay. The Shield south of the North Bay area supported moderate densities; its density in the Great Lakes–St. Lawrence Forest Region south of the Shield was low (Friesen in Cadman et al. 2007).

Breeding Bird Survey data indicate that the Hermit Thrush decreased at annual rates of 0.987% in Canada and 0.242% in Ontario 1970-2021. The 2011-21 trends were annual decreases of 3.05% in Canada and 5.01% in Ontario. All estimates were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

In Michigan, Akresh et al. (2009) netted birds in riparian habitat (a mix of alder, honeysuckle, and trembling aspen) and in upland trembling aspen stands during the postbreeding period. Seventy-nine percent of Hermit Thrush juveniles were caught in riparian habitat and most adults occurred in the shrubbier habitat. In Minnesota, Streby et al. (2011b) captured only 4 Hermit Thrushes in regenerating clear-cuts during the breeding season, but caught 18 adults and 32 fledglings during the postbreeding period, suggesting that dense woody vegetation is important during that period. During the postfledging period in Pennsylvania, Stoleson (2013) caught 9 adults and 23 fledglings in clear-cuts and 3 adults and 27 fledglings in mature forests. Capture rates in clear-cuts and forests were identical. Some birds that were recaptured had switched habitats.

MIGRATION

The Hermit Thrush migrates mostly at night, stopping to rest during the day, but moves more during the day than other thrushes in the same genus and the Wood Thrush. Nocturnal spring migration occurs when the maximum daily air temperature is 21°C or higher. It is rarely seen in conspecific flocks during migration, but individuals may occur in flocks of chickadees, kinglets, and titmice. In spring, males arrive about 2 weeks before females. In autumn, females migrate slightly sooner than males. Autumn migration is often precipitated by cold fronts, high pressure, clear skies, and strong northerly winds. In Louisiana, adults arrive in autumn before juveniles (D.R. Brown et al. 2002; Campbell et al. 1997; Dellinger et al. 2020; Graber et al. 1971; Gross in Bent 1949; Stouffer and Dwyer 2003).

The Hermit Thrush arrives in southern Ontario in mid-April and spring migration continues until early or mid-May. The midpoint of migration at Long Point is 27 April (Mills 2005b). In the Hudson Bay Lowland, a bird seen on 27 July was presumed to be an autumn migrant, and other migrants were seen 3-12 September. In the southern Shield, autumn migration occurs mainly in September and early to mid-October. In the south, autumn migrants may appear as early as mid-August but the average arrival is early to mid-September, with the peak in October. Stragglers persist into November and December and some overwinter (Black and Roy 2010; Curry 2006; LaForest 1993; Mills 1981; Tozer 2012; Weir 2008; Wilson and McRae 1993). At Long Point, the midpoint of autumn migration was 13 October 1975-2000 (Mills 2005b) and was 12 October in 2008 (Mills et al. 2011).

Mills (2005b) examined migration timing of the Hermit Thrush at Long Point in relation to global warming for 1975-2000. The date of first spring arrival tended to be earlier in later periods, but not

significantly. When spring migration data were analyzed by quartile, there was a nonsignificant tendency to migrate later with time. In autumn, it departed significantly later over time. Smith and Paton (2011) analyzed 48 years of data from a Rhode Island banding station and found that the Hermit Thrush departed significantly later in autumn in recent years. They attributed the delay in migration to climate change.

At Long Point Bird Observatory (LPBO), spring stopover times of Hermit Thrushes were 2.42-4.30 days. Stopover duration may be related to habitat features including food and shelter (Dellinger et al. 2020). During autumn migration at Long Point, the duration of stay averaged 8.9 days (range 0.8-20.5 days). Some birds made nocturnal local landscape-scale flights. The mean duration of time from capture until a landscape-scale flight was 3.6 days compared with the mean duration of 9.9 days from capture to final detection. Landscape-scale movements exceeded 1 km. Most flights were from the tip of Long Point which offers lower-quality habitat than the other 2 LPBO banding stations (Mills et al. 2011). In Michigan, the average duration of autumn stopover was 5.4 days. Birds that were lean when they arrived stayed significantly longer (average 6.4 days) than those that were fatter (4.8 days; Craves 2009). One bird stayed in the same location for 2 weeks in northeastern Illinois in October (Graber et al. 1971).

The Hermit Thrush may occupy a variety of habitats during migration including city parks, urban churchyards and gardens, university campuses, and several natural habitats. These may include old shrubby fields and forests of all types, but especially those with moderately dense understorey and an abundance of fruit. It may prefer edges and openings in woodlands. It is often associated with moist areas such as lakeshores, floodplains, and margins of ponds and marshes (Campbell et al. 1997; Craves 2009; Dellinger et al. 2020; Gross in Bent 1949; Leighton et al. 2002; Sinclair et al. 2003; Weir 2008). In Pennsylvania, it was detected significantly more on transects through forests than in shrub habitat during spring migration. There was no significant difference in capture rates of nets placed in forest or shrub habitat although more birds were captured in shrubby areas (Smith and Hatch 2008).

Few Hermit Thrushes inhabit cities. Urban areas may pose constraints such as human disturbance which may interfere with foraging time. In addition, urban-adapted bird species compete for fruit. Nonnative fruits predominate and high-quality fruits are usually depleted earlier in the season leaving Hermit Thrushes to rely heavily on low-lipid nonnative fruits (Craves 2009).

During migration, the Hermit Thrush may establish small foraging areas that are approximately 100 m in radius, an area of about 3 ha (Dellinger et al. 2020).

S.B. Smith et al. (2007) studied the diet of autumn migrants in Rhode Island. Daily dry food intake was 8.67 g for autumn olive, 8.06 g for pokeweed, 7.65 g for roses, 7.39 g for chokecherry, 7.20 g for bittersweet, 6.80 g for winterberry holly, 6.04 g for Virginia creeper, 4.97 g for southern arrowwood, and 4.71 g for bayberry. Fruit selection may have been due in part to availability. In Illinois, 21 stomachs collected during spring migration contained 84% insects. Of these, 20-30% were beetles, with timing of spring arrival coinciding with the emergence of many beetles. Lepidopterans (18-19%) and ants (13-15%) constituted much of the rest of the diet. It ate more millipedes (12%) than most other bird species. The spring diet also included 7-8% grasshoppers, 7-8% bugs, and 4%

spiders. In autumn, it fed on grapes and was particularly fond of pokeweed berries (Graber et al. 1971). In subalpine areas of British Columbia, blueberries were an important source of food for autumn migrants (Evans Ogden et al. 2013).

During migration, the Hermit Thrush may strike tall structures such as buildings, television and communications towers, and lighthouses. A 3-year study in Toronto found 139 at the bases of tall buildings. Fifty-five died; 84 were alive but possibly injured. In Arkansas, 127 were killed in 1 night at a transmission tower. Few casualties occurred at Illinois television towers with the Hermit Thrush representing 0.02% of victims (Graber et al. 1971; Gross in Bent 1949; Dellinger et al. 2020).

Snowstorms accompanied by cold weather may result in mass mortality during migration, especially if food supplies are covered up. After a heavy snow and cold temperatures on 10 October 1906, there was a massive kill of birds on the Ontario shoreline of Lake Huron. Although the bulk of Hermit Thrushes had already passed through by 6 October, they were still well represented among the dead. In Illinois, there was a large kill of Hermit Thrushes by a storm at the southern end of Lake Michigan on 16 April 1960 (Dellinger et al. 2020; Graber et al. 1971; Gross in Bent 1949).

The Hermit Thrush is a common migrant in Ontario (James 1991), although it is an uncommon spring and autumn migrant in Elgin County (Lancaster et al. 2004). Spring numbers are generally lower than those in autumn.

LPBO data suggest that numbers of the Hermit Thrush are stable or increasing during migration. Hussell et al. (1992) reported a net change of 0.0% 1961-88. Changes within different time intervals were: 1961-70, –4%; 1970-79, +0.5%; 1978-88, +3.2%. From 1961 to 1994, there was a significant increase of 1.26% per year with increases in both spring and autumn (Dellinger et al. 2020). From 1967 to 2007, it increased at a rate of 1.0% per year (Anonymous 2009b).

WINTER

The Hermit Thrush prefers to winter south of where snow stays on the ground for a prolonged period and usually winters south of latitude 40°N. Christmas Bird Count (CBC) data indicated that it is mostly absent from regions with January temperatures below –4°C, but there are 3 populations, including southern Ontario, that winter in areas colder than this. It requires open water in winter and is common only in forests that rarely get below –1°C in January. Females migrate further south than males, but there appears to be no difference in winter distribution between age classes. The mean December to February latitude of males is about 1.2° north of that of females; the mean winter latitude of the sexes differs by 130 km. In Louisiana, 75% of winter birds were females. It is most likely that birds overwintering in Ontario are males (Gross in Bent 1949; Root 1988; Stouffer and Dwyer 2003).

In the Hamilton area, wintering birds are often found in ravines with open water and abundant fruit (Curry 2006). During winter, the Hermit Thrush tends to inhabit dense, moist forests and concentrate in forest openings and at forest edges, possibly because fruit may be more abundant in these areas. In the southeast, it is most common in woodlands with a moderate density of understorey, especially where broad-leaved evergreens are present. In the Midwest, it winters among dense berry-bearing vegetation, particularly in ravines and other sheltered locations. In Louisiana, it was most abundant in pole-stage pine stands and least abundant in hardwoods, which

had an open understorey and low fruit availability. There was no difference in the habitats selected by males and females, or adults and juveniles. During winter, it may also occur in well-vegetated residential areas surrounded by a wooded landscape (D.R. Brown et al. 2002; Dellinger et al. 2020; Dunn and Tessaglia-Hymes 1999; Root 1988; Stouffer and Dwyer 2003). In South Carolina, winter distribution of the Hermit Thrush was largely explained by the dry mass of ripe fruit, habitat types, and interactions between habitat and year. Abundance was positively associated with the mass of dry pulp. Twice as many were detected in bottomland hardwood stands than in regeneration, pine plantations, and upland hardwoods. Although habitats differed in the number of Hermit Thrushes they supported, each habitat exhibited an increase in thrushes with increasing dry pulp mass. Much of the variation in abundance among habitats was independent of fruit biomass indicating that other factors are important. Some habitats that were not sampled, such as 10-40-year-old pine plantations, may be important wintering sites in South Carolina (Kwit et al. 2004).

Some Hermit Thrushes defend a territory in winter; others are non-territorial floaters. In Louisiana, 86% of birds were territorial and 14% were floaters. There is little territory overlap, averaging 15.9% (range 0-79%). In Louisiana, the territory size of 34 birds was 0.55 ha (range 0.22-0.97 ha). Territory size did not vary by sex or age class, but did by habitat. Average territory sizes were 0.69 ha in hardwoods, 6.78 ha in sapling-stage pines, 0.48 ha in mature pine, and 0.45 ha in pole-stage pines. Pole-stage pines appeared to be superior habitat due to the smaller territories and the fact that they were settled first. In South Carolina, territory size was unrelated to the availability of either fruit or arthropods. Home ranges of floater birds averaged 5.83 ha (range 2.53-11.3 ha). Floaters included both sexes and age classes. The average distance between consecutive locations was 55.30 m for territorial birds and 121.28 m for floaters. Floaters often had very small core home ranges from which they wandered widely. Many birds were site faithful from November until March. Vacated territories were quickly occupied by either expanding or shifting of neighbouring territories, or by floaters (Brown and Long 2007; D.R. Brown et al. 2000, 2002; Diggs et al. 2011).

The Hermit Thrush has a tendency to return to the same wintering area in successive years. In South Carolina, 10 of 81 birds (12.3%) returned the following winter. In California, 18% of 306 returned to the same site the next winter and in Mexico several were captured in the same mist net over a 3-year period. In Louisiana, 18% of individuals returned to winter in the same plot. Of 25 returns, only 2 were captured more than 30 m from where they were originally caught. No marked bird was captured or observed at more than 1 plot or more than 1 point count location. Returning birds used the same territory that they defended the previous winter (Brown et al. 2000; Dellinger et al. 2020; Gross in Bent 1949).

The Hermit Thrush is largely frugivorous in winter, even in the south where arthropods are still available. The diet consists mostly of fruit until just prior to spring migration when it eats invertebrates almost exclusively. Wild fruits, berries, and seeds consumed in winter include those of dogwoods, pokeweed, juneberries, hollies, blueberries, mistletoe, grapes, elderberries, viburnums, spicebush, mulberries, greenbriers, Virginia creeper, sumacs, poison ivy, and privet (Gross in Bent 1949; Kwit et al. 2004; Long and Stouffer 2003). Over 2 winters near Branchton, one fed regularly on the fruit of staghorn sumac (personal observation). In South Carolina, larger birds (mostly males) occupied territories with more arthropods and had a diet with a higher proportion of arthropods

than smaller birds, often females. Arthropods were a critical component of the winter diet. Smaller-bodied females may be excluded from optimal territories and be forced to spend more time foraging to meet their energy requirements (Diggs et al. 2011).

The Hermit Thrush is a rare visitor to winter bird feeders. Even in the core of its winter range usually only one comes to an individual feeder on a casual basis. One that spent the winter of 1941-42 at London fed on currants supplemented by suet crumbs from under the feeder. A bird at a Toronto feeder in February 2002 fed on bits of suet dropped by woodpeckers. It also seemed to feed on bits of sunflower seeds after finches and cardinals had opened the shells. It took bits of suet and shelled sunflowers from the feeder. Feeders are most likely to be visited in midwinter or during spring migration; most visits are for water rather than food. Infrequent items consumed at feeders include mixed seeds, niger, bird puddings, peanut butter mixes, dried fruit, suet bits, and bread crumbs (Dunn and Tessaglia-Hymes 1999; Gross in Bent 1949; Iron and Pittaway 2002).

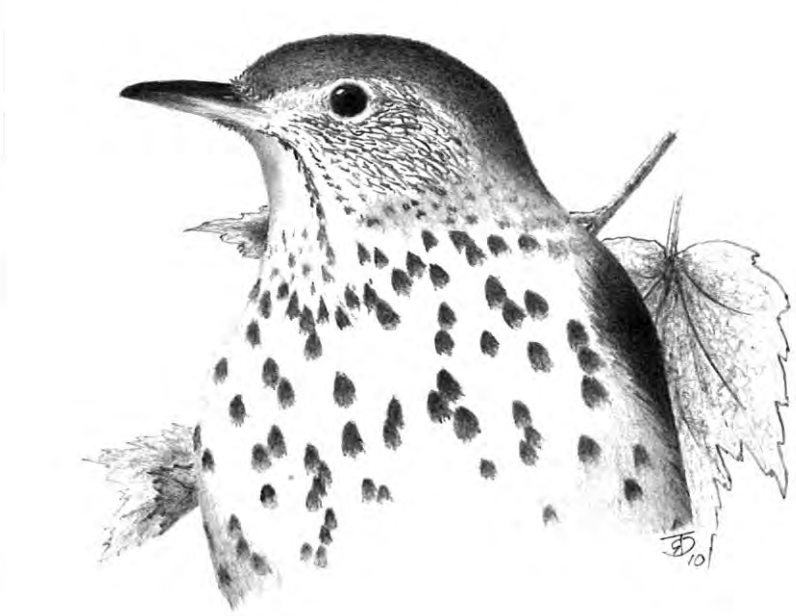
Severe winter weather is probably the most significant limiting factor to the Hermit Thrush. Populations may experience significant declines after a severe winter. Large numbers perished in South Carolina during cold temperatures in February 1899 and hundreds died in January and February 1895 due to cold weather even though food was abundant. Population declines in the Maritimes in the late 1950s were attributed to severe winter weather in the southeastern states. Low populations in Illinois in 1958, 1959, and 1960 were thought to be a result of severe winter weather. During a severe winter storm in Illinois, its density declined from 7.9 birds per km^2 to 0. It was concluded that the storm resulted in 100% mortality (Dellinger et al. 2020; Graber and Graber 1979; Graber et al. 1971; Gross in Bent 1949; Stouffer and Dwyer 2003).

The Hermit Thrush is local and rare in winter in Ontario and the northern portion of its winter range (Dellinger et al. 2020; James 1991). Beginning in the 1970s, it began to overwinter with increasing frequency in the Hamilton area and at least 1 or 2 are found each winter now (Curry 2006). It was reported in Elgin County on 7 of the last 10 CBCs (Lancaster et al. 2004). Dellinger et al. (2020) reported that it wintered regularly on islands in western Lake Erie. Of 7 CBCs when data were collected on Pelee Island, it was observed 5 years. Numbers present ranged from 1-21 and averaged 5.9 birds over all 7 years and 8.2 birds if only the years when it was detected are considered (Allen Woodliffe, unpublished data).

Based on Project FeederWatch data, the Hermit Thrush increased in abundance in the 30 years prior to 1996 despite cold winters (Dunn and Tessaglia-Hymes 1999).

Wood Thrush

Hylocichla mustelina

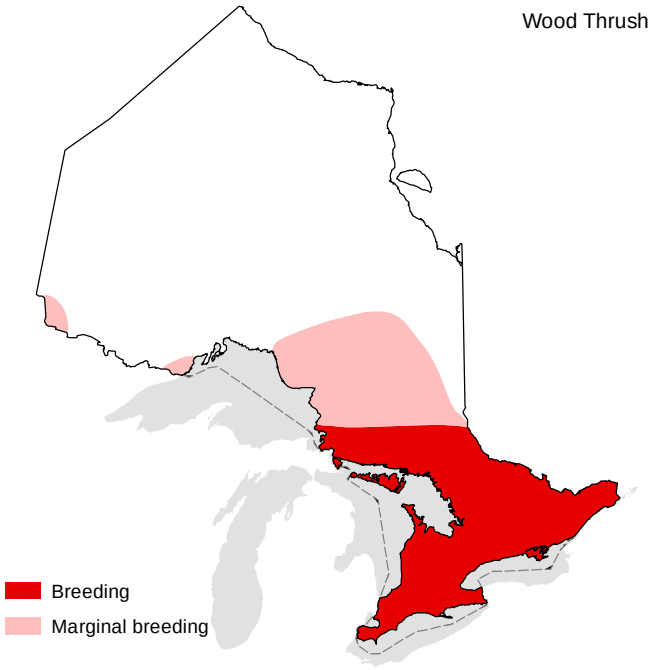


BREEDING SEASON

Habitat Requirements

In Ontario, the Wood Thrush breeds predominantly in forested areas. Deciduous (58.6% of nests) and mixed (37.9%) woodlands were preferred for nesting over coniferous woods and plantations (3.4%). Nesting occurred in wet and dry forests; second-growth woodlands were selected over mature woods. Four nests were in overgrown fields, 2 in fencerows, and 2 in alder swamps (Peck and James 1987).

McIlwraith (1894) stated that the Wood Thrush preferred moist beech woods for nesting. It nests in small woodlots surrounded by agriculture, in some urban woodlots, and in contiguous forest such as along the Niagara Escarpment and the southern Canadian Shield (Friesen et al. 1995). Woodlots where it nested in the Peterborough and Ottawa areas were dominated by sugar maple, with white ash and basswood frequent in the canopy. Peterborough sites contained some hophornbeam, white cedar, and beech in the canopy (Phillips et al. 2005). In the Region of Waterloo and along the Niagara Escarpment, it nested in upland deciduous forests dominated by sugar maple, beech, and white ash, with lesser amounts of hemlock and white cedar. These were early to mid-successional forests with occasional pockets of older growth. They had openings created by selective logging with an understorey of sugar maple and white ash saplings, alternate-leaved dogwood, and red



elderberry (Friesen and Campbell 2002; Friesen et al. 1999a, 1999b). Near Metcalfe, occupied woodlots were mostly dominated by sugar maple, white ash, basswood, and hophornbeam (Villard et al. 1995). In Algonquin Park, it was most likely to occur in half-open second growth and heavily culled areas (MacLulich 1938). Also in Algonquin Park, it was detected only in pure hardwood stands or in hardwoods mixed with balsam fir and spruce. It was absent from stands dominated by poplar and white birch, balsam fir and spruce, immature white pine, and hemlock (Martin 1960). In Durham Region it occurred, in order of decreasing abundance, in mature sugar maple–red oak forest; a woodlot with an open canopy and a rank growth of ferns and raspberries; mature white cedar–elm swamp; a farm woodlot dominated by beech; mature beech-maple with a sparse understorey; mature pine plantation with a small sugar maple–red oak forest; and sugar maple forest sloping down into white cedar–balsam fir–spruce swamp (Speirs and Orenstein 1975).

F.G. Weaver (1939) and Weaver (in Bent 1949) summarized Wood Thrush habitat as cool, damp woodlands, often near streams. Moisture is considered essential to provide mud for nest building; it tends to avoid sandy areas. Presence of understorey shrubs and saplings are important habitat components. Nests have been reported in bogs and rarely in dense thickets. Some Wood Thrushes nest in cities near human habitation. Nests were often only 1 or 2 m from a house, but in all cases houses were near gorges, streams, woods, or damp places. In Maryland, it was common for nests to be 244-610 m, or even 975 m, from water in suburban areas (Brackbill 1943). M.L. Evans et al. (2020) characterized its habitat as interior and edges of deciduous and mixed forests, especially well-developed mesic ones. The key elements in sites frequently used were trees taller than 16 m, a high variety of deciduous tree species, moderate subcanopy and shrub density, shade, a fairly open forest floor, and decaying leaf litter.

The average characteristics of 165 territories were: ground cover, 44.9% (range 32.3-71.6%); shrub stems per 0.002 ha, 6.6 (range 3.8-25.1); trees 7.5-15 cm diameter at breast height (DBH) per 0.04 ha, 11.2 (range 7.4-13.8); trees 15-22.5 cm DBH per 0.04 ha, 5.9 (range 3.5-7.0); trees 22.5-37.5 cm DBH per 0.04 ha, 5.6 (range 4.1-6.7); trees larger than 37.5 cm DBH per 0.04 ha, 2.8 (range 0.6-3.8); species of trees per 0.04 ha, 5.6 (range 3.4-6.8); canopy height, 21.3 m (range 16.6-25.7 m); and canopy cover, 87.2% (range 81.2-98.1%). There were regional differences in all vegetation parameters except the number of small trees. Canopy height and shrubbiness varied most among regions, but there was considerable variation in number of tree species present. It occupied many

types of deciduous forest, but all had a well-shaded understorey that contained at least a few small trees with low, exposed branches and a fairly open forest floor with moist, decaying leafy litter. These were probably the primary determinants of its distribution and abundance. Highest densities occurred in upland mesic forests with a well-developed but sparse understorey and greater canopy height and fewer small trees. Bottomland swamps supported fewer pairs than upland mesic stands. There is a narrow range in the number of medium-sized trees in forests that support the Wood Thrush. Its range coincides with areas that receive more than 15 cm of rain during June when the birds are nesting; this may be important in providing mud for nests (James et al. 1984).

Due to regional differences in habitat preferences, there are numerous and occasionally conflicting descriptions of the Wood Thrush's habitat. In Illinois, lowland forest appeared to be preferred, although it nested in upland forests, residential areas, and shrubby areas (Graber et al. 1971). In New Jersey, it was significantly more abundant in hardwood swamps than in upland oak-pine forests (Rich et al. 1994). In New York, it required an abundance of sapling growth and was most abundant in edge situations associated with undisturbed hardwood forests. It tended to avoid drier habitats (Dilger 1956). Beal (1915b) stated that it preferred open groves and bushy pastures and could be found along little-travelled roads and near low, shrubby swamps. In Connecticut, territories tended to be clustered along streams and wetter areas at 1 area but not at another site with no water. Presence of water appeared to be important in areas that had water because the earliest established territories tended to be along small streams. Small seeps and springs sometimes led birds to establish territories in habitats that would otherwise be unoccupied. Mean vegetation parameters of territories were 43.9% shrub coverage, 16.3 m tree height, 16.2% of territory in early succession, 9.6% in late succession, moderate moisture regime (average 2.8 on a scale of 1 [dry] to 7 [wet]), and 2.4% exposed earth. Moisture, tree diameter, herbaceous cover, and shrub cover were significant determinants of its abundance (Bertin 1977). In New Hampshire and Maine, it was positively correlated with the number of trees 2-10 cm DBH, total foliage density of both deciduous and coniferous trees larger than 10 cm DBH, and total foliage volume of deciduous trees smaller than 2 cm DBH. It was negatively correlated with canopy closure, percent ground cover, number of coniferous trees larger than 10 cm DBH, and total foliage volume of deciduous trees 2-10 cm DBH (DeGraaf et al. 1998). In South Dakota, it was absent from isolated woodlots near farmsteads, but nested in floodplains dominated by Manitoba maple, elm, silver maple, green ash, cottonwood, and hackberry (Gentry et al. 2006). Within the city limits of Newark, Delaware, it nested in upland areas of tulip tree, sweet gum, oaks, and hickories, and lowland areas of red maple, sweet gum, and pin oak (Longcore and Jones 1969). In Baltimore, Maryland, it was a common breeder in wooded residential areas. Nesting occurred on lots of occupied houses, on vacant lots between houses, in trees growing at the curb, and at the edges of a park near houses (Brackbill 1958). In Michigan, it occurred in wide bands of riparian wetland forest but was most abundant in the outer edge of upland forest (Inman et al. 2002). In New Jersey, it preferred second growth but occurred in wet, disturbed forest and climax logged forest. It was the most abundant species in a climax forest of beech, red maple, and several oak species with an understorey of red maple, spicebush, and black raspberry. It first appeared in successional fields 40 years after they had been abandoned. It increased as shrubs choked out open spaces or trees shaded out herbaceous areas. It also increased in climax woods as the understorey became more open (Suthers 1988). In Wisconsin, it preferred

closed or semi-open canopy with patches of dense saplings in upland forests. It preferred moderate understorey growth and moister conditions than occur in dry-mesic oak forests. Small openings filled with saplings create favourable habitat if enough canopy remains intact (Mossman and Hoffman 1989). In the mid-Atlantic states, its abundance was positively correlated with mean canopy height, forest area, and number of trees per 0.04 ha. It was negatively correlated with the percentage of forest cover within 2 km, number of trees larger than 3 cm DBH per ha, the percentage of canopy cover by conifers, and the number of trees larger than 38 cm DBH (Robbins et al. 1989). In Wisconsin, it inhabited primarily younger and intermediate-age stands dominated by climax species (maple, oak, beech). It occupied a wide range of habitats but was uncommon in most pioneer stages (birch, poplar). It was more common in mesic than xeric forests but was uncommon in damper forests. It exhibited a wide tolerance to moisture regime (Bond 1957). In Wisconsin, it was scarce in coniferous plantations (Bielefeldt and Rosenfield 1994). Also in Wisconsin, it was uncommon in mesic forests and first appeared once trees became pole-sized (12.5-22.9 cm DBH). At this stage, the canopy is nearly closed but the self-thinning process has begun, allowing a shrub layer to develop (Hoffman 1989a). In Maryland, it was positively correlated with canopy height and total basal area of trees but negatively associated with woodlot isolation (Lynch 1987). In Indiana regenerating 7-9-year-old clear-cuts, its abundance was positively correlated with fruit availability and negatively with vegetation density (Ruhl et al. 2020).

In a New Hampshire northern hardwoods forest over a 30-year period, the Wood Thrush was common the first 15 years, declined through the next quarter of the study, and disappeared completely in the last quarter due to natural succession. Initially, the forest was mature and characterized by a dense, fairly closed canopy with an open subcanopy and a low, dense shrub layer. At the end of the study, it was more open with a patchy canopy with a denser and taller shrub and subcanopy layer and a sparser low shrub layer. It remained in an adjacent area that had been damaged by a hurricane for 10-15 years after disappearing from the plot (Holmes and Sherry 2001). In a Connecticut woodlot over a 59-year period, there was a progressive shift to larger trees, a sparser shrub layer, and a less diverse tree canopy dominated more by oaks and maples. There was no change in its population despite the decline in shrubs (Buchanan et al. 2016).

The Wood Thrush nests in a variety of forest types in the northeast. In northern hardwoods, Noon et al. (1979) documented it in 80% of mature, undisturbed forests and 47% of disturbed and successional habitats. It nested in lowland hardwoods dominated by ash and basswood in New York (Samson 1979). It was rare in sapling-pole-size aspen-birch stands and absent in other stages of this forest type (Back 1979). In northeastern pine stands, it was absent in pitch pine and most pine stands but occurred in low densities in mature pine in 1 study (Capen 1979). It is absent or rare in upland balsam fir–spruce stands and lowland conifers but may use lowland white cedar stands, tamarack, and other conifers if there are deciduous species mixed among the conifers (Crawford and Titterington 1979; Dawson 1979). It is more common in mixed stands dominated by combinations of sugar maple, beech, yellow birch, hemlock, spruce, balsam fir, and pine (Temple et al. 1979).

Some authors considered the Wood Thrush a late-successional species (Speirs and Orenstein 1975) or to require mature forests (Temple et al. 1979). Sugar maple stands are climax forest types, so it is appropriate to term it a late successional species, but it is not typically associated with older

forests. In Pennsylvania, it occurred in 18.2% of old-growth forests compared with 91.2% of forests state-wide and 89.2% of forests on the Appalachian Plateau. Haney (1999) considered it to have negative old-growth forest affinities. Bond (1957) found that it was most abundant in intermediate-aged stands where the sapling layer was well developed. It occurred almost exclusively in mature bottomland forests in South Carolina and was rarely detected in younger stands of similar composition (Buffington et al. 1997).

In Virginia, Wood Thrushes tended to avoid areas dominated by oaks and pines. The oaks were associated with xeric soils and they may have been avoiding dry areas rather than the oaks and pines. It was positively correlated with worm biomass; worms were associated with moist soils close to streams. It appeared to prefer mesic areas within its home range, which also offered a high biomass of one of its preferred prey (Jirinec et al. 2016a).

Detailed vegetation analyses have been completed comparing characteristics around the nest to random areas in the territory. In Delaware, vegetative cover within 6 m of the nest was denser 1 m above the nest than at the same height of random non-nest sites (M.L. Evans et al. 2020). In Ohio, nest sites had a greater density of small deciduous and coniferous trees and a higher amount of coniferous canopy cover than perch sites. Nests were sometimes in small hemlock trees but foraging areas were almost exclusively in surrounding deciduous woodlands. Densities of trees per m^2 were: in 1-m radius plots, 1.42 at nests and 0.58 at perches; in 5-m radius plots, 0.90 at nests and 0.43 at perches; and in 11.3-m radius plots, 0.55 at nests and 0.31 at perches. The Wood Thrush did not exhibit a preference for any size of nesting microhabitat, but nests were often in microhabitat patches of about 5-m radius (Petit et al. 1988b). In Pennsylvania, nests were in areas that had higher densities of trees, higher canopy heights, higher density of shrub stems, and higher average shrub height than randomly selected points. It selected areas that had taller trees and shrubs than generally available (Hoover and Brittingham 1998).

The Wood Thrush may nest throughout forests, but is more likely to occur at forest edges. It is more likely to use forest edges bordering on service corridors and agriculture than those along roads. Growth rates of nestlings may be faster on edges than in the interior, probably due to more abundant food resources (Kaiser and Lindell 2007). In small woodlots in Pennsylvania, it spent more than 80% of its time within 20 m of edge. Use of edge habitat was significantly more than expected based upon its availability (MacIntosh et al. 2011). In Maine, it was most abundant within 100 m of Interstate 95 and was negatively correlated with increasing distance from the highway (Ferris 1979). Hayden et al. (1985) considered it an edge species in Missouri. In Tennessee, it was more abundant near a hydro corridor through large forests than distant from the edge (Kroodsma 1984). In Maryland, Gates and Giffen (1991) studied edge effects at a forest-stream ecotone. The Wood Thrush was most abundant near the stream and edge of the forest. The forest canopy was dominated by hemlock and had hemlock and rhododendrons in the understorey. Its presence was negatively associated with deciduous cover. In New York, it used edges in the habitats it occupied (Dilger 1956).

In Ontario, the Wood Thrush is not particularly area sensitive and regularly breeds successfully in woodlots as small as 3-4 ha (Friesen et al. 1999a; Wyatt 1998). In the Ottawa area, its abundance was best predicted by forest size; the amount of surrounding forest cover was not a significant factor. Density of thrushes decreased with increasing forest size (Lee et al. 2002). In southwestern Ontario,

its probability of detection was positively correlated with the amount of forest 100 m from edge and negatively correlated with woodlot size, the amount of forest within 2 km, and the amount of regional forest cover. Only the latter 2 relationships were significant (Austen et al. 2001). In Pennsylvania, Keller and Yahner (2007) classified it as area sensitive and associated with increasing forest size. M.L. Evans et al. (2020) stated that it was more likely to occur in larger woods, but that it may nest in 1-ha fragments and semi-wooded residential areas and parks. In Maryland, its abundance declined significantly once forest size declined below 10 ha. Robbins (1979) considered its critical forest size to be 100 ha. In the mid-Atlantic states, the forest area at which its probability of observation reached its maximum was 500 ha; probability was reduced by 50% at 1.0 ha. The 3 smallest woodlots where it was detected were 0.8, 0.8, and 0.2 ha. There was a 70% chance of detecting it in a 10-30-ha woodlot (Robbins et al. 1989). In Illinois, its presence was correlated with forest size (Blake and Karr 1987). In Wisconsin, it was at least 50% more common in large than small woodlots. Frequency of occurrence was 2.3 in 6.1-14.2-ha woodlands, 11.5 in 16.2-32.4 ha, and 20.0 in woodlots larger than 32.4 ha. In mesic stands, it occurred almost exclusively in large woodlands (Bond 1957). In Iowa, Stauffer and Best (1980) considered the Wood Thrush restricted by habitat patch size. It was absent in woodlands less than 145 m wide. In Missouri, the minimum forest size it was found in was 341 ha; the minimum size threshold reported in New Jersey was only 0.8 ha (Hayden et al. 1985). In Maryland, its probability of observation was 18% in a 0.1-ha forest, reaching a maximum of 80% at approximately 150 ha (Lynch 1987). In Rhode Island, Golet et al. (2001) examined its abundance in differently sized red maple swamps. The swamps were not isolated and were bordered by upland forest. It occurred in 5.6% of swamps smaller than 1 ha, 1.2% of those 1-5 ha, 0.5% in 6-10 ha, and 1.4% in 11-20 ha. There was no significant relationship between swamp size and its abundance. In Maryland and Delaware, its probability of occurrence in riparian forests increased significantly as corridor width increased. Its probability of observation was 76% in 50-m wide corridors, 84% in 100 m, 93% in 200 m, 97% in 300 m, and 100% in 800 m (Keller et al. 1993).

In southern Ontario, the probability of a smaller woodlot being occupied by the Wood Thrush was significantly correlated with proximity to large woodlands that were a source of thrushes. Occupancy rates were highest close to large woodlands and declined with distance. The occupancy rate adjacent to large woodlands was 30%, declining to 20% at approximately 7.5 km, and less than 10% at 20 km. Occupied fragments were mostly less than 14 km from large forests and much closer on average. There was no significant relationship between regional forest cover and percent occupancy of small fragments (Nol et al. 2005). In southeastern Ontario, the amount of forest cover within 2 km was positively correlated with its density and nesting success, but negatively correlated with pairing success (Richmond et al. 2012). In New York, it selected landscapes that were 82-100% forested (Cunningham and Johnson 2019). The Wood Thrush sings more frequently in continuous forests than in forest fragments. Birds in smaller forests or where densities of thrushes are lower are more likely to be undetected than those in large contiguous forest blocks. This may affect survey results and conclusions regarding area sensitivity, density, and overall abundance (McShea and Rappole 1997).

Several studies examined habitat partitioning between the Wood Thrush and other thrush species. In New York, the Wood Thrush had no positive associations with other thrush species'

habitat, but it was least negatively associated with the Veery (Dilger 1956). James et al. (1984) stated that none of the other thrush species occurred where the Wood Thrush occupied its average habitat. The Wood Thrush and Veery were most similar in their habitat requirements.

Noon (1981) found that the distribution of the Veery was very similar to that of the Wood Thrush on an elevational gradient, with both most abundant at low elevations and reaching their upper limit together at the lowest ecotone where sugar maple and beech disappeared and spruce and yellow birch increased. The Wood Thrush occupied the lowest gradient but the Veery did not appear until mid-elevation. The 2 species had almost exclusive ranges with only about 300 m overlapping. In New York, the Wood Thrush selected mature deciduous forests with high canopy height and cover dominated by a few large trees. The Veery occupied similar habitats but occurred in more open or disturbed areas where shrub coverage was significantly higher (Dilger 1956). In Tennessee and North Carolina, Wood Thrush habitat differed from that of the Veery in having a taller canopy and more tree species present. Most differences in their locations were due to spatial separation with the Veery occupying higher altitudes. The 1 factor that consistently separated the Wood Thrush and Veery was their differential response to shrub density, with the Wood Thrush selecting lower shrub density. When both species are present, the Wood Thrush may be competitively constrained by the Veery from using habitats with a particular structural configuration. It responded by expanding its habitat niche to include additional habitat types where the Veery was nesting at higher altitudes. The Wood Thrush had the lowest niche breadth of the thrushes studied, suggesting that it is a habitat specialist. In Maine, the Wood Thrush colonized an area inhabited by the Veery and Hermit Thrush. The Wood Thrush occupied both deciduous and coniferous areas that were moister than those used by the Hermit Thrush and drier than those used by the Veery. The Wood Thrush was not found in any habitats to the exclusion of the other 2 thrush species although it occupied young white pine–alder sites almost to the exclusion of the other species. In 2 cases, a Wood Thrush used essentially the same territory that had been occupied the previous year by a Veery or Hermit Thrush and therefore appeared to be socially dominant to both species. The Wood Thrush may be able to establish territories upon spring arrival even in areas that are already occupied by the Veery or Hermit Thrush (Morse 1971a). James et al. (1984) concluded that the Wood Thrush had similar habitat requirements to the Veery except that the Wood Thrush was more restricted to closed canopy forests. In Connecticut, the Wood Thrush preferred lower shrub density, less early- and late-successional habitat, less moisture, and less exposed soil than the Veery, but selected areas with taller canopy. Successional stage appeared to be the main difference between Wood Thrush and Veery territories, with the Veery appearing earlier in succession. Plants significantly more common in Wood Thrush territories than those of the Veery were typical of more mature forests and drier sites, and included American chestnut, flowering dogwood, large-toothed aspen, chestnut oak, red oak, black oak, and sassafras; plants in Veery territories were typical of early successional and wetter areas. The Wood Thrush was associated with flowering dogwood in mature forests compared with striped maple for Veery. Shrub coverage was the single-most important factor reflecting the absence of Wood Thrush in thickets and early successional areas. The Wood Thrush appeared to require 1 or more trees at least 12 m tall, possibly for song perches; the Veery usually sang at heights of 2-8 m (Bertin 1977). In West Virginia, the Wood Thrush and Veery nested at different heights (higher than 1.6 m for Wood Thrush and lower than 1.6 m for Veery). Some Veery nests had less than

2.5% woody debris on the ground; other Veery nests and Wood Thrushes had more than 2.5% woody debris. Some Veery nests had more than 222.5 saplings; Wood Thrush and some Veery nests had fewer than 222.5 saplings in the vicinity. Wood Thrush and Veery nests were separated by percent canopy cover, with more than 42.5% for Wood Thrush and less than 42.5% for Veery. There was more woody debris ground cover, fewer saplings, and more canopy cover at Wood Thrush than Veery nests. The Wood Thrush nested at the lowest altitude and the Veery at intermediate altitudes; the Wood Thrush was isolated in the lower portion of its range. Wood Thrush nests were usually higher and in a crotch; Veery nests were lower in epicormic branches. The Wood Thrush did not nest in raspberries, greenbriers, or roses, but the Veery did. In summary, the Wood Thrush and Veery have similar habitat preferences but the Wood Thrush prefers higher canopy, taller trees, drier areas, less dense shrub coverage, and more ground coverage by plants and woody debris than the Veery (Dellinger et al. 2007).

Both the Swainson's Thrush and Hermit Thrush are separated from the Wood Thrush through their preference for coniferous cover versus deciduous cover for the Wood Thrush. On elevational gradients, both the Swainson's Thrush and Hermit Thrush occur at higher altitudes than the Wood Thrush. There is typically no overlap in habitat used by the Swainson's and Wood thrushes, but the Wood Thrush and Hermit Thrush overlap in the upper portion of the Wood Thrush's range and the lower portion of the Hermit Thrush's range. The Wood Thrush nests in moister areas than the Hermit Thrush. Wood Thrush nests averaged more than 2.8 m from edge; Hermit Thrush nests were closer than 2.8 m to edge (Dellinger et al. 2007; Morse 1971a; Noon 1981).

The Wood Thrush and American Robin occasionally occur together in woodlands in agricultural or natural settings but co-occurrence is greatest in urban woodlots. The robin is most common in areas with intermediate canopy closure and limited understorey. The Wood Thrush prefers a more closed canopy and a well-developed shrub or sapling layer. The robin tends to nest closer to edge (less than 2.8 m) than the Wood Thrush (more than 2.8 m). The Wood Thrush is dominant to the robin and is usually successful in driving it out of its territory (Dellinger et al. 2007; James et al. 1984; F.G. Weaver 1939).

In Virginia, average nocturnal roost height of males was 6.8 m (range 2.0-26.5 m). The Wood Thrush usually used different roosts on different nights. Roosts were located twice 12 days apart; the mean distance between roosts was 158 m (range 2-607 m). This excluded an outlier of 1,301 m where a male relocated to a new territory. Only 8% of males roosted in the same location on both nights. Roosts were distributed throughout the daily home range and 31% were located outside it. The mean distance of external roosts to the edge of the daily home range was 91 m (range 9-322 m). Roosts within the daily home range were not in areas of high diurnal use. The mean distance of roost sites from peak diurnal use areas was 140.4 m for yearlings and 70.2 m for older males. Roosts were in areas with significantly higher vegetation density than random sites, approximately 7% denser at roosts than random sites. Females with active nests roosted exclusively in the nest; males roosted an average of 121.8 m away (range 72.6-204.2 m). Once nests failed or young fledged, the mean distance between roosts of the sexes was only 10.6 m (range 2.2-51.9 m). In most cases, members of the pair roosted side by side within the daily home range (Jirinec et al. 2016b).

All Ontario nests were above ground in living saplings (52.8% of nests), in trees (22.0%), in shrubs (22.8%), and on tops of dead stubs (2.4%). Deciduous trees and shrubs (83.5% of nests) of 17 species were used for nesting compared with 16.5% of nests in 6 species of conifers. Species selected most frequently for nesting were 54.2% maples, 18.3% beech, 12.2% hawthorns, 8.4% hemlock, and 6.9% white cedar. Nests were randomly situated from the lowest part of a tree or shrub to its top, and were on lateral branches (52.0% of nests) and in crotches or forks (48.0%). Nests were at or near the trunk (61.0% of nests) or distant from it. Distances from the trunk ranged from 0.3 to 4.5 m, but mostly 1.2-3 m. Nests were 0.3-9 m from the ground, with most 1.8-3 m up (Peck and James 1987, 1998a). Red elderberry is an important nesting shrub in early spring. This is one of the first woody species to leaf out and it provides good concealment for nests (Savignac 2012b). Friesen et al. (1999b) reported the average height of Wood Thrush nests in Waterloo Region to be 3.1 m (range 1.2-6.4 m). Reuse of nests has rarely been reported (Craves 1998). Two nests in Waterloo Region were reused during the same breeding season. Five of 61 nests (8%) survived the year intact and 2 were reused the following year. One nest was reused to fledge 2 broods within the same breeding season (Friesen et al. 1999c; Wyatt 1997).

Throughout its range, the Wood Thrush nests in shrubs, saplings, and deciduous trees and, to a lesser extent, coniferous species. Growth characteristics of the tree or shrub are probably more important than the species. It has nested in elms, tree-of-heaven, spicebush, witch-hazel, tartarian honeysuckle, black cherry, black gum, maple-leaved viburnum, sassafras, multiflora rose, white ash, white mulberry, southern arrowwood, flowering dogwood, oaks, blue spruce, snowball bush, privet, juneberry, basswood, locust, and grapevines. Spicebush was important for nesting in many areas. In North Carolina and Tennessee, 84% of nests were in hemlocks and 11.3% were in rhododendrons. Eighty-four percent of nests were in trees with a DBH less than 10 cm. There were significantly more shrubs at nest sites than non-nest sites. Hemlock comprised more than 51% of the shrubs or small trees at nest sites but only 33% at non-nest sites. It nested in hemlock more than its availability (Farnsworth and Simons 1999). Nests in Maryland were all on the lowest available branch, in forks in saplings, or saddled on a horizontal branch either near or distant from the trunk. Nests may be 0.3 m to more than 20 m above ground, but most are lower than 6 m, with about half 1.5-4 m up. There is 1 report of a nest on the ground. Individual birds do not favour any particular characteristics for nest-site placement. Subsequent nests may be placed very close to the previous one and the exact site of a previous nest may be selected. Subsequent nests of individuals may vary greatly in height, whether they are in a shrub or tree, whether they are in a fork or on a branch, and by species selected (Brackbill 1943, 1950a, 1958; M.L. Evans et al. 2020; Graber et al. 1971; Hoover and Brittingham 1998; Newell and Kostalos 2007; Nolan 1974; Stouffer and Best 1980; F.G. Weaver 1939; Weaver in Bent 1949). In Pennsylvania, mean nest concealment was 86% laterally and 82% from above and below, but there was a large range in values. Average nest site characteristics were: nest height, 2.2 m (range 1.0-6.5 m); 61.3 m to edge (range 1-300 m); supporting vegetation DBH 4.8 cm (range 0.8-55.9 cm); 7.6 cm from the nest to the main stem (range 0-182.9 cm); 13.8% horizontal exposure (range 0-65%); 17.5% vertical exposure (range 0-70%); and 15.0% total exposure (range 0-60%; Hoover and Brittingham 1998). Nests may be occur the interior of forests to the very edge, or in shrubby areas beyond the edge (Brackbill 1958; M.L. Evans et al. 2020; Hoover and Brittingham 1998; A.F. Riggs 1947; F.G. Weaver 1939).

The Wood Thrush is territorial but may trespass frequently in adjacent territories. In Algonquin Park, it occupied areas from the ground to a height of approximately 11.9 m, about 30 cm below the bottom of the canopy (Martin 1960). In Illinois, territories were 0.8-2.8 ha in 1 area; another study reported average size of territories as 1.2 ha (range 0.7-1.7 ha). In New York, territories ranged from 0.08 to 0.8 ha. In suburban Baltimore, territories were 0.8-1.1 ha. These territories included an entire city block, excluding areas where paved driveways and close spacing of buildings reduced the amount of lawns and shrubbery. In Kansas, 1 male sang over an area of 5.1 ha, but only small portions of this area were used. The territory consisted of 2 separate parcels that were several times longer than wide. The combined area was about 0.6 ha (0.4 and 0.14 ha), with both patches along woodland edge with an intervening 45-m wide field. In Pennsylvania, territories averaged 2.4 ha (range 1.5-4.0 ha). Mean nearest neighbour distance was 90 m with a range of 50-150 m (Brackbill 1943; Evans et al. 2008; Fitch 1958; Graber et al. 1971; F.G. Weaver 1939). In Virginia from May until late July, the median home range size of 37 males was 10.4 ha (Jirinec et al. 2016a).

The Wood Thrush may maintain the same territory for its second brood of the season, or move considerable distances. In Waterloo Region, all females stayed in the same woodlot to raise their second brood except one that moved across a highway to another woodlot. Distances between successive nests in a season averaged 72.6 m (range 0-400 m). Fifty-one percent of second nests were within 50 m of the first. In Delaware second nests averaged 35 m apart if the first nest was successful and 50 m if the first nest failed. In Virginia, the same numbers were 67 m for successful nests and 122 m for unsuccessful nests, excluding 2 long-distance movements of 1.5 and 4.3 km (Brackbill 1943; M.L. Evans et al. 2020; Friesen et al. 2000; Nolan 1974; Vega Rivera et al. 1998; Wyatt 1997). In Georgia, birds occasionally wandered long distances from the nest. Maximum recorded distance from the nest was 624 m for males and 539 m for females, but both sexes were found within 100 m of the nest on 50-60% of observations. The probability of a female staying the entire breeding season within a 400-ha area was less than 20%. Sixty-three instances of emigration of males and females from study areas were documented with the mean distance travelled between nests or after the end of the breeding season being 3,353 m. Thirty percent of adults moved less than 1 km and 20% moved 1-2 km. Some moved from a 14,000-ha contiguous forest to small, fragmented woodlots or residential areas. Within a breeding season, females moved 1-17,388 m (median 251 m) between nest sites; 80% travelled less than 1 km. Females renesting after successful nests did not move as far as those with previous failed nests (424 m compared with 1,130 m), but this difference was not significant (Lang et al. 2002). In Pennsylvania, 4 of 12 females (33.3%) with unsuccessful first nests moved a mean of 418 m (range 250-628 m) for their renesting attempt. Three of 11 females (27.3%) with successful first broods moved a mean of 381 m (range 250-558 m) for their second broods. There were more significant movements to nest sites with few large trees, short canopy height, high percent canopy cover, and high percent ground cover. This occurred for both birds that remained in territories and those that moved off territories. Dispersal was not influenced by female age, success of the first nest, or clutch size. Overall, 30% of females dispersed to different territories during the breeding season; this appeared to be solely to upgrade their habitat (Gow and Stutchbury 2013a).

In Pennsylvania, males, females, and pairs frequently made off-territory forays. Foray distances were more than 250 m for 17% of lone females, 17% of pairs, and 3% of lone males (range 300-2,200 m). All long-distance forays occurred after a recent nest failure. In 60% of cases, the foraying birds returned to breed in their original territory, but 2 females (40%) disappeared from the study area. Most forays during active nesting were shorter and to adjacent territories (Evans et al. 2008). In small woodlots in Delaware, more than half of pairs had only 1 nest and left the site after that attempt, which was typically a failure. New birds continued to arrive throughout the breeding season suggesting that they had attempted a previous nest in another location. Birds that emigrated from these woodlots did not appear in a 15-ha forest 1.6 km away, nor did emigrants from the larger forest appear in the smaller woodlots. This suggested that emigrants may move considerable distances. None of the birds that emigrated from any of the woodlots were found in other forests within 10 km. Two males that remained residents throughout the breeding season in the large forest were recovered 4 and 43 km away indicating that extensive movement may occur within the breeding season (Roth and Johnson 1993; Weinburg and Roth 1998). In Virginia, 56% of males relocated their home ranges during the breeding season at least once. Birds moved as far as 4.29 km from their original territory (Jirinec et al. 2016b). In Pennsylvania, Wood Thrushes nesting in woodlots smaller than 5 ha occasionally moved outside the territorial woodlot. Eighty-two percent of males and 33% of females made at least 1 foray outside their resident woodlot. In 2 cases, unmated males acquired a mate midway through the breeding season, but in different woodlots 50 and 700 m distant. Most forays by males were more than 150 m 1 way, with a maximum of 392 m. Males crossed open gaps as wide as 615 m, but most gaps were less than 100 m across. Most female forays were less than 150 m (range 40-1,400 m); they crossed gaps of 30-300 m. For females, the incidence of gap-crossing decreased significantly with gap width. Males in small woodlots spent more time off their territory (23.5%) than those in contiguous forest (4.8%) and travelled further (392 m compared with 9.9 m; MacIntosh et al. 2011).

The rate of natal philopatry may be 0% in some areas and fair high for a passerine species in other areas. Brackbill (1958) banded 26 nestlings in Maryland and 0 returned. In Delaware, 13 females and 21 males banded as young returned to breed, with an overall return rate of 5%. These included 4 females and 1 male that did not return until their second year after fledging. Over 8 years, 0 or 1 young returned in most years, with annual return rates varying from 0% to 12%. The maximum number returning in a year was 7, 4 of which hatched the previous year and 3 2 years previously. Yearlings and 2-year-olds were captured 1.3-4.2 km from the natal site, except for a female that was recovered 39 km away. Annual return rates of fledglings may vary and some may not return until 2 years after fledging (Roth and Johnson 1993). In New Jersey, 5 of 74 fledglings (6.8%) returned to breed the following year (Suthers 1988).

Adult site fidelity may vary geographically and annually at individual sites. Schlossberg (2009) estimated adult site fidelity at 41% based on 456 birds in 3 different studies. In Maryland, 4 of 10 (40%) males and 1 of 10 (10%) females returned (Brackbill 1943). In Delaware, mean return rates were 49% for females and 59% for males. Rates of return varied considerably year to year (Roth and Johnson 1993). At the same area, 64% of 39 females present for their third consecutive year returned the next year and 71% of 28 males that had been present for 4 years returned. For females, 64% of

4-year birds and 75% of 5-year birds returned. One female nested in the same 0.2 ha in 5 consecutive years with 1 male and then with another male in the same area for an additional 3 years. It was assumed that there was strong site fidelity and that return rates equalled survival rates (M.L. Evans et al. 2020). In New York, 1 male used the same territory in 3 successive years (F.G. Weaver 1939). In Illinois only 19.2% of 26 adults returned the following year even though 67-79% of all adults were captured in subsequent years. These data suggest a high turnover rate, but Robinson (1992) acknowledged that low return rates may have been due to net or territory shifts, or birds becoming net-shy.

Studies in the Ottawa area (Villard et al. 1992, 1995) provided insight into the variability of fidelity rates that have been reported. They studied the presence-absence of Wood Thrushes over 2 years in all woodlots in a 10 x 10 km square. Size of woodlots ranged from 3.0-129.8 ha (median 11.8 ha). There were local extinctions and recolonizations in 16-28% of the forest fragments. Extinctions and recolonizations even occurred in fairly large woodlots (25.3-53.3 ha). Although the woodlots that supported Wood Thrushes changed each year, the number of woodlots occupied within the larger study area remained constant. This has important implications because a single-year survey may conclude that a given woodlot does not support the Wood Thrush and is therefore unimportant to it. The same woodlot may have the potential to become recolonized and contribute to the metapopulation.

Limiting Factors

Eggs have been found in Ontario nests from the beginning of May until early August, with most present in the first 3 weeks of June (Peck and James 1987, 1998a). In Waterloo Region, 44% of nests had egg dates in July and early August. The average first egg date for double-brooded birds was 24 May (range 13 May to 7 June) for first nests and 1 July (13 June to 16 July) for second nests. First broods in Ontario fledge around 20 June. The first egg of second broods was laid an average of 13.4 days after young had fledged from the first nest (range 7-31 days; Friesen et al. 1999a, 1999c, 2000).

Nest construction takes 3-8 days but mostly 5 days or less. Three or 4 days may elapse between nest completion and initiation of egg laying. Eggs are laid at 1-day intervals. Incubation begins consistently with laying of the penultimate egg, although short periods of incubating may occur as soon as the first egg is laid. The incubation period at 8 Ontario nests was 10-12 days. Elsewhere, incubation periods of 11-14 days have been reported; average incubation periods at 3 different study areas were 12.7-12.75 days. Young leave the nest when they are 12-15 days old. It takes approximately 51 days from nest building to fledgling independence (Anders et al. 1997; Brackbill 1943, 1958; M.L. Evans et al. 2020; Longcore and Jones 1969; Nolan 1974; Peck and James 1987, 1998a; Vega Rivera et al. 1998, 2000: F.G. Weaver 1939; Weaver in Bent 1949).

The Wood Thrush typically attempts to raise 2 broods per season and very rarely 3. Double broods were suspected in Ontario based upon egg dates (Friesen et al. 1999a; Peck and James 1987, 1998a) and were confirmed by Wyatt (1997) and Friesen et al. (2000). Over 2 years, 74% of females in a Waterloo study area initiated a second clutch after successfully raising a first brood: 64% in the first year and 86% the following year. It was likely that some nests were missed, so the incidence of double brooding may have been close to 100% (Friesen et al. 2000). A similar rate of double brooding was reported in Pennsylvania, with 74% of birds that successfully raised a first brood

attempting a second (Gow and Stutchbury 2013b). Friesen et al. (2001) confirmed triple brooding in Waterloo Region and all 3 nests successfully produced young. The triple-brooded pair did not initiate nesting earlier than other birds (15 May) and the fledging date of their last brood (19 August) was only 2 days later than for several other pairs. Over 3 years, only 1 of 73 females (1.3%) was triple brooded. In Pennsylvania, 1 female successfully raised 3 broods (Gow and Stutchbury 2013b). Throughout the Wood Thrush's range, 2 broods are typically raised, but occasionally only 1 and rarely 3. About half of females are successful in raising a second brood. It is a persistent renester and may make several nesting attempts. In Waterloo, 2 females fledged a first brood and made unsuccessful attempts to raise a second; 13% of females did not attempt a second brood. Of females that were unsuccessful in raising the first brood, 35% renested in the study area and 65% were not encountered again (Brackbill 1958; M.L. Evans et al. 2020; Friesen et al. 2000; Longcore and Jones 1969; Powell and Knutson 2006; Powell et al. 1999; F.G. Weaver 1939). Clutches of 2-5 eggs have been reported in Ontario with most containing 4 eggs (Peck and James 1987). Clutches of 1-5 eggs have been documented throughout its range with 3 or 4 eggs typical. Single-egg clutches are usually in late nests or nests that have been parasitized by the Brown-headed Cowbird. In Delaware, mean clutch size for first nests was 3.7 eggs (range 1-5), 3.0 for second clutches (range 1-4), 2.8 for third nests (range 2-3), and 2.6 for fourth nests (range 2-3). Modes for successive nests were 4 eggs (72% of clutches) for second clutches, 3 eggs (83%) for third clutches, and 3 eggs (60%) for fourth clutches. In another Delaware study, mean clutch size was 3.7 eggs in May, 2.8 in June, and 2.8 in July with an overall mean of 3.3 eggs. In Maryland, all clutches smaller than 3 eggs followed a disturbance such as nest loss or parasitism (Brackbill 1958; M.L. Evans et al. 2020; Graber et al. 1971; Longcore and Jones 1969; F.G. Weaver 1939; Weaver in Bent 1949). The number of young fledged in a season is strongly related to when the moult is initiated. The most productive individuals moulted about 3 weeks later than average (Gow and Stutchbury 2013b).

The age at first breeding is 1 year, and the Wood Thrush nests annually thereafter. The mating system is monogamous, although polgyny rarely occurs. One male in Delaware had nests 50 m apart with 2 different females. The first female successfully raised 2 broods; the second female raised 1 fledgling in the first brood but her second nest failed. The low productivity of the second female may have been because the male seldom fed her young. In Delaware, polygynous males were detected 6 times in 945 nestings (0.6%). One male was a bigamist in 2 non-consecutive years. Two other males were bigamists for 2 nesting periods within a single season. The pair bond is typically maintained throughout a breeding season regardless of the number of nesting attempts or if the pair moves between successive nests. Divorce does occur; 13 of 417 females (3.1%) and 17 of 416 males (4.1%) renesting the same year did so with another mate. Most returning birds have a new mate annually, but 3-8% of pairs may be of birds that were mated the previous year. One pair is known to have stayed together for 5 breeding seasons (Brackbill 1943, 1958; M.L. Evans et al. 2020; R.K. Johnson et al. 1991; Lang et al. 2002). In Pennsylvania, 9 of 151 young (6%) were extra-pair; 7 of 51 nests (14%) contained extra-pair young. All 151 nestlings were related to their mother suggesting that intraspecific parasitism does not occur or is rare. Two extra-pair fathers occupied an adjacent territory 200-250 m away; another's territory was 650 m away. In Ontario, the rate of extra-pair paternity was 40% (45 of 112 nestlings). Twenty-four of 36 pairs (67%) had extra-pair young. The 2 extra-pair males that were identified each held territories adjacent to those containing nests with

their extra-pair young. Densities of Wood Thrushes were similar in Pennsylvania and Ontario, but the rate of extra-pair young in Ontario was 6.7 times that in Pennsylvania (Evans et al. 2008, 2009).

Young from early nests typically forage on the ground, often along logs. Later-fledging birds depend heavily on fruit for food and spend most of their time foraging 5-10 m high in trees. Upon first arrival at the breeding grounds, adults may feed from the foliage of newly leaved trees but later forage mostly on the ground. The Wood Thrush mostly probes and gleans and occasionally hovers or hawks insects and fruit that cannot be reached from the ground. It may also use bill swipes or pick up leaves to expose prey. In urban areas, it may forage on lawns in a manner similar to that of the American Robin (M.L. Evans et al. 2020; Vega Rivera et al. 2000; Weaver in Bent 1949). Dilger (1956) studied the foraging tactics of closely related thrushes in New York. The Wood Thrush and Hermit Thrush were primarily ground foragers in edge habitat. The Veery and Swainson's Thrush were predominantly arboreal foragers, occasionally flycatching, and occurred in forest interior.

The mean length of food given to young increases gradually with age: 9.8 mm in days 3 and 4 and 12.3 mm in days 8 and 9. Nestlings are fed caterpillars, earthworms, ants, spiders, soldier beetles, millipedes, cankerworms, and moths. Fruit provided to young includes red and white mulberries, honeysuckle berries, and black cherries. By days 7-9, young are fed more ants, spiders, soldier bugs, earthworms, and millipedes than at days 3-6, probably reflecting either selectivity by adults or different prey availability. In addition to these foods, fledglings may be fed Japanese beetles and June beetle larvae (Brackbill 1943; M.L. Evans et al. 2020; Lagassé and Ryder 2016; Powell et al. 1996; Vega Rivera et al. 2000; Weaver in Bent 1949).

Adult Wood Thrushes feed mostly on soil invertebrates with greater use of fruits in late summer and autumn (M.L. Evans et al. 2020). They also eat small salamanders, snails, and some arboreal insects. The diet of 22 birds in Illinois consisted of 71% insects and 19-21% fruit. It was exceptional among the thrushes in the number of millipedes it consumed (13% of the diet) and it also fed heavily on ants (15%) compared with other thrush species. Beetles were important, comprising 18% of the diet, mostly ground and scarab beetles, click beetle larvae and adults, and weevils. Other food items included 12% crane and march fly larvae, 1% spiders and harvestmen, 1% molluscs, and 1% bugs. Another study in Illinois found that bugs were more important, comprising 10-20% of the diet. In autumn, it has fed on fruits of spicebush and pokeweed (Graber et al. 1971). Beal (1915b) examined 171 stomachs taken throughout its breeding range. The diet consisted of 59.6% animal matter and 40.4% vegetable matter. The greatest amount of animal food was eaten during the month after arrival in spring and the least in October during autumn migration. Beetles were the most prevalent animal food at 20.4%, including scarab beetles (10.2%), ground beetles (2.2%), weevils (2.2%), click beetles (2.1%) and occasionally Colorado potato beetles. Caterpillars comprised 9.4% of the diet, with most taken in July (16.3% of that month's food items). Ants averaged 8.9% for the season, beginning with 18.1% in April, gradually declining through the summer and disappearing from the diet in October. Other hymenopterans were eaten regularly but in small quantities (3.9%). Other animal prey included 2.7% flies (mostly crane flies), 1.3% bugs, 2.3% grasshoppers, less than 1% other insects, 8.5% spiders and millipedes (which comprised 20-94% of April food, but gradually decreased in importance through September), and 1.8% isopods, snails, and earthworms. More than 90% of the vegetable matter eaten was fruit, predominantly wild fruit (33.5%), but some domestic fruit was

consumed (3.7%). Fruit comprised only 1.2% of the diet in April and gradually increased to 87.2% in October. Dominant fruits in the diet included blackberries and raspberries, mulberries, chokecherries, blueberries, spicebush, frost grapes, and dogwoods. In addition to fruit, it ate a few seeds and rose haws. In Illinois over 3 years, frugivory comprised 71-83% of foraging attempts; 74% of fruit foraging was in forest gaps created by treefalls and other disturbances. The percentage of fruit consumed was 3% elderberries, 58% Virginia creeper, and 39% spicebush in year 1; 20% grapes and 80% spicebush in year 2; and 8% grapes, 9% Virginia creeper, and 83% spicebush in year 3. Malmborg and Willson (1988) considered it an understorey-foraging species that foraged significantly more for fruits in gaps and for insects in forest interior. It favoured clumped areas of fruit when feeding in gaps rather than single stems. In Pennsylvania, it was rarely seen on red elderberry bushes despite being detected at 80% of elderberry sites during surveys. It was detected foraging at 5.9% of elderberry sites on only 0.9% of visits (Stutchbury et al. 2005a). Other fruits it eats include holly, jack-in-the-pulpit, and black gum (M.L. Evans et al. 2020). In Delaware, Ladin et al. (2015) used stable isotopes to determine the diet of adult and nestling Wood Thrushes. They compared diets of nestlings in nests with and without a Brown-headed Cowbird nestling. The diet of adults was composed largely of protein-rich and calcium-rich foods (51-62%), including snails, isopods, and myriapods, as well as spiders (23-33%). They ate 7 times the snails, 4 times the spiders, and 17 times the isopods than expected by availability, and 7.1% of the available insects and 5.9% of the available caterpillars. Earthworms and myriapods were consumed at expected frequencies. Nestlings without cowbirds in the nest ate snails, spiders, and myriapods at expected frequencies but only 20% of available insects and 12.5% of available caterpillars. Nestlings with cowbirds ate snails, spiders, isopods, and caterpillars at expected frequencies and 33% of available insects. Nestling diets where cowbirds were absent contained a greater proportion of calcium-rich foods and spiders compared with those accompanied by cowbird nestlings. Brood parasitism affects nestling diet and may have negative effects on development through nutritional stress that may subsequently affect survival and fecundity.

The Wood Thrush is commonly parasitized by the Brown-headed Cowbird. Parasitism rates generally decline with distance from the cowbird's historic range west of the Mississippi River. Hoover and Brittingham (1993) defined 3 general regions: the Midwest region, which in Ontario is approximately the area west of Rossport; the mid-Atlantic region, which extends from Rossport to the Toronto area; and the northeast region, which is east of Toronto in Ontario. Parasitism rates were 42.1% in the Midwest, 26.5% in the mid-Atlantic, and 14.7% in the northeast. The Ontario range of the Wood Thrush does not extend to the Midwest region. The percentage of parasitized nests was positively correlated with the number of cowbirds detected on Breeding Bird Survey (BBS) routes and negatively correlated with the number of Wood Thrushes detected. In Delaware, parasitism rates were 60% or more 1985-87 but 0% 1989-91 with no apparent reason for the change (M.L. Evans et al. 2020). Parasitism rates in a large Pennsylvania forest varied significantly annually with values of 0-23% (Hoover et al. 1995). In Ontario, 110 of 384 nests (28.6%) were parasitized (Peck and James 1998a). Parasitism rates vary geographically across the province and with woodland size. On the Niagara Escarpment, 41% of nests were parasitized, with no significant difference in parasitism rates by year. There was a significant difference in parasitism rates in large (8%) and small (57%) woodlots (Friesen and Campbell 2002). In Waterloo Region, Friesen et al. (1999a) reported an overall parasitism

rate of 47% and no significant difference in rates between large and small woodlands. Phillips et al. (2005) reported parasitism rates of 26-46% at Peterborough over 4 years and 20-39% at Ottawa over 3 years. Woodlands with houses in them had significantly higher parasitism rates than those with no nearby development or those with adjacent houses. In south-central Ontario, Burke and Nol (2000) reported parasitism rates of 4.4% in small woodlands and 2.8% in large woodlands. Wyatt (1998) reported on the outcome of 338 nests in Waterloo Region, Port Severn, and the Halton Region portion of the Niagara Escarpment, each with different amounts of forest cover (14%, 29%, and 48%, respectively). Parasitism rates were 14% in Waterloo, 12% in Severn Sound, and 28% on the Niagara Escarpment. Parasitism was most severe in woodlands smaller than 50 ha: 39% in 4-14-ha woodlots; 61% in 20-50 ha; 23% in 140-440 ha, and 0% in woodlands larger than 1,300 ha. In Norfolk County, 47 of 186 nests (25.3%) were parasitized. Nest concealment was not correlated with parasitism rates. Nests in 11-69-ha forests were parasitized at a significantly higher rate than those in 162-500-ha forests (Israel et al. 2023). Increased parasitism rates in smaller woodlots have been documented in Delaware (Weinberg and Roth 1998), Pennsylvania (Hoover et al. 1995), Missouri, Minnesota, and Wisconsin (Donovan et al. 1995). There was no relationship between forest area and parasitism rates in Indiana, with rates ranging from 58% to 100%. This may have been because the area is saturated with cowbirds (Fauth 2000). In Illinois woodlots, all nests were parasitized and nests contained 4 times as many cowbird as thrush eggs (Robinson 1992). Where the cowbird is very abundant, amount of forest cover and forest size are not significant due to the overall high rate of parasitism. Most studies found no relationships between parasitism rates and distance from forest edge. In Michigan, parasitism rates were higher along abrupt edges such as roads than along gradual edges such as wetlands and utility rights-of-way. In Virginia, where parasitism rates were 29%, parasitism increased with the percent of agricultural land and road density within 500 m (Etterson et al 2014; Kaiser and Lindell 2007; Simons et al. 2000). Occasionally parasitism rates may be inexplicably low, even when cowbirds are present and parasitism rates are high in the general region. In 1 Delaware woodlot, there was no parasitism of Wood Thrush nests, but nests of Red-eyed Vireos, Eastern Towhees, Common Yellowthroat, and Kentucky Warbler were parasitized (Artman and Downhower 2003; Hahn and Hatfield 1995; Longcore and Jones 1969). The Wood Thrush generally accepts cowbird eggs, although nests may occasionally be abandoned and there are accounts of it ejecting eggs or imbedding them in the nest (Brackbill 1958; M.L. Evans et al. 2020; Weaver in Bent 1949). It is a larger host and can raise its own young in parasitized nests. The incubation period of the 2 species is similar so that the cowbird does not have a competitive edge by hatching sooner, and the Wood Thrush can renest and increase its chance of successful reproduction. Parasitism has no effect on Wood Thrush nestling growth. Numerous studies demonstrated that the percentage of nests successfully fledging a Wood Thrush is not significantly affected by parasitism (Burke and Nol 2000; M.L. Evans et al. 2020; Farnsworth and Simons 1999; Fauth 2000; Friesen and Campbell 2002; Hoover and Brittingham 1993; Hoover et al. 1995; Kaiser and Lindell 2007; Lowther 1997; Phillips et al. 2005; Roth and Johnson 1993; Simons et al. 2000; Weinberg and Roth 1998). Although parasitism may not greatly affect nest success, the number of thrushes produced per nest declines as a result of parasitism. The cowbird frequently removes thrush eggs and these are not replaced, resulting in smaller clutch sizes. Presence of a cowbird egg may also inhibit the Wood Thrush from laying a full clutch. In Waterloo Region, parasitized nests produced significantly fewer thrushes than

unparasitized nests, and this relationship was also observed on the Niagara Escarpment. In the Peterborough area, parasitized nests produced almost 17% fewer thrush fledglings per nest (2.3) than unparasitized nests. In Missouri, Wisconsin, and Minnesota, parasitized nests fledged significantly fewer Wood Thrushes than unparasitized nests (Brackbill 1958; Donovan et al. 1995; M.L. Evans et al. 2020; Friesen and Campbell 2002; Friesen et al. 1999a; Phillips et al. 2005; Wyatt 1998).

Predation appears to be the greatest limiting factor to the Wood Thrush. In most areas, about half of nests fail and produce no young. Predation is the main cause of nest failure and accounts for 66-100% of losses in different study areas. Ontario studies reported nest success rates (fledging of at least 1 young) of 47-51%, with 74-85% of losses due to predation. These rates appear to be fairly typical for North America, but success rates as low as 37.6% and as high as 60.3% have been reported. The high rate of predation may be sufficient to result in a woodland being a sink area rather than a source in many cases. On the Halton section of the Niagara Escarpment, there was no difference in predation rates between small (20 ha) and large (1,300 ha) woodlands but the predation rate was 58.3% in small central Ontario woodlots compared with 27.8% in large woodlots. In woodlots in Waterloo Region, predation risk decreased with increased urbanization. The abundance of alternative food sources associated with humans may divert the attention of predators from bird nests. In Tennessee and North Carolina, high rates of predation were associated with areas with only 20% forest cover; predation rates were lower in contiguous forest. The lack of difference in predation rates between nests in large and small forests in some areas may be because large contiguous forests may support a more diverse and abundant predator community. In West Virginia, the southern flying squirrel was the most common predator. This species is restricted to large forest patches, particularly those with abundant mast, and may potentially be a greater predator than raccoons and cowbirds in large, contiguous forests. In Delaware, predation rates in small forest fragments were 1.88-2.28 times those in larger forests. Most studies found that predation rates are not affected by edge, with nests in forest interior having similar predation rates as those on edges, but in Pennsylvania, predation rates decreased significantly with distance from edge. Results of this study may have been somewhat confounded by the fact that thrushes nesting in forest interior nested an average of 2 m higher than those on edges, and higher nests were more successful than lower ones. In Virginia, elevated predation rates occurred within 50 m of agricultural edges; nest predation rates increased with increasing nest height. There may often be no difference in predation rates in relation to edge but the type of edge may influence predation. In Michigan, nests near abrupt edges such as roads and marshes were more likely to be depredated than those near gradual edges such as clear-cuts and hydro rights-of-way. The species of predators present may also influence predation rates at different distances from edge and at different nest heights (Artman and Downhower 2003; Burke and Nol 2000; Etterson et al. 2014; M.L. Evans et al. 2020; Farnsworth and Simons 1999; Fauth 2000; Friesen and Campbell 2002; Friesen et al. 1999a, 2013; Hoover and Brittingham 1998; Kaiser and Lindell 2007; Longcore and Jones 1969; Newell and Kostalos 2007; Phillips et al. 2005; Richmond et al. 2011; Simons et al. 2000; Weinberg and Roth 1998; Williams and Wood 2002).

Forest fragmentation has been considered to be highly detrimental to the Wood Thrush, but results may vary significantly geographically. The general pattern is less reproductive success in

small forests, in less forested landscapes, and in the Midwest than the east, but there are many exceptions to this (M.L. Evans et al. 2020). In the eastern United States, almost 35% of Wood Thrushes detected on BBS routes were in fragmented habitats (Donovan and Flather 2002). Studies undertaken in Ontario demonstrated that there are geographic differences within the province and much smaller woodlands than generally reported support viable populations. In Waterloo Region, which has approximately 14% forest cover, pairing success was essentially 100% in woodlots ranging in size from 3 to 12 ha. Nesting success was sufficient in these small patches that they acted as sources. A pair successfully reared 3 broods in a year in a 1.8-ha woodlot. Nest success and productivity were not affected by forest size or nest location relative to edge. Even in the smallest woodlands in an agricultural matrix, Wood Thrushes nested successfully. It was concluded that severe reproduction impairment is not a general phenomenon of all settled landscapes (Friesen and Campbell 2002; Friesen et al. 1997, 1999a, 1999b, 2001; Wyatt 1998). In Norfolk County, Wood Thrushes nesting in small fragments were not subject to strong negative effects on body condition, reproductive success, or timing of the last nest of the season. Annual survival was not linked to breeding fragment size and autumn migration was not delayed for birds nesting in small fragments (Boyd et al. 2023; Hayes et al. 2023). In central Ontario, woodland size was the most important factor affecting reproductive success. The amount of forest cover in the local landscape had no significant effect. Small forests were sinks and large ones were sources. Only 1% of the locally available forest fragments were sources (larger than 200 ha). The source areas occupied less than 30% of the total forest cover (Burke and Nol 2000). Nesting success rates from elsewhere are less than 18% in Illinois in 14-65-ha woodlands, about 25% in Missouri in 181-1,872-ha woodlands, 28% in Pennsylvania in 10-30-ha woodlands, 30% in Wisconsin in 181-1,872-ha woodlands, 41% in Missouri in 26,000-ha woodlands, about 60% in Wisconsin in 29,000-ha woodlands, and about 85% in Pennsylvania in a woodland larger than 10,000 ha. In rural Pennsylvania, nesting success in forests smaller than 80 ha was usually below the sustainable level. In central Illinois with 10% regional cover and Missouri with 31% forest cover, forest fragments 25-1,600 ha were population sinks. A 15-ha urban woodlot in Delaware was a source and nesting success there was equal to or greater than in the Smoky Mountains, the largest contiguous forest in the eastern United States. In Missouri, Wisconsin, and Minnesota, forest fragments had higher daily nest mortality due to predation and parasitism than contiguous forest. The primary reasons for decreased productivity in some forest patches are increased parasitism and predation. Predation and parasitism rates may vary annually, such that some woodlots are sinks some years and sources in others. Another factor that may affect reproductive success in small woodlots is that the return rate of experienced birds may be much lower than in large woodlands. Small woodlands may be regarded as inferior habitat and be populated by less experienced breeders (Anders et al. 1997; Donovan et al. 1995; M.L. Evans et al. 2020; Fauth 2000; Friesen et al. 1999a; Hoover et al. 1995; Roth and Johnson 1993; Weinberg and Roth 1998).

Forest fragmentation creates edge. The effects of edges on the Wood Thrush are variable. In Waterloo Region, Friesen et al. (1999b) found no edge effects, with nests on edges as successful as those in forest interior. In Michigan, nestlings in nests near gradual edges grew faster than those at abrupt edges and in forest interior. There was no difference in survival rates between nests in the interior and on edges (Kaiser and Lindell 2007). Nest success increased significantly with distance

from edge in Pennsylvania. Nesting success was 46% within 50 m of edge, 67% 50-100 m from edge, and 79% more than 100 m from edge (Hoover et al. 1995). In Illinois, reproductive success of Wood Thrushes nesting near an agricultural corridor was less than in contiguous forest (Ford et al. 2001). In an extensive forest in Pennsylvania, Wood Thrushes nesting near agricultural disturbances had lower success rates than those nesting near disturbances caused by forestry practices. The difference may have been related to greater abundance of predators within the agricultural land (Rodewald and Yahner 2001). In New Jersey, it was significantly more abundant near unpaved roads than paved roads or power lines. The widths of these corridors were 8, 16, and 23 m, respectively. Its abundance was significantly reduced along edge corridors 16-23 m wide, but not along 8-m wide corridors (Rich et al. 1994). In contiguous forest in West Virginia, the Wood Thrush avoided roads and pipelines and was significantly more abundant distant from them (Farwell et al. 2019).

In the Missouri Ozarks, the Wood Thrush shifted its breeding territories so they were closer to large openings such as clear-cuts. This resulted in high breeding densities around clear-cuts and low densities distant from clear-cuts. In large forests, there was an increase in mortality as juveniles became independent and wandered through the forest looking for suitable postfledging habitat. Wood Thrushes inhabiting forest fragments in Missouri did not have to wander far to find shrubby habitat and did not experience a similar increase in mortality. It may have lower annual reproductive success when it nests far from thickets and other habitats required by the young after independence. The growing maturation and homogeneity of deciduous forests in the east, where mature forests next to clearings have become increasingly rare, is leading to a decline in the Wood Thrush. In New Hampshire, it has disappeared from mature forests but is still present in forests near second growth or clearings (Ahlering and Faaborg 2006). Near Ottawa, its density declined with increasing forest size, supporting the theory that nesting density is greater at forest edges (Lee et al. 2002).

Hames et al. (2002) demonstrated that acid rain plays an important role in declines of birds, particularly in areas with low pH soils. Decreases of calcium in the soil may alter the quantity and quality of available prey, lead to toxicity due to release of heavy metals, and substantially decrease the biomass of prey in the litter (especially snails and slugs). Acid precipitation may be a limiting factor to the Wood Thrush in the Canadian Shield area of Ontario where soil pH is naturally low.

Nest success may vary depending upon vegetative characteristics around the nest, nest height, and how well the nest is concealed. In Delaware, nests initiated later in the breeding season were more likely to be successful than early nests. Spicebush and black gum were most often associated with successful nesting. Red maple and spicebush were used for nesting mostly early in the season, black gum was used most in mid-season, and arrowwood in July. Success was lowest in red maple, possibly due to the high average height of nests in this species, the early use of this species, and that these nests were highly conspicuous until foliage developed. Success was inversely proportional to nest height. Greatest nest success (53%) occurred below 1.6 m and was least (15%) at 5.0-7.6 m (Longcore and Jones 1969). In Pennsylvania, nesting success was highest where shrub density was lowest. The only factor affecting nest success was visibility of the nest from above and below, with better concealed nests having lower predation rates (Hoover and Brittingham 1998). In another Pennsylvania area, successful nests averaged more than 1 m higher and had approximately

a third fewer small stems surrounding the nest than unsuccessful nests. Success was 20% higher for nests placed above the median nest height of 3 m. High shrub density around nests was associated with high rates of predation. Nest concealment, forest canopy trees, or percent urban land use in the surrounding landscape did not affect nest success. Predators in this area were predominantly ground-foraging mammals and snakes, which probably explains why higher nests were more successful. Lower nests may be more successful in areas where avian predators are prevalent (Newell and Kostalos 2007). In Delaware, better nest concealment reduced predation. The plant used most frequently for nesting was southern arrowwood which could not support the weight of most mammalian predators (Johnson 1977).

In the Kawartha Lakes area, Wood Thrush nest success was positively correlated with invertebrate biomass. Nests in sites with higher prey biomass were more likely to succeed, but only in areas with low squirrel abundance. Squirrel density was positively associated with housing density within 100 m of the site perimeter; raccoon density increased with housing density within 2 km. Forests with greater amounts of less intensive agriculture (hay, old field, and pasture) nearby supported a higher biomass of invertebrate prey (Richmond et al. 2011).

In southeastern Ontario, density and productivity of the Wood Thrush was negatively correlated with housing density (Richmond et al. 2012). At Peterborough, the number of fledglings produced 1 year was significantly higher in undeveloped woodlots (2.7) than those with embedded (1.8) or adjacent (1.7) houses, but differences were not significant in other years or overall. When results for woodlots with embedded and adjacent (within 100 m) houses were combined, they had significantly lower productivity (2.6 fledglings per female) than undeveloped sites (4.0 fledglings per female). Decreased productivity was due to an increase in brood parasitism and nest predation in woodlands affected by development. Near Ottawa, Wood Thrushes in developed woodlands produced fewer fledglings than those nesting in undeveloped woodlots. Parasitism rates increased with development but there were no significant differences in predation rates. Phillips et al. (2005) concluded that the effects of housing developments appear to be region-specific and may depend on other factors influencing the overall abundance of cowbirds and rates of parasitism. Impacts of residential development appeared to be more significant in Waterloo Region, which has less forest cover than the Peterborough and Ottawa areas. Presence or absence of the Wood Thrush in Waterloo Region was estimated in 3 development classes (1-3 houses, 8-15 houses, and more than 25 houses) and 3 forest-size classes (3-4 ha, 8-15 ha, and 20-50 ha). It exhibited the most dramatic response of all species. Over 2 years, it was found in 43-67% of small woodlots with no development, 0-33% of small woodlots with 1-3 houses, 33% of small woodlots with 8-15 houses, and 0% of small woodlots with more than 25 houses. In medium-sized woodlots, it was present in 37-100% of woodlots with no development, 57-83% with 1-3 houses, 33-50% with 8-15 houses, and 0% with more than 25 houses. The same numbers for large forests were 83% with no development, 100% with 1-3 houses, 17-67% with 8-15 houses, and 0-40% with more than 25 houses. Friesen et al. (1995) considered it virtually absent in urban forests in Waterloo Region and concluded that cats and gray squirrels may have been factors. A more recent study in Waterloo Region found that the degree of predation did not differ in urban and rural areas. The probability of predation was unaffected by forest size or percent forest cover, but this may have been because all study woodlots were fairly

small and the regional forest cover was low. Nests in woodlots within areas of higher urban pressure were less likely to be depredated than those in rural areas, possibly because of abundant alternate food sources for predators (Friesen et al. 2013). In Waterloo Region, its historical abundance was almost 3 times greater than 20 years later. The decline was steepest (79%) in woodlots that had experienced housing development within 1 km since the first survey. The decline in woodlots without recent nearby development was 57%. There was no decline in daily nest survival over time with or without development. Urbanization near breeding habitat contributed to a decline in the Wood Thrush (Heidi et al. 2023). In Pennsylvania, there was no difference in nest success rates along an urban to forested gradient. The amount of urban area within the surrounding landscape was not a factor. Highest success rates occurred at suburban sites. At 1 contiguous forest, success was 2 times as high for interior nests than for those along an edge adjacent to a small housing development. This may have been due to increased predation by raccoons along suburban forest edges (Newell and Kostalos 2007). In North Carolina, it declined with density of buildings within 200 m (Lumpkin and Pearson 2013). In a residential area in Delaware, variables that were significant in predicting presence of the Wood Thrush were dense tree canopy, a shrubby understorey, wet soil, and amount of leaf litter. Parameters for having more than 50% chance of providing nesting habitat for it in residential areas included a minimum of 0.08 ha of tree cover, preferably contiguous and with at least 70% canopy closure, under which the natural leaf litter, native shrubs, and moist soil were maintained (Roth 1987).

Activities that remove overhead canopy or result in thinning of shrubs or saplings could be detrimental to the Wood Thrush. Removal of understorey growth is a common practice on cottage lots and this may affect habitat suitability (Stauffer and Best 1980). One factor that may affect the suitability of suburban and urban woodlots is the lack of management. Once development occurs, they are usually preserved with no harvesting of timber or firewood cutting. Over time, these woodlots become more park-like with very limited understorey, thereby making them unsuitable for the Wood Thrush.

The effects of forest management on the Wood Thrush vary considerably, with impacts on shrub density being most important. There appears to be a fine line between having an adequate number of shrubs and too high a density of shrubs. Selective thinning or fuelwood cuts that create small openings in forests are beneficial. More intensive management (diameter cuts, removal of a percentage of merchantable timber, and clear-cuts) may be deleterious. Forests that are retained with no management tend to become very close-canopied with minimal shrubs and become unsuitable. In Waterloo Region, the small woodlots studied by Friesen et al. (1999b) were lightly logged and managed for firewood and maple sugar production. These provided ideal habitat. In the Boreal Forest Region of Ontario, there was no effect on the Wood Thrush when 30% of trees were removed, but it declined when 50% or 70% of trees were removed (Vanderwel et al. 2009). In the Carolinian Forest Region in Ontario, it greatly preferred woodlots that had been thinned to those that were uncut. Heavy treatments, such as diameter-limit cuts, were preferred to woodlots that were thinned using standard techniques (Holmes et al. 2004). In Illinois, Robinson and Robinson (1999) created 0.02-0.04-ha openings within a 2,000-ha forest. This had no effect on the Wood Thrush; it was equally abundant in recently cut areas (1-5 years), older cuts (10-15 years), and in uncut

forest. In Pennsylvania where snags were retained in thinned forests, Wood Thrushes were present; none were recorded where snags were not retained. Woodlands where snags were retained had a more patchy and open canopy and significantly more woody vegetation 0-1.5 m from the ground (Stribling et al. 1990). In New York, Webb et al. (1977) examined the effects of removing 25%, 50%, 75%, and 100% of merchantable timber from woodlands. Populations of Wood Thrushes were significantly lower in the 25%, 75%, and 100% treatments than in uncut areas, but there was no significant difference in abundance in the uncut areas and the 50% cut. Presence of the Wood Thrush was an indicator of undisturbed forest conditions. It was negatively and equally affected by all levels of this type of logging. In Quebec, 10% fewer Wood Thrushes occurred in sugar maple forests affected by dieback than in healthy forests. In the affected woodlots, 78% of trees were affected favouring the development of more abundant regeneration (DesGranges et al. 1987). In Minnesota, it declined in riparian areas when adjacent upland forests were clear-cut, and it also declined when riparian areas were thinned (Hanowski et al. 2005).

Georgia forests that were thinned and burned resulted in adults using managed areas less than those that remained unmanaged (Lang et al. 2002). In Ohio, Artman and Downhower (2003) studied the effects on the Wood Thrush of prescribed burning in mixed oak forests. In unburned areas, there were few differences in vegetation parameters at nest sites compared with random sites. In burned areas, it selected sites with higher leaf litter, lower coverage by bare ground and grasses, higher densities of large shrubs and saplings, and lower density of snags than available at random sites. Nests were higher from the ground and in taller and larger diameter trees and shrubs in burned than unburned areas. In unburned areas, nests were more frequent in intermediate and mesic areas and less frequent in xeric areas than expected. In burned areas, nests were more frequent in mesic areas and where burn intensity was low or moderate. Nest success rates were similar in burned and unburned areas. In both unburned and burned forests, successful nests were higher and in lower density of shrubs and seedlings than failed nests. Successful nests in unburned areas had high coverage by ferns; the opposite was true in burned areas. Successful nests in unburned areas had lower tree and snag densities, with the opposite in burned areas. Low-intensity fires in closed-canopy forest appeared to have no adverse effects.

In New Jersey and Pennsylvania, hemlock declined from 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The Wood Thrush exhibited one of the most positive associations with hemlock decline, increasing due to the increased deciduous understorey (Toenies et al. 2018).

Overbrowsing by white-tailed deer reduces shrub and sapling density and impairs habitat for nesting Wood Thrushes. In Rondeau Provincial Park, there was limited recruitment of small trees and declines in basal area of species that were sensitive to browsing. Wood Thrush numbers were very low in the park when there were 55 deer per km^2. Following deer control efforts that reduced deer densities to 7 per km^2, thrush numbers increased in response to a modest increase in understorey regeneration (Savignac 2012b). In Delaware, Tymkiw et al. (2013) compared Wood Thrush abundance within areas of low (10 or fewer per km^2), moderate (11-19 per km^2), and high (20 or more per km^2) deer densities. Its abundance was significantly higher in areas of low and high deer

density than in areas of moderate deer density. It was very common in this area may be better adapted to using exotic shrubs than most species.

In Georgia, Crawford (1986) compared the amount of rainfall received in April and May with the number of singing males and found a positive correlation. The amount of spring rainfall could affect abundance of breeding Wood Thrushes. Dry springs could possibly limit opportunities to find mud for nest construction.

DesGranges and Morneau (2010) considered the Wood Thrush sensitive to climate change in Quebec.

Status

The Wood Thrush was formerly a much less common breeding species in Ontario and occupied a smaller range. McIlwraith (1894) knew it only as a migrant in the Hamilton area. Fleming (1907) considered it a rare breeder in the Toronto area, with only 3 records. In Niagara, Sheppard et al. (1936) had no breeding records for the Wood Thrush. It was recorded from the Kingston area dating back to 1858 (Weir 2008). In Elgin County in 1891, it was a fairly abundant summer resident; in 1954, it was a fairly common summer resident that nested mostly in larger woodlands; and in 2000 it was a common but declining breeder (Lancaster et al. 2004). Baillie and Harrington (1937) considered it a common breeder only in the extreme southwestern portion of the province. Elsewhere, it was found in small numbers from Lakes Erie and Ontario north to Parry Sound District and Ottawa. There were records of it from Sault Ste. Marie, Lake Nipissing, Nipissing District, and Manitoulin Island. MacLulich (1938) stated that it was an uncommon summer resident in Algonquin Park, where it was near the northern extent of its range. It was regular and moderately common in the Hamilton area in the 1930s and 1940s and is now a ubiquitous breeder (Curry 2006). A major range expansion of the Wood Thrush in Ontario started in the 1950s (M.L. Evans et al. 2020). During the first atlas, its breeding range was further north than indicated by Godfrey (1986). It occurred in almost every square north to approximately Lake Nipissing; the most northerly record was from near Kapuskasing (Sadler in Cadman et al. 1987). James (1991) considered the Wood Thrush a common summer resident north to about Georgian Bay and Ottawa, becoming rare north to Sault Ste. Marie and Sudbury. There were records north to Rainy River, Thunder Bay, Wawa, and Cochrane.

The second atlas revealed that there had been no significant change in the distribution of the Wood Thrush since the first atlas. It was found in virtually every square south of the Canadian Shield, including large urban areas such as Toronto and Ottawa. It continued to be widespread in the Shield north to the Lake Nipissing area, with another pocket of abundance around Sault Ste. Marie. It occurred north to New Liskeard and along the northern shoreline of Georgian Bay and eastern Lake Superior to Wawa. A small isolated population was present near Lake of the Woods. Its probability of observation did not change significantly since the first atlas. A significant decline occurred in the southern Shield that may have been due to the effects of acid precipitation or forest maturation. It was most abundant south of the Shield, although there were pockets of high abundance in the southern portion of the Shield. A large area of eastern Ontario was struck by a severe ice storm in 1998. This devastated many forests that are now regenerating. This region had the most extensive area of high-density Wood Thrush populations in the province (Friesen in Cadman et al. 2007).

From 1989 to 2014, Wood Thrush frequency of occurrence in the Canadian Shield of Ontario was high and stable. It occurred in 72.3% and 75.5% of forest fragments during the 2 sampling periods. Local extinction rates were 21.2% in the Shield and 2.5% south of the Shield. The probability of continuous detection increased with the amount of forest within an atlas square in the Shield, but this trend was much weaker south of the Shield. The probability of continuous detection increased with forest cover within 1 km. It was almost 2 times as abundant south of the Shield as in the Shield. It decreased at annual rates of 1.75% south of the Shield and 3.75% in the Shield (Torrenta et al. 2022).

BBS results indicate that the Wood Thrush decreased at annual rates of 2.69% in Canada and 2.33% in Ontario 1970-2021. The trends 2011-21 were annual decreases of 0.353% in Canada and 0.45% in Ontario. The long-term trends were highly reliable; the short-term trends were of medium reliability (A.C. Smith et al. 2023).

The Wood Thrush has been designated threatened nationally and special concern provincially.

POSTFLEDGING PERIOD

Fledglings may be fed by adults until they are 25-32 days old, but may start feeding themselves at age 17-20 days. For first nests, the brood remains together and individual young are fed by both parents. The second brood is often split with each adult caring for half the brood. In 1 case where there were only 2 fledglings, the male left and the female raised the young. In 1 case where there was only 1 fledgling, the female left. Young are usually independent when they are 31-32 days old, although some are independent as early as 21-28 days (M.L. Evans et al. 2020).

In Missouri, juveniles dispersed 3 weeks after fledging. They moved from forest-interior natal territories into areas of denser vegetation, such as mature wooded riparian habitat, young deciduous and pine forests (clear-cuts), and forest-field edges. Two different movement types were used by family groups prior to dispersal. Five of 7 broods had stationary home ranges centred around the nest site and 2 broods had drifting home ranges where adults and young moved progressively further from the nest. Mean brood home range was 4.46 ha for stationary home ranges and 19.5 ha for drifting home ranges, with an overall range of 2.6-24.8 ha. Siblings remained together until dispersal and moved separately from their natal areas. Mean dispersal distance was 2.08 km (range 0.21-4.65 km). Juveniles took an average of 4 days (range 1-9 days) to move to the post-dispersal home range. Habitats used by juveniles after dispersal were early successional oak-hickory or pine forests resulting from clear-cutting, with dense stands of saplings and shrubs; mid-successional pine forests with dense patches of oak, hickory, and sassafras in the understorey with continuous shrub coverage; high-graded oak-hickory forest with large, open patches supporting dense growth of understorey; mature riparian sycamore and black walnut forest with continuous ground cover; abrupt forest–old field and forest-pasture edges with dense canopy, understorey, and ground cover where juveniles were always under forest cover; and mature oak-hickory forests where juveniles selected dense stands of 3-4-m tall understorey trees along drainage courses or dense patches of ground cover 0.5-2 m high. Each juvenile settled into one of these habitats. Its post-dispersal home range occurred entirely within that habitat with areas of denser undergrowth or shrub and sapling coverage selected more than their availability. Mean dispersal home range size was 1.53 ha. Two juveniles moved to second post-dispersal areas and had home ranges of 0.21 and

0.26 ha. Post-dispersal home ranges were occupied for 4-30 days. In all habitats, juveniles remained on or near the ground within dense vegetation. Dense cover provides protection from predators and abundant food in the form of insects and raspberries (Anders et al. 1997, 1998). In Virginia, fledglings 12-15 days old were able to climb shrubs but were incapable of sustained flight. During this time, they perched quietly 1-5 m above ground. The distance the brood and adults moved from the nest after fledging and before independence varied depending upon whether parents remained in the nesting area to moult (104 m) or moved elsewhere (332 m). After independence, most fledglings dispersed 1.5 km from natal sites and joined flocks of conspecifics. Young either remained at the distant site or moved further away (Vega Rivera et al. 2000). In Georgia, the average pre-dispersal movements of fledglings were 131, 208, and 117 m over 3 years. Juvenile dispersal occurred between 3 and 4 weeks after fledging, although 1 fledgling did not disperse in each of the 3 years. The average dispersal distance for juveniles was 2,189 m; probabilities of dispersing different distances were 35% for 0-1 km, 30% for 1-2 km, and 20% for 4-5 km. After dispersal, most fledglings remained within 172, 360, and 390 m of their initial dispersal locations, but 3 juveniles made a second long-distance movement of about 5 km 18-20 days after dispersal. The longest distance travelled by a juvenile was 6,524 m; the average daily distance travelled was 140 m. No second-year birds were recaptured in their juvenile dispersal areas. Juveniles preferred a moderate overstorey taller than 2 m in 11-30% coverage, and avoided sparse (0-10%) overstorey. Of the 3 most common midstorey trees and shrubs, juveniles used areas with dogwoods more frequently than expected. Juveniles dispersed in random directions and not to a juvenile grouping site (Lang et al. 2002).

In Norfolk County, 93 of 119 juvenile Wood Thrushes (78.2%) made premigratory flights greater than 5 km. Ninety percent of movements were at night. The age of first detection more than 5 km from the natal woodlot varied. Birds that fledged in June were first detected distant from the natal woodlots 24-93 days postfledging. Later-fledging birds tended to disperse at a younger age postfledging and there was less variation in the timing. The average maximum distance juveniles were detected from the natal woodlot was 21.8 km, with 21 of 93 (22.6%) detected more than 30 km away. One moved 85 km from the natal site but returned prior to autumn migration. The direction of movements was random and not small-scale migration movements which would be southerly in orientation. Most premigratory dispersal occurred during the 2 weeks before departure on autumn migration (Hayes et al. 2024).

In Ohio, both juvenile and adult Wood Thrushes were frequently caught in regenerating clear-cuts during the postfledging period. Capture rates were more than 6 times as high in nets 4.5 m from the ground than those 2.5 m up. It was the sixth-most abundant forest-breeding bird captured in clear-cuts. Capture rates were 2.5 times higher in small (4-9 ha) than large (13-18 ha) clear-cuts. Capture rates in differently sized clear-cuts were significantly different for juveniles but not for adults. There were no differences in habitat characteristics, vegetation density, arthropod abundance, or fruit abundance between small and large clear-cuts. Birds were more abundant 50 m or more from the edge of clear-cuts than closer to adjacent forest habitat. There were no differences in habitat associated with distance from edge; birds may avoid edges if predators are concentrated along them (Vitz and Rodewald 2006, 2007).

In Minnesota, Streby et al. (2011b) captured no Wood Thrushes in regenerating clear-cuts during the breeding season, but caught 10 adults and 2 fledglings during the postbreeding season. In Virginia and West Virginia, Marshall et al. (2003) captured adults, juveniles, and a family group in regenerating clear-cuts. It was one of the most abundant forest-breeding species captured in clear-cuts. During the postfledging period in Pennsylvania, Stoleson (2013) captured 5 adults and 10 fledglings in clear-cuts compared with 4 adults and 0 fledgling in mature, closed-canopy forests with a dense understorey. Its capture rate was significantly higher in clear-cuts than in forests. Shrub density was not significantly different between clear-cuts and forests, but birds captured in clear-cuts were in significantly better condition. Clear-cuts supported high densities of fruit-bearing shrubs that may have provided a superior food source. In Missouri, Porneluzi et al. (2014) netted birds during the postfledging period in an oak-pine-hickory forest 2-15 years after it was clear-cut. The Wood Thrush exhibited a nonsignificant trend of gradually increasing to a peak about 6-9 years after harvest followed by a gradual decline.

In Georgia, adult males used all forest overstorey types available during the fledgling stage, but were most often present in sparse or moderately dense vegetation (Lang et al. 2002). In Virginia, males may move long distances (300, 400, and 855 m) from the nesting area with the brood and then either return to the nesting area or immature deciduous woods to moult (Vega Rivera et al. 2000). Of 30 birds in Virginia that remained to moult, 11 moulted where they nested and 19 moulted in different areas. Of birds that moved, 4 males used deciduous sapling stands near their territory and 15 (4 females, 11 males) used moulting sites an average of 2,015 m from their nesting territories (range 545-7,291 m). The moult began 1-4 days after young reached independence and lasted an average of 52.0 days (53.2 days for males and 49.2 days for females). Birds could barely fly for 10 days. During the moult, birds hid on the ground in the densest available vegetation, frequently among branches of fallen trees. Once the moult started, birds moved less (67 m compared with 114 m) and had smaller (1.4 ha compared with 2.6 ha) home ranges than during nesting. After moulting, most adults maintained similar movement patterns and remained in the moulting area. Others had different movement patterns: 1 moved 500 m to a site not visited before, remained there for 2 days, then returned to the nesting territory; 2 moved 4.4 km and 500 m back to their nesting areas and then left the study area; and 4 males that moulted in sapling stands adjacent to their territory moved back into the forest prior to autumn migration departure. None of the birds that returned to their nesting area exhibited any territoriality. These birds restricted their activities to sites characterized by the presence of at least 1 tree species with ripe fruit (black gum, flowering dogwood, and sassafras). The density of woody stems, understorey vegetation, and saplings was much higher in moulting areas than in nesting areas and provided cover from predators when birds' flight abilities were impaired. Large forested areas with a mix of forest types and ages may provide nesting and moulting habitat. Fragmented landscapes may provide nesting habitat but not moulting habitat. The time available for nesting is constrained by the requirement to moult prior to migration (Vega Rivera et al. 1998, 1999). In New York, 18 of 46 birds (39.1%) moulted on their breeding territory, 15 (32.6%) moulted off territory within the study area, and 13 (28.3%) moved more than 1 km from the study area. Moulting habitat differed significantly from nesting habitat by having a low percent canopy cover, more shrubs shorter than 60 cm, and more fruiting trees. Females were more likely to moult off territory than males and first-year breeders tended to moult off territory more than older

birds (86% compared with 52%), but these differences were not significant (Gow and Stutchbury 2013a).

Vitz and Rodewald (2012) examined the diet of several Wood Thrushes in 6-10-year-old clear-cuts in Ohio. There was no evidence that they had switched from a diet consisting of arthropods to one dominated by fruit.

In Indiana, Vernasco et al. (2018) examined the effects of cowbird parasitism, drought, amount of forest cover, understorey vegetation density, and nestling condition on postfledging survival of the Wood Thrush. Brood parasitism and nestling condition were not strongly linked to fledgling survival. Decreases in survival occurred during a year of drought and were most pronounced in fledglings 0-3 days out of the nest. During drought years, birds in areas with lower forest cover exhibited the steepest decline in survival. Fledglings of the same age in more forested habitats had similar survival rates in drought and non-drought years. In non-drought years, survival declined as the amount of forest cover increased, possibly because growth rates are higher closer to forest edge. Nestlings were in significantly poorer condition in parasitized nests and in drought years but were unaffected by vegetation parameters. Nest vegetation structure and parasitism had little effect on fledgling survival but forest cover and breeding season precipitation interacted to affect fledglings.

The breeding and postbreeding habitat requirements of the Wood Thrush are complex. Due to local extinctions and recolonizations, woodlots may support breeders some years but not in others. Although most pairs remain in the same woodland to raise their second brood, others may move several kilometres between successive nests within a breeding season. These within-season movements may occur in large, contiguous forests as well as in small fragments. Once they are independent, fledglings move to areas with dense understorey vegetation, often where there is limited overhead canopy. Many of these habitats would not support breeding pairs of Wood Thrushes, but are essential to fledglings. Adults also move to areas of thick cover during the moult. Many smaller forest fragments may not provide all the essential habitats for Wood Thrushes throughout the breeding season. They may still contribute young to the metapopulation or provide habitat for fledglings or moulting adults even if they are not used for breeding.

MIGRATION

The Wood Thrush migrates at night, except at the end of trans-Gulf flights (M.L. Evans et al. 2020). Early in the season, males arrive on the breeding grounds 2-3 days before females. Later in spring, arrivals of both sexes overlap (Dilger 1956; M.L. Evans et al. 2020; Weaver in Bent 1949). Most birds arrive in early May in southern Ontario with most on territories by mid-May; migrants may occur as early as mid-April. In the southern Shield, most arrive in mid-May and start moving south in August with migration continuing until early September and late birds persisting until the end of September. Autumn migrants may occur in the south as early as mid-July and move through in low numbers until early October (Black and Roy 2010; Curry 2006; LaForest 1993; Mills 1981; Tozer 2012; Weir 2008). In Norfolk County, the average departure date for juveniles was 19 September (range 25 August to 15 October). Juveniles that fledged by 22 June departed on autumn migration 9 days earlier than those that fledged later (Hayes et al. 2023).

During migration, the Wood Thrush may occur in both forested and shrubby habitat. In Pennsylvania, it was captured significantly more often in shrub than forested habitat during spring migration. Invertebrate biomass was higher in shrub habitats than in forest (Smith and Hatch 2008). During autumn in Pennsylvania, its highest abundance was in forest-agricultural edge habitat, where it was significantly more abundant than all other habitats except suburban forest. Abundance in shrub-sapling-stage forest was greater than in pole-stage forest, but the differences between these habitats as well as suburban forests were not significant. No Wood Thrushes were encountered in forest interior (Rodewald and Brittingham 2004). In Minnesota and Wisconsin during spring migration, it was detected in upland forests but not in floodplain forests (Kirsch et al. 2013).

The Wood Thrush is vulnerable to striking windows and tall towers and buildings during migration but may be less vulnerable than many migrants. Sixteen were killed at the Lennox generating station near Kingston. In Illinois, it represented 0.5% of birds killed at towers in autumn (Graber et al. 1971; M.L. Evans et al. 2020; Weir 2008). In the United States it was much more vulnerable to striking residences than average. It was 41.0 times more likely to strike residences 1-3 stories tall than the average for all birds (Loss et al. 2014).

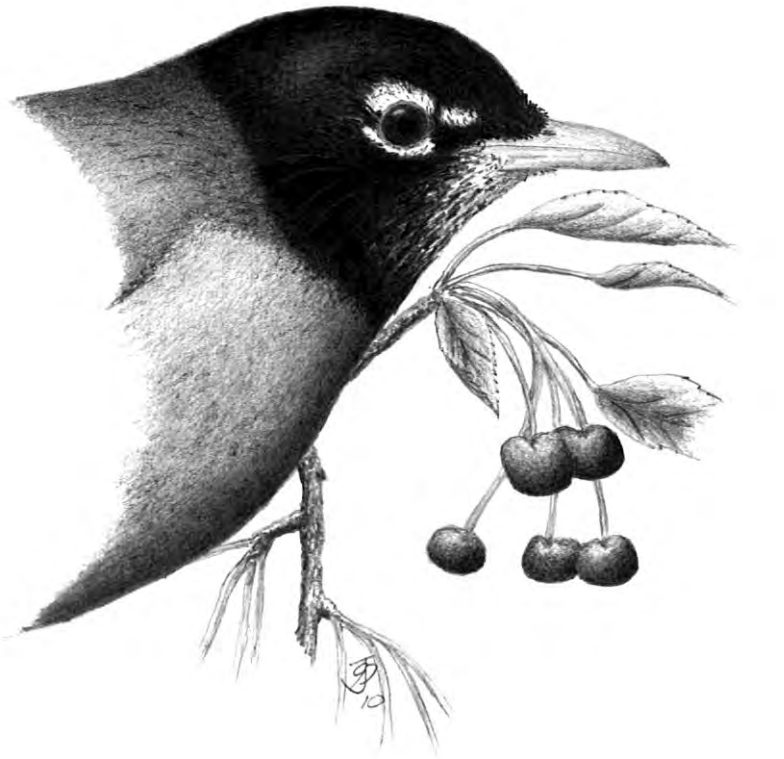
In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season for 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming during the second period. The Wood Thrush departed significantly later in autumn during the second period, but there were no significant differences in its spring arrival dates or length of the breeding season. In Concord, Massachusetts, it arrived later in warm years, averaging 1.3 days later for each 1°C increase in temperature (Ellwood et al. 2010).

The Wood Thrush is a common migrant in Ontario (James 1991), although it is an uncommon migrant in Elgin County (Lancaster et al. 2004). Although it is common during migration, large numbers seldom occur.

Hussell et al. (1992) noted a significant decline of migrating Wood Thrushes of 6.0% 1966-88 at Long Point Bird Observatory. Rates of change during different periods were: 1961-70, −9.4%; 1970-70, −0.6%; and 1978-88, −15.0%.

American Robin

Turdus migratorius

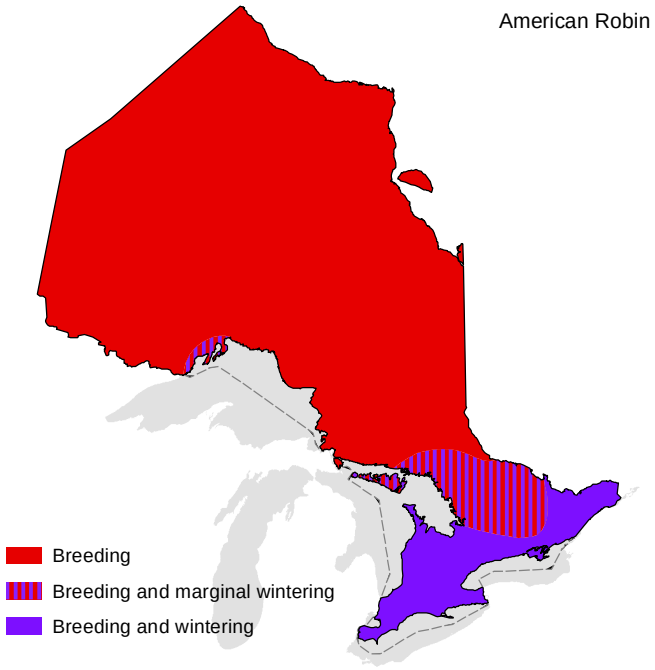


BREEDING SEASON

Habitat Requirements

In Ontario, American Robin nests have been found in urban, rural, and wilderness areas. Habitats where nests have been found include residential gardens, buildings, and tree-lined streets (38% of nests); open areas, including farm fields and orchards, roadsides, campgrounds, and mine buildings (35.1%); woodlands and swamps (25.1%); and bogs, marshes, and beaver ponds (1.8%). Coniferous forests were preferred for nesting and supported 50.2% of nests compared with 22.8% for deciduous woods, 21.4% for mixed stands, and 5.6% for treed swamps. It greatly preferred dry sites for nesting (90.0% of nests) over wet sites (Peck and James 1987).

In the Hudson Bay Lowland, Wilson and McRae (1993) recorded the robin at all forested sites they examined, but it was most abundant in and near Moosonee. Along the west James Bay coast and the southern Hudson Bay coast, it nested inland along forest edges in drier locations and was particularly plentiful around settlements. It also nested in willow thickets along the Moose River (Manning 1952).



In the Ontario portion of the Clay Belt, the robin occurred in all forest types except for a few black spruce–jack pine, jack pine, and trembling aspen stands (Welsh and Lougheed 1996). In Quetico Park, it was most abundant in early successional forests (1-23 years old), occurred at lower density in mature stands, and was not recorded in intermediate-aged or old-growth stands (Apfelbaum and Haney 1985).

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the robin nests in mature and old-growth white pine stands (Kirk et al. 2012). Near Gogama, it was rare in areas forested with jack pine and absent in older pine and mixed stands except at edges. It was most abundant in young plantations where there was open ground suitable for foraging (James and Peck 1995a). It was present in most open jack pine stands mixed with deciduous cover in Parry Sound District (James 1979a). In Algonquin Park, it was common near settlements and scarce in contiguous mature forest (MacLulich 1938). In Algonquin Park, Martin (1960) found it in most forest types but it was most abundant in edge habitat. In Muskoka District and Haliburton County, singing posts were in areas of low canopy volume, low tree density, and low amounts of understorey. It was associated with lawns. Its ability to nest on buildings and ledges and its preference for foraging in the open allowed it to be successful where most natural vegetation had been removed (Clark et al. 1983).

Near Kingston, upland white cedar stands provided quality breeding habitat (McLeish and Robertson 1997). Tozer (2002b) reported a robin nesting in a large cattail marsh associated with the Beaver River in Durham Region. It occurred in all habitats sampled by Speirs and Orenstein (1975) in Durham Region and did not show any special affinity for conifers or any particular level of succession.

In southern Ontario, the robin was more abundant on conventional than organic farms. It was positively associated with hedgerows, pasture, amount of riparian and upland woods, and row crops. It was significantly negatively associated with grassy strips between fields that often included a fence (Kirk et al. 2011).

The American Robin is the most widespread thrush in Canada and North America, breeding throughout except for a few areas north of the treeline and in the extreme south. It may be found in almost every habitat type. It is most frequent in urban and suburban areas, rural residential areas, and where there are wooded areas suitable for a nest site adjacent to open areas that provide foraging habitat. The most commonly used type of these habitats is small, isolated woodlots in agricultural settings but natural or anthropogenic openings in forests may be used including clear-cuts and burns. It may nest in any forest type, but prefers deciduous and mixed stands to pure

coniferous stands. Densities are considerably lower in large contiguous forests than in isolated stands in fragmented landscapes. It may nest in riparian and upland forests and treed swamps and, less frequently, in thicket swamps, but tends to be more common in upland habitats. Nesting may occur in old fields regenerating with trees and shrubs, hedgerows, plantations, Christmas tree farms, oak savannahs, pine and oak barrens, orchards, lightly grazed pastures, and alpine meadows. Other habitats it may nest in occasionally include marshes dominated by cattails or common reed, fens, bogs, and on low cliffs in treeless areas. Active agricultural land may not be used for nesting, but adjacent hedgerows and woodlots frequently are and the open fields may be important foraging habitat. In the Yukon, its abundance was positively correlated with density of trees and shrubs (Back 1979; Beals 1960; Bielefeldt and Rosenfield 1994; Bock and Lynch 1970; Campbell et al. 1997; Capen 1979; Crawford and Titterington 1979; Crozier and Niemi 2003; Dawson 1979; Erskine 1977; Gentry et al. 2006; Golet et al. 2001; Graber and Graber 1963; Graber et al. 1971; Grundel and Pavlovic 2007a; Hoffman 1989a, 1989b; Howell 1942; Hudson 1994; Hughes and Hudson 1997; Inman et al. 2002; Noon et al. 1979; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991; Rotenberry and Wiens 1980; Rumble and Gobeille 1998; Samson 1979; Shirley 2005; Sinclair et al. 2003; Suthers 1988; Tardif and Lanoue in Gauthier and Aubry 1996; Taylor and Taylor 1979; Temple et al. 1979; Turner 2013; Tyler in Bent 1949; Walk et al. 2011; Wood et al. 2013).

The robin is most abundant in cities, suburban areas, towns and villages, and rural residential areas. In southern Illinois, 80% of the population nested in towns and cities compared with 60-70% in the northern portion of the state. Overall, 75% of the population was associated with residential areas and farmyards (Graber and Graber 1963; Graber et al. 1971). In urbanizing areas of Washington State, it was most abundant in forested neighbourhoods and forest patches where squirrels were uncommon. It avoided areas within forest patches where a single predator was abundant or where there were several species of predators (Marzluff et al. 2007). In suburban areas of Massachusetts, its abundance was correlated with the amount of coniferous tree volume in the 1.5-6.1-m height range and the amount of deciduous volume 3.4-6.1 m from the ground. The number of gardens and distance to the nearest fallow field were significant predictors and were probably related to suitable foraging sites (Thomas et al. 1977). In 2 Nevada cities, nest success was positively correlated with the amount of canopy cover within 20 m of the nest (Becker and Weisberg 2015).

The American Robin is an edge species that forages mostly in open habitats. Some authors considered it an obligate edge species, but it also occurs in forest interior and in contiguous forest at much lower densities. In Wisconsin, 75.9% of nests were at the edge of white cedar plantings, and a tree directly on the edge was frequently selected for nesting. In West Virginia forests, nests tended to average less than 2.8 m from edge, including roads and skid trails. Nesting close to edge separated the robin from all other thrushes except the Hermit Thrush. Robin nests had fewer than 2-5 medium-sized trees around nest sites; the Hermit Thrush had more. In California, the robin was more common in open burns than adjacent unburned forest. It nested in residual trees in the burn or the edge of forest and foraged in the burn. Despite a preference for edge, its abundance was negatively correlated with the complexity of the shape of the habitat patch (Bock and Lynch 1970; Campbell et al. 1997; Crozier and Niemi 2003; Dellinger et al. 2007; Suthers 1988; Young 1955). Erskine (1977) considered the robin one of the most common species along edges in the Boreal Forest Region.

The robin is more common in fragmented landscapes than contiguous woodlands. In southern Ontario, its probability of detection was significantly negatively correlated with woodlot size, amount of forest within 2 km, and regional amount of forest. It was also negatively correlated with the amount of forest habitat 100 m or more from edge but not significantly (Austen et al. 2001). In Vermont, it was significantly more abundant in Christmas tree farms surrounded by agriculture than those encompassed by forest (Hughes and Hudson 1997). In Saskatchewan, it was more common in small forest fragments and areas with a low percentage of forest cover (Hobson and Bayne 2000). In Quebec boreal forest, its abundance was significantly correlated with poorly forested landscapes (Drolet et al. 1999). In Newfoundland, its presence was not correlated with the amount of forest within 2.5 km, but was negatively associated with the amount of forest and shrub areas within 150 m (Taylor and Krawchuk 2006). In Pennsylvania, there were no correlations between robin abundance and the amount of fragmentation or patch size (Keller and Yahner 2007).

In North Dakota in 400-m landscapes with less than 30% tree cover, the robin increased with increasing tree cover within 100 m. The response in wooded landscapes was somewhat similar but much weaker (Cunningham and Johnson 2016). It preferred areas with 52-75% forest cover in North Dakota and 44-92% in New York. In North Dakota, there were no areas with more than 75% tree cover (Cunningham and Johnson 2019).

Virtually all studies concur that the robin prefers small to large forests. In North Dakota aspen stands, its probability of observation was approximately 35% in 1-ha woodlots and almost zero in 1,000-ha woodlands (Grant and Berkey 1999). In Maryland and Delaware, it was more likely to occur in narrow riparian forests than wide ones. Its probability of detection was 83% in 50-m wide forests, 79% in 100-m wide, 70% in 200-m wide, 59% in 300-m wide, and 11% in 800-m wide forests (Keller et al. 1993). In the mid-Atlantic states, its probabilities of detection were 78% in 0.3-ha woodlots, 50% in 10-ha woodlots, 35% in 100-ha woodlands, and 20% in 3,200-ha woodlands (Robbins et al. 1989). Blake and Karr (1987) reported that the abundance of the robin was negatively correlated with forest size.

Most authors reported that the robin is more likely to be found in young than old stands, but some (Morgan and Freedman 1986; Rumble and Gobeille 1988; Speirs and Orenstein 1975) reported it equally common in all age classes; Temple et al. (1979) considered it a late-successional species in mixed-wood forests. Erskine (1977) considered the robin associated with young stands in the Boreal Forest Region. Crawford and Titterington (1979) reported that it was common in young upland spruce-fir stands in the northeast, but sparse in mature forests. In western boreal areas, it was absent in stands younger than 10 years and in mature stands, common in stands 15-20 years old, and uncommon in older-growth forests. It was associated with younger than older stands (Kirk et al. 1996). In Newfoundland and Wisconsin it was associated with young clear-cuts (Hoffman 1989b; Taylor and Krawchuk 2006). In Pennsylvania, its presence was negatively correlated with old-growth forest. It occurred in 36.4% of old-growth forests compared with 99.1% of forests statewide and 98.7% of forests in the Appalachian Plateau (Haney 1999). In New Jersey old fields, Suthers (1988) found it in equal numbers in fields aged 10, 20, and 40 years. In New York, Brooks and Bonter (2010) surveyed a regenerating field, forest, and Christmas tree plantation over a 35-year period. Over this

time, the number of robins declined significantly in the regenerating area but did not change in forest. Numbers increased in the plantation where the trees were allowed to grow taller.

In New York, water was usually present in robins' territories (Dellinger et al. 2007; Howell 1942) and in many British Columbia habitats it tends to nest near streams, marshes, or ponds (Campbell et al. 1997). In Rhode Island, McKinney and Paton (2009) studied birds associated with small (less than 0.1 ha) seasonal pools that dried up in summer. The robin was 1 of 3 species detected most often. It was more abundant at urban seasonal pools suggesting that it may take advantage of the available resources in the absence of competition from non-tolerant species. Seasonal pools were surrounded by denser shrub coverage, possibly providing enhanced food resources and shelter. Presence of water is important to the robin due to its need for mud to construct the nest.

A number of microhabitat requirements have been identified for the robin. In Indiana savannahs, it was most abundant in areas with a high proportion of low ground cover and a low proportion of high ground cover. Increased fire frequency increased the density of vermivores, with the robin dominating this guild (Grundel and Pavlovic 2007a, 2007b). In northern mixed forests, it increased with increasing abundance of sugar maple and yellow birch (Temple et al. 1979). In the northeast, it was associated with a low density of trees and saplings and a high density of shrubs (Niemi and Pfannmuller 1979). In western boreal forests, it preferred open areas. It was associated with slightly drier than average stands with a low nutrient status (Kirk et al. 1996). In the mid-Atlantic states, its abundance was positively correlated with percent canopy closure but negatively associated with the number of trees and percent canopy coverage by conifers (Robbins et al. 1989). In Wyoming, its abundance was negatively associated with shrub density indicating an affinity for a more open understorey (Finch 1991a).

In balsam fir stands in the Boreal Forest Region of Quebec, the robin was observed almost exclusively in riparian areas near water (LaRue et al. 1995). It was ubiquitous in balsam fir–white cedar stands in Newfoundland, occurring in both riparian and non-riparian stands (Whitaker and Montevecchi 1997, 1999). In British Columbia coniferous stands, it was associated with riparian habitat during winter and spring and autumn migration, but it was not significantly associated with riparian stands during the breeding season (Wiebe and Martin 1998).

Communal nocturnal roosts are used by the robin year-round and are frequently shared with European Starlings and Common Grackles. Less frequently, it roosts with Brown-headed Cowbirds, Red-winged Blackbirds, Eastern Kingbirds, Baltimore Orioles, Cedar Waxwings, and Brown Thrashers. Adult males roost together during the breeding season and adult females join them once nesting is complete. Juveniles of both sexes join a roost as soon as they are capable of flying, and all birds roost communally during winter. During spring and early summer, small roosts near the breeding territory are used, but robins move to more protective habitat (from lawns to forests) in preparation for the moult in August and September. It selects roosts primarily for their proximity to a good food source, especially once the diet becomes dominated by fruit. Breeding-season roosts in Massachusetts were typically in low-lying swampy woods. Most roosts are in deciduous trees, but it has roosted in pines and white cedar. Night-roosting has been reported from a hayfield dominated by bluestem in Kansas. In 1 case, 400-500 roosted in lilacs near a house. In New York, the mean distance of breeding-season roosts from the centre of the daily activity centre was 0.48 km. The

mean distance moved between sightings on consecutive days was 0.36 km. Four of 7 robins moved their daily activity centres 7-9 km at the end of the breeding season and also switched roosts. Roosts were switched 12.3% of the time, but only 4 of 56 birds (7.1%) moved more than 2 km. Roosts may contain as many as 250,000 robins but 20-200 birds is more typical. Large roosts may be used year after year. In winter, nocturnal roosts provide both foraging and antipredator benefits. During winter, flocks of roosting birds may break up in the day and fan out over an area of more than 1,100 km², then gather again to roost in trees (Applegate 2001; Dunn and Tessaglia-Hymes 1999; Graber et al. 1971; Hirth et al. 1969; Howell 1942; Morrison and Caccamise 1990; Pitts 1984; Tyler in Bent 1949; Vanderhoff et al. 2020). Common (1947) reported a male that roosted singly in an apple tree near the nest.

Ontario nests were in trees, shrubs, and vines, and on stumps, fallen trees, and roots (78.8% of nests); on or in buildings and other human-made structures (21.0%); on cliff or quarry ledges (0.1%); and on the ground (0.1%). Of nests in trees, 70.7% were in crotches and 29.3% were on horizontal branches 0.2-6 m from the trunk, with most 0.9-2 m from the trunk. There was a tendency for nests to be near the midpoint of the nest tree. Nests were placed equally often in deciduous and coniferous trees. Tree species used most often were spruce (338 nests), white cedar (234), hawthorn (217), pine (182), maple (182), and apple (123). Four nests were in tree cavities. Most tree nests were over ground, but some were over water. Heights of nests ranged from 0 to 21 m, with most 1.4-3 m up. Some nests were reused, and old nests of Eastern Phoebe, Barn Swallow, Blue Jay, Gray Catbird, and Common Grackle were used (Peck and James 1987). Savard and Falls (1981) examined nest-site selection of robins in Toronto. Nests were found in more than 30 species of trees. Of 171 nests, 105 were in deciduous trees, 57 in conifers, and 9 on human-made structures. Norway maple was the most common deciduous species used and blue spruce was the most common conifer used which was probably a reflection of the abundance of these trees. In May, 63% of nests were in conifers compared with 15% in June and 4% in July. Nests were at heights of 1.52-13.41 m (average 5.00 m). Nest height was similar to that reported from other urban areas, but higher than in non-urban areas, probably due to the scarcity of low vegetation in urban areas. Most nests were in the layer of foliage just below the layer with the largest volume. Average nest height was significantly lower in conifers (3.82 m) than in deciduous species (5.57 m). Taylor (1959) reported a nest in a tree cavity in Toronto. In Muskoka and Parry Sound districts, nests were in dead and alive trees, on stumps, and on buildings at heights of 0.15-15 m (Mills 1981). Dance (2008) reported 2 Ontario nests in black alder. Woodliffe (1996) found a nest on the ground at the base of a black oak tree at Rondeau. At that time, only 3 of 6,358 nests (0.05%) reported to the Ontario Nest Records Scheme were on the ground. Tozer (2002b) reported a nest in a cattail marsh in Durham Region.

Nest-site selection by the robin is variable. Most nests are in trees or shrubs, but it may nest on a wide variety of human-made structures. Almost any species of tree or shrub may be used for nesting. Individual birds may have successive nests that are in different species and at different heights. In some areas, it has shown a preference for particular tree species, but often tree species are used in proportion to their availability. In Minnesota shelterbelts, spruce was selected over maple and ash. In Maine, 62% of nests were in conifers although they represented only 45% of available trees. In Christmas tree farms in Vermont, 4 times as many nests were in spruce than fir trees. In

Manitoba, about half of nests were in Manitoba maple but it was 25% of available trees. Peach-leaved and sandbar willow were 55% of available trees but supported only 25% of nests. In Nevada, trembling aspen was used less than expected for nesting and pine was used more than expected. In Colorado, spruce was preferred and cottonwood was avoided. In Iowa riparian habitat, all nests were in deciduous trees and none were in conifers, saplings, or shrubs. In most areas, coniferous trees are selected early in the spring but deciduous species are used predominantly later on. In Nevada, there was no seasonal change in usage of deciduous and coniferous trees. Most nests are near the centre of the tree at 50-60% of the tree height. Nests in trees are usually in a fork or on a horizontal branch. Half or more are at the trunk and the remainder are distant from the trunk. In Colorado Springs, 345 of more than 500 nests were on tree branches overhanging streets, alleys, and driveways; 107 were on branches over sidewalks; and 54 were in vertical forks. For nests overhanging streets and sidewalks, the lower branch was usually selected, 4.6-7.2 m from the ground. Nests have been reported on the ground to a height of 24 m, but most are 2-4 m up. In Illinois, rural nests averaged 2.1 m in height compared with 3 m in urban areas; Vancouver nests averaged 3.8 m from the ground, higher than the provincial average. Ground nests are rare even where trees are almost absent. Nests in wooded areas tend to be within 5 m of an opening or edge and are frequently near water, even if it is a temporary source such as a puddle. Most studies found that nest orientation is random, but nests in Minnesota and Nevada faced between south and east, presumably to take advantage of the morning sun. The Cornell Nest Record Scheme revealed that only 1 of 16,000 nests was in common reed. Ten nests in a marsh in Boston were supported by common reed and were 0.9-1.8 m from the ground. Other unusual nesting locations include under plants in a garden; at the base of trees, shrubs, or logs; on exposed roots at road cuts; on leaves on the ground with no evidence of a nest; in a knothole in a tree; in old woodpecker cavities where the top or side had broken off; within a split in a stump; on top of nests of Baltimore Oriole, Northern House Wren, Red-winged Blackbird, Western Kingbird, Gray Catbird, and hornets; on a slight shelf on the bare trunk of a maple tree; in crevices of rock walls and caves; on fallen trees leaning against other trees; and on witch's-brooms (Brackbill 1947a, 1950a; Campbell et al. 1997; Common 1947; Graber et al. 1971; Howe 1898; Howell 1942; Hoyt 1948; Hudson 1994; Hughes and Hudson 1997; Klimstra and Stieglitz 1957; Knupp et al. 1977; MacKenzie et al. 1982; Mousley 1916a; Stauffer and Best 1980; Tyler in Bent 1949; Vanderhoff et al. 2020; Warkentin et al. 2003b; Webb 1946; Weber 1975; Yahner 1983; Young 1955). The robin may nest on or in buildings anywhere there is a flat surface to support the nest. It has nested on arms of utility poles, on top of bird nest boxes, in the hub of a wagon, in a smoke pipe, on a railway tank car that was occasionally moved, on fence rails and posts, on a chandelier at the entrance to a library, at the intersection of 3 cables of a trolley line with trolleys passing every few minutes a few centimeters below the nest, on a gate that frequently swung back and forth, on the arm of a railway signal that was raised 50 times a day, on a steel crane that was constantly swinging to load railway cars, on a figure over a grave, in old horse carriages; in woodpiles, on a set of antlers hung over a frequently used garage door, on ornamental vines growing on trellises, on bridges, on abandoned equipment, in underground parking garages, in tunnels, on billboards, on steps of a ladder, on boards in lumber piles, and in hanging bird feeders and flower baskets (Campbell et al. 1997; Eiserer 1976; Howe 1898; Howell 1942; Leighton et al. 2002).

The robin defends a small territory from which other robins are expelled, but foraging and roosting occur in undefended areas outside the territory. Peck and James (1987) reported a group of about 25 pairs nesting on steel beams beneath a concrete bridge over a river suggesting coloniality. Nests were often separated only by the thickness of the steel, but birds could not see others while they were on their nests. R.G.B. Brown (1972) reported what he termed a colony of robins breeding at Vineland. A total of 13-14 pairs bred in 15.4 ha of cedar hedge and cherry orchard. There were only 8-13 pairs in the remaining 27.1 ha of the farm, which was similar habitat. In Quebec, robin territories were evenly spaced in forested habitat, with no evidence of grouping (Bourque and Desrochers 2006). Territory sizes vary inversely with population density and habitat quality, with most territories 0.1-0.3 ha. Reported territory sizes are 0.11-0.21 ha in New York, 0.04-0.24 in Wisconsin, 0.12-0.84 ha in Tennessee, and 4.00 in spruce forest in Maine. In Tennessee, 1 male had territories of 0.43 and 0.50 ha during 2 nestings within a season. Another had territories of 0.53 and 0.48 ha in the same territory in consecutive years. The mean size of territories in this population was 0.42 ha, larger than reported from most locations. Habitat was less than ideal because there were a limited number of suitable nest trees. Nests were rarely at the centre of territories and usually near the edge. Nests of neighbouring females may be as close as 5 m to each other and in 1 case nests were touching each other. In Tennessee, overlapping of territories occurred in 5 of 7 years. The amount of overlap was 0.03-0.08 ha with the largest overlap being 21% of the smaller of the 2 territories involved. In Algonquin Park, depth of territories in white birch–poplar forest was 0-10.7 m, corresponding to the area from the ground to the top of the canopy. Neighbours may join together to attack an intruder (Bourque and Desrochers 2006; Howell 1942; Martin 1960; Morse 1977; Pitts 1984; Vanderhoff et al. 2020). Home ranges are larger than the territory. Most birds have to leave the territory to find sufficient food and nocturnal roosts are typically outside the territory. Birds may feed and roost as far as 400 m from the territory (Howell 1942; Pitts 1984).

Few juveniles return to their natal site to breed, but a high proportion return to the general vicinity. In British Columbia, 0 of 35 fledglings returned; 4 of 90 juveniles (4.4%) returned to a New Jersey study area. In New York cherry orchards, return rates of juveniles depended upon the quality of the cherry crop. After a good crop year, 17 of 61 nestlings (27.9%) returned; only 6% returned the following year after a poor crop. In Massachusetts, 4 of 250 nestlings (1.6%) returned. In North Dakota, 33 of 368 young (9.0%) returned to breed. None nested in their natal shelterbelt. Mean distance of first nests from the natal area was 3.5 km (range 0.1-9.4 km). In Massachusetts, 61 nestlings were recovered; 54% were found within 1.6 km of their natal nest and an additional 20% were found 1.6-16 km away (Campbell et al. 1997; Haas 1995; Hirth et al. 1969; Johnson et al. 1976; Suthers 1988). Farner (1949) analyzed 428 recoveries of breeding robins that were banded as young east of the Mississippi River from Pennsylvania northward. Of 422 breeding record returns, 387 (91.7%) were 0-40 km from the natal site, 13 (3.1%) 40-80 km away, 10 (2.4%) 80-160 km away, 10 (2.4%) 160-320 km away, and 2 (0.48%) more than 320 km away. Some were found 233-684 km from the natal site and they had dispersed in all compass directions. Of 121 birds, 120 (99.2%) were retrapped at the banding location. Of birds found dead, 387 of 428 (86.9%) occurred within 40 km of the banding area. This figure increased to 89% if doubtful breeding records were removed. Of 115 recovered away from the original banding site, 75 (65%) were found within 40 km of the natal site, or 69% when doubtful breeding records were removed. These data suggest that juveniles tend

to return to the same general area and may return to breed in the last place they occupied prior to autumn migration. Older adults return sooner which may prevent first-year birds from establishing territories in their natal areas. Weir (2008) reported that 10.5% of robins banded at Prince Edward Point returned 1 year later to nest, 3.3% returned 2 years later, and 1.3% returned 3 years later.

Adults typically return to the same area to breed every year. There are several records of distinctly plumaged birds nesting in the same territory for as many as 6 years (Farner 1945; Graber et al. 1971; Howell 1942). In Vancouver, 14 of 20 adults (70.0%) returned to breed, 5 of 11 (45.5%) returned in New York, and 11 of 22 (50.0%) returned in Tennessee; 93 of 100 (93.0%) were rediscovered in a North Dakota study area, although not all birds returned to the same breeding area. Some birds nest in the identical spot each year and may build a new nest on top of the old one. In 1 case, 7 nests were built on top of each other (Brackbill 1952; Campbell et al. 1997; Haas 1998; Howell 1942; Pitts 1984). In Tennessee, several birds that did not return to the same nesting area were found nesting nearby; some skipped a year before returning to nest again (Pitts 1984). In Maryland, 1 male returned to his previous territory, but moved a considerable distance away a month later (Brackbill 1952a). In New York, females returned to the general location of their previous territory; males returned to the same territory (Howell 1942). Of returning robins in North Dakota, 56% returned to the same shelterbelt and 75% of these used the same nest site, 18% moved to woody draws between shelterbelts, and 7% moved to a different site. Return rates were dependent upon breeding success the previous year. Return rates for successful birds were 46% for males, 43% for females, and 44% overall. Return rates for birds whose nests failed due to natural causes were 12% for males, 27% for females, and 22% overall; and for experimentally induced failures, 20% for males, 17% for females, and 18% overall. Distances moved between nests in successive years were 0-1,300 m. Means were 66 m for successful birds, 152 m for natural failures, and 125 m for induced failure. Distances moved between successive nests within a breeding season were 0-1,200 m, with means of 42 m, 71 m, and 125 m for successful, naturally unsuccessful, and experimentally failed nests, respectively. The relationship between nesting success and dispersal distance was significant only for within-season movements (Haas 1995, 1998).

Limiting Factors

Eggs have been found in Ontario nests from early April until the third week of August, with most present in May and the first half of June (Peck and James 1987, 1998a). In Algonquin Park, nests are under construction from mid-April to mid-June, eggs are present from late April to late July, nestlings are present from mid-May to early August, and dependent fledglings have been observed from early June to mid-August (Tozer 2012). Nesting in late autumn and in very early spring or late winter has been documented elsewhere. In Iowa and Illinois, late dates for nest establishment were 3, 9, and 26 August (Klimstra and Stieglitz 1957). In Virginia, Bedell (1999) found a dead nestling in February and a newly constructed nest that was estimated to have been initiated on 31 January. Winter nesting by the robin is rare, but has been reported from Pennsylvania (nest with eggs on 4 January [Berger 1966]), Ohio, and North Carolina; all these attempts were unsuccessful. In Missouri, Gardali and White (2003) reported a nest that fledged young on 12 and 15 October. They reviewed 11,113 Cornell University nest records for the robin and found 15 records for September and 3 later than September. Most September records were in the later stages of nesting, but 3 of 5 from Alaska

contained eggs. The 3 later nests were 3 October in Massachusetts, 18 November in West Virginia, and 8 January in Ohio. About 23,000 nest records for Canada yielded only 2 records from September, 1 each from Quebec and Manitoba.

Nest construction may take as little as 1 day or as long as 20 days, with average times reported as 3-6 days, 7 days, and 3.5 days. Nest construction takes longer early in the season. Work may be halted for a few days during periods of snow or other adverse weather. Second or third nests are usually built in 2-3 days. Initiation of nesting is delayed by 3 days per degree of increasing latitude in the east, but there is no difference in timing in the west (Common 1947; Graber et al. 1971; Howe 1898; Howell 1942; Klimstra and Stieglitz 1957; Tyler in Bent 1949; Vanderhoff et al. 2020; Young 1955). Egg laying may begin the day after the nest is completed or be delayed as long as 15 days. The time elapsed between nest completion and initiation of egg laying is 1-4 days. The egg-laying interval is approximately 1 day. Most females begin incubation with the laying of the last egg, but some start with laying of the first egg resulting in a wide range of reported incubation periods. In California, nocturnal incubation began with laying of the first egg and the amount of time spent on the nest increased with each egg that was laid, with full incubation beginning with laying of the last egg. The incubation period of 109 Ontario nests was 9-15 days (average 11-13 days). There was only 1 record of a 9-day incubation period. In British Columbia, the incubation period was 11-16 days (median 13 days); mean incubation periods at 1 site over 2 years were 12.7 and 13.1 days. Of 233 nests reported to Cornell University, most eggs hatched in 10-12 days. The incubation period is longer earlier in the nesting season. There is a nonsignificant tendency for the incubation period to increase with latitude; the incubation period decreases with increasing clutch size. In the Yukon, the incubation period averaged 11 days; that study concluded that the incubation period decreased with latitude. Eggs hatch over a 2-3-day period (Brackbill 1977; Butcher 1988; Campbell et al. 1997; Graber et al. 1971; Howe 1898; Howell 1942; Klimstra and Stieglitz 1957; Morton and Pereyra 2010; Peck and James 1987; Tyler in Bent 1949; Young 1955). Young may leave the nest when they are 10-21 days old, but mostly in 12-15 days. In British Columbia, the nestling period ranged from 11 to 21 days (median 15 days). Young usually stayed in the nest longer earlier in the season or during periods of inclement weather. The mean nestling period at 1 site over 2 years was 13.2 and 13.5 days; it was 14 days at another site. In the Yukon, the nestling period was only 11 days. All young leave the nest on the same day even though there may be 1 or 2 days difference in their ages. The time for a nesting cycle from initiation of nest building to fledging of young is 33-49 days, but mostly about 37-39 days (Campbell et al. 1997; Graber et al. 1971; Brackbill 1947b; Howell 1942; Turner et al. 2017; Tyler in Bent 1942; Young 1955).

The American Robin typically raises 2 broods and occasionally 3. In Ontario, 8 double broods and 1 triple brood have been confirmed. In British Columbia, 2 broods are reared except in the north near the Yukon boundary where only a single brood is raised; 3 broods are occasionally reared in the south. In New York, 4 of 27 pairs (14.8%) raised 3 broods. A new nest is usually built for subsequent clutches 15-60 m from the first nest. Occasionally the first nest is used to raise a second brood and there is 1 record of a pair using the same nest to raise 3 broods in a season. The first egg is laid in the second nest 37-43 days after laying the first egg in the first nest; second broods fledge about 5 weeks after the first. Renesting is common if a nest fails, with an average of 1.2 days elapsing

between nest failure and the start of the next nesting attempt. A full clutch may be completed 9-16 days after loss. Although the robin will nest repeatedly after failures, it can make no more than 5 attempts (Campbell et al. 1997; Graber et al. 1971; Howe 1898; Howell 1942; Nickell 1957; Peck and James 1987; Pitts 1984; Sinclair et al. 2003; Vanderhoff et al. 2020; Young 1955). Clutches of 2-8 eggs have been found in Ontario with most containing 3 or 4 eggs (Peck and James 1987). Overall, clutches of 1-8 eggs have been reported, but 1-egg clutches have usually been partially depredated. Clutches larger than 5 eggs are likely due to the efforts of more than 1 female. Throughout its range, the robin typically lays 3 or 4 eggs per clutch, and 2 or 5 much less frequently (3-4% of clutches). Clutch size declines with season but increases with latitude. In Illinois, 74% of April and May clutches had 4 eggs and 23% had 3 eggs; in June and July, 46% had 4 eggs and 48% had 3. After mid-May, more 3-egg than 4-egg clutches are laid in New York. If a third clutch is laid, it almost always contains 3 eggs. In Illinois, the mean clutch size was 3.17 eggs; it was 3.44 in Iowa, and 3.16 in Maine. In Quebec, first nests had a mean clutch size of 3.7 eggs compared with 3.2 for second nests. Clutch sizes in the Maritime provinces (3.0 in Prince Edward Island, 3.2 in Nova Scotia, and 3.3 in New Brunswick) are significantly lower than those in the remainder of the east. This may be due to the later springs and resulting poorer food supply (Campbell et al. 1997; Eiserer 1979; Graber et al. 1971; Howard 1967; Howe 1898; Howell 1942; Klimstra and Stieglitz 1957; Knupp et al. 1977; Tardif and Lanoue in Gauthier and Aubry 1996; Tyler in Bent 1949; Vanderhoff et al. 2020; Young 1955).

The age at first breeding is 1 year and breeding occurs every year thereafter. The mating system is monogamous although there are a few anecdotal incidents that suggest polygyny. Birds typically remain mated throughout a breeding season but mates are quickly replaced if one dies. Divorce occasionally occurs during a breeding season. Returning members of a pair usually do not reunite, but remating in subsequent years occurs occasionally. In Wisconsin, only 1 pair of 18 (5.6%) remated the following year. Both returned in the third year but selected different mates. None of 18 pairs returning to the Kingston area remated. In Maryland, 1 of 8 returning pairs remated. To remate, both birds need to be faithful to their previous territory and arrive at approximately the same time in spring (Brackbill 1952a; Howell 1942; Vanderhoff et al. 2020; Weatherhead and McRae 1990; Young 1955). Over 2 seasons in Illinois, 62% and 72% of broods contained at least 1 offspring from an extra-pair copulation, and as many as 48% of young were the result of an extra-pair fertilization (Vanderhoff et al. 2020).

Young begin to peck at the ground at age 20 days but are not effective in obtaining food. By age 24-30 days, juveniles are capable of capturing prey. Adults move less, spend less time foraging in shaded areas, and capture more worms on wet surfaces and after rain than juveniles. Adults were more successful at capturing arthropods than juveniles. Juveniles only captured worms in the most saturated soils. Both age groups spent more time foraging in the most saturated soils: 59.3% for juveniles and 45.5% for adults. In Kentucky, juveniles were successful in picking mulberry fruit only 23% of the time compared with 69% for adults (Brackbill 1947b; Vanderhoff and Eason 2008a, 2008b). The robin exploits 3 primary food resources: invertebrates on the ground, fruit in trees and shrubs, and invertebrates in trees and shrubs. While foraging on arthropods in foliage, it tends to sit and wait to observe and capture prey. On the ground, it wanders and actively seeks prey. It may bill-sweep to move litter to find prey. Lawns are a preferred foraging substrate where it captures

earthworms visually. Progressively less time is spent foraging on lawns as the grass grows taller. Robins consistently selected short grass when offered a choice between tall and short lawns (Clark 1983; Eiserer 1980; Heppner 1965; Morton 1968; Paszkowski 1982). It selects larger fruit; mean widths of fruits consumed were 3.7-9.0 mm in diameter, all below the main gape width of the robin (White and Stiles 1991). In a laboratory, the robin selected fruits with the highest percentages of protein. It significantly preferred fruits of autumn olive and multiflora rose to those of native plants. Some fleshy-fruited invasive plants may receive more dispersal service from the robin than native plants with similar fruits (Lafleur et al. 2007). There are 2 groups of fruits: those that are high in sugars relative to lipids and those high in lipids relative to sugar. Sugar-rich fruits are common throughout the fruiting season and lipid-rich fruits are common from late summer through early winter. It selected sugar-rich fruits in both summer and autumn. There was only a slight (6%) increase in the consumption rate of sugar-rich fruits from summer to autumn but a more substantial (46%) but nonsignificant increase in consumption of lipid-rich fruits. Energy assimilation did not change seasonally for sugar-rich fruits but increased for lipid-rich fruits from summer to autumn. Birds obtained more energy from the same fruit in autumn than earlier which may be important in preparation for migration. Robins tended to prefer red to purple fruits in summer and had no colour preference in autumn (Lepczyk et al. 2000). The nutritional value of fruit may be increased by selecting those that are infested with insects (Vanderhoff et al. 2020). The robin may defend food resources when they are scarce. A single robin successfully defended a crabapple tree against flocks of 2-15 Cedar Waxwings and also a Purple Finch and Blue Jay over a 2-week period in spring. Later, when the waxwing flock increased to 30-36 birds, the robin was no longer capable of defending the food supply (Pietz and Pietz 1987).

Adults split the territory roughly in half when collecting food for nestlings. They tend to bring young larger prey items than they consume themselves. Near Kingston, the percentage of food provided to nestlings in May was 38% worms, 33% caterpillars, 11% beetles, 5% millipedes, 4% hymenopterans, 3% odonates, and 2% each for snails, isopods, and spiders. The percentages in June were 37% caterpillars, 22% beetles, 14% worms, 12% orthopterans, 6% hymenopterans, 4% spiders, 3% odonates, and 2% millipedes. In some areas, nestlings are fed mainly cutworms. In Illinois, food brought to nestlings consisted of 50% caterpillars, 29% earthworms, 7% ants, 6% flies, and small percentages of adult lepidopterans, beetles, and millipedes. In New York, young were fed earthworms, grubs, fruit, caterpillars, grasshoppers, cutworms, June beetles, crickets, insect larvae and adults, and spiders as well as large numbers of crane flies and ripe cherries. The food of 15 young aged 3-35 days consisted of 70.2% animal matter and 29.8% plant matter. Animal food consisted of 44.1% insects, 15% earthworms, 3.1% millipedes, 2.3% spiders, 1.7% isopods, and a trace of pseudoscorpions. The insects included 24.7% caterpillars, 11.6% beetles (ground, soldier, click, pill, darkling, and scarab beetles plus weevils), 4.9% short-horned grasshoppers, 3.2% ants and ichneumonid wasps, and 0.5% bugs. Plant material consisted of 19.5% grass blades, stems, and roots; 3.2% mulberries; 2.4% honeysuckle seeds; 0.5% aster family seeds; and traces of strawberry seeds, clover leaves, and plantain seeds. The grasses may be brought along with other food and ingested incidentally. Nestlings 5-7 days old were fed exclusively green darners (a large dragonfly) in 1 afternoon. Earthworms were scarce in this area which may have explained the unusual diet. Nestlings in an October Missouri nest were fed hawthorn fruits. There are several accounts of young

being fed small garter snakes and a red-bellied snake; adults have been seen consuming a 20-25 cm ribbon snake and attacking a red-bellied snake (Burton 1963; Gardali and White 2003; Graber et al. 1971; Gullion 1950a; Howell 1942; James 2011; Johnson et al. 1976; Keast 1990; Kilham 1958; Richmond 1975; Tyler in Bent 1949; Vanderhoff et al. 2020; Whitford 1998).

Beal (1897a) analyzed the contents of 330 robin stomachs collected in the United States. The diet consisted of 42% animal matter and 58% vegetable matter, predominantly small fruits or berries. Nineteen percent of the diet consisted of beetles and about one-third of them were ground beetles. Grasshoppers constituted 10% of the annual diet but over 30% of the August diet. Caterpillars represented 6% of the diet. The remaining animal food consisted of a variety of insects with a few snails, spiders, and earthworms. Of the 58% plant material in the diet, 47% was wild fruit and 4% was cultivated fruit. Cultivated fruit was eaten predominantly in June and July; wild fruits were consumed year round. Forty-one species of fruit were eaten with the most important being 4 species of dogwoods, 3 of cherries, 3 of wild grapes, 4 of greenbriers, 4 of sumacs, and 2 of elderberries, plus cranberries, huckleberries, blueberries, juneberries, and hackberries. It also ate some seeds. Wheelwright (1986) summarized contents of robin stomachs in 3 geographic areas. The eastern area included the Atlantic states and coast westward to Ontario and Minnesota in the north and Louisiana in the south. The robin was documented eating fruit of at least 51 genera and 28 families; 34% of fruit consumed belonged to the rose family. Twenty percent of food items consisted of cherries; 5% were raspberries. Also important were sumac and poison ivy (10%), grape (6%), and dogwood (5%). Invertebrates were represented in the diet by 107 families and 14 insect orders. Beetles occurred at a frequency of 40%. Important beetles were ground beetles (10%), weevils (8%), and scarab beetles (7%). Beetles were followed in frequency by lepidopterans (13%) and hymenopterans (9%), with these 3 orders accounting for more than half of food items. Lepidopteran prey was almost exclusively caterpillars. Adults were most frequently eaten in other orders, although it occasionally ate larval scarab beetles. Caterpillars and earthworms were likely under-represented in the samples due to their rapid digestion. In the northeast, fruit from at least 37 plant genera and 12 families was eaten and the robin preyed upon invertebrates of 72 families and 12 orders of insects. The most common fruits eaten were those of the rose (43% of fruit records), dogwood (12%), heath (19%), and sumac and poison ivy (7%) families. Invertebrates most commonly consumed were ground beetles (9% of invertebrates), ants (8%), weevils (7%), scarab beetles (6%), and click beetles (6%). Fruit and sumac was eaten in every month. Sumac was most prevalent in the diet in spring, fruits of the rose family dominated the fruit diet in mid- to late summer and were replaced by dogwoods and grapes in autumn. Within the rose family, cherries and raspberries were commonly eaten in June, July, and August; hawthorn fruits were eaten in late autumn and again in spring. During autumn and early winter, 80-99% of the diet consisted of fruit; the change in diet was abrupt, climbing from less than 10% to more than 80% in 1-2 months. Fruit was most commonly eaten in autumn (96%), followed by winter (93%), summer (66%), and spring (6%). Four to 6 taxa of fruit occurred in the diet during the breeding season compared with 2-3 in winter. There was no difference in the diet of the sexes. Stomachs of juveniles contained a higher proportion of fruit than those of adults. Stomachs contained different proportions of fruit depending upon habitat. The proportion of fruit consumed was highest in orchards (96.0%), native fruiting trees (90.0%), and forests (80.0%) than in agricultural lands (10.5%). Birds in meadows and edge habitats ate

intermediate amounts of fruit: 60.0% and 31.0%, respectively. Habitat differences in fruit consumption were greatest in spring and early autumn. In August, the amount of fruit eaten began to become similar among habitats and by October birds collected in all habitats ate 80-99% fruit. Beetles were eaten most frequently in open habitats (fields and lawns) and infrequently in edge habitats; the reverse was true for hymenopterans and lepidopterans. It preyed upon bugs more than expected in forested habitat and less than expected in open habitats. In Illinois, the robin fed almost exclusively on invertebrates in spring. The most frequent prey items were earthworms and march fly larvae early in the spring. Later in spring, cutworms, tussock moth egg masses, ground beetles, and click beetle larvae became prevalent in the diet. It also ate cankerworms and cicadas. In June, it switched to a predominantly fruit diet, and fruit was important through summer and autumn. Dominant fruits in the diet in late summer and autumn were grape, black cherry, Virginia creeper, hackberry, dogwood, multiflora rose, pokeweed, elderberry, and red cedar. Other fruits commonly eaten were those of mountain-ash, sumac, barberry, bittersweet, holly, snowberry, pear, apple, and greenbrier (Graber et al. 1971). Breiding (1946) reported the robin eating Canada moonseed fruit. In a New York residential area, Hamilton (1940) analyzed 700 fecal samples collected from late June to early July. The frequency of occurrence was 80.1% for animals and 73.1% for plant material. Animal matter consisted of 74.1% insects including 38.4% hymenopterans (mostly ants), 11.3% beetles (mostly weevils and leaf beetles), 6.9% lepidopterans (mostly cutworms), 5.6% orthopterans, 0.7% lacewings, 0.7% bugs; 3.4% spiders; 3.3% molluscs; 0.6% earthworms; and 0.4% centipedes. Frequency of fruits consumed was 58.2% chokecherry, 40.0% Allegheny blackberry, 21.1% red raspberry, 17.0% pin cherry, 11.7% black cherry, 8.3% honeysuckle, 5.9% nightshade, 2.4% Canada juneberry, 1.3% strawberry, and 1.1% red currant. In Nova Scotia and eastern Canada, the robin is considered the most important consumer of lowbush blueberries (Crossland and Vander Koet 1996). In an Illinois forest, 100% of robins ate fruit, and all fruit was consumed in forest gaps. In the first year, 58% of frugivory was on grapes and 42% was on Virginia creeper; the following year, 81% was on grapes, 13% on pokeweed, and 6% on Virginia creeper. It was not observed feeding on elderberries, poison ivy, greenbrier, moonseed, or spicebush. It strongly favoured isolated grape plants for foraging and was the most important species for dispersal of grape (Malmborg and Willson 1988). Stutchbury et al. (2005a) studied its frugivory on red elderberry in forest gaps in Pennsylvania. It was observed foraging at only 5.9% of sites on 1.9% of visits. The low level of frugivory probably reflected the low abundance of the robin in the study area. In New Jersey, it commonly fed on the fruit of winged sumac, red cedar, multiflora rose, fox grape, spicebush, black gum, apples, pears, and viburnums (White and Stiles 1991). Near Ithaca, New York, preferred fruits were those of northern arrowwood and spicebush. Changes in fruit consumption occurred seasonally even for captive birds when offered constant food quality and abundance (Wheelwright 1988). Jung (1992) offered captive robins choices between white mulberry, bella honeysuckle, and red-osier dogwood. Thirty-five birds ate 318 mulberries, 150 dogwood fruits, and only 28 honeysuckle berries. Some birds showed a preference for 1 species of fruit: 15 ate mostly mulberries, 2 ate mostly dogwood, and 0 ate mostly honeysuckle. Unusual food items that have been reported in the robin's diet include skinks, snakes, mice, shrews, trout fry and other fish, and damselfly nymphs (Eiserer 1976; Tyler in Bent 1949; Vanderhoff 2007; Vanderhoff et al. 2020). In New Brunswick, there was no relationship between the abundance of the robin and spruce budworm numbers (Morris et al. 1958). Over 2 years in Maine,

spruce budworm larvae and pupae constituted 23.7% and 29.1% of the robin's invertebrate diet (Mitchell 1952).

The American Robin and Cedar Waxwing eat many of the same fruits, but the robin consistently eats less fruit throughout the year. Cherries were the most common fruit in the diet of both species in summer and autumn and the relative consumption of cherries was also similar. During winter and spring, robins ate fewer red cedar berries than waxwings, and waxwings did not eat sumacs. In autumn, 4 species of dogwoods were prominent in the robin's diet, but the waxwing ate only flowering dogwood berries. The 2 species showed strong differences in their selection of insect orders and ate different families of beetles and bugs. The most terrestrial insects eaten by robins, stink bugs and ground beetles, were not eaten by waxwings (Witmer 1996a). In Michigan, robins visited cherry orchards less frequently than waxwings (on 6% of days compared with 21% of days for waxwings). Robins visited orchards a mean of 2% of daylight hours compared with 5% for waxwings. The difference in times spent within orchards by the 2 species was probably a reflection of their diets. Robins consume larger proportions of invertebrates and prefer lipid-rich fruits; waxwings prefer sugary fruits such as cherries (Eaton et al. 2016).

The reported percentage of robins' nests that are parasitized is very low but the robin is a known rejecter of cowbird eggs. The female cowbird typically removes a robin's egg when laying one of her own. Even if the robin ejects the egg, there is a decrease in productivity because robins do not replace single eggs that are lost. When a cowbird successfully parasitizes a nest, robins are usually capable of fledging their own young as well as those of the cowbird. In Ontario, 17 of 6,004 nests (0.3%) were parasitized and 0.1% of 4,522 British Columbia nests were parasitized. Other reported parasitism rates are 0.25% in Illinois, 0.8% in Ohio, 0.5% in Louisiana, 4.3% in Oklahoma, and 40% in Kansas. The sample size was only 5 nests in Kansas, but parasitism rates are higher there than reported elsewhere (Campbell et al. 1997; Graber et al. 1971; Hodges 1949b; Howard 1967; Howell 1942; Leighton et al. 2002; Lowther 1991; Peck and James 1998a; Rasmussen et al. 2009; Rothstein 1975; Vanderhoff et al. 2020; Wolfe 1994).

The robin is vulnerable to the effects of a wide range of environmental contaminants and can be useful as an indicator of chemical pollution. Starting in the 1950s, severe die-offs and reduced reproductive success occurred due to spraying of DDT in an attempt to control Dutch elm disease. DDT was also widely used in orchards until the late 1960s. It takes 10-17 years for robin populations to return to pre-DDT levels. The robin is poisoned primarily by residues in earthworms. DDT may continue to cycle from the soil through earthworms to robins for as long as 30 years after a single application. In New York orchards where DDT had been applied as recently as 7-8 years previously, robins produced significantly smaller clutches and raised fewer nestlings than robins from the same area during the pre-pesticide era. Robins did not forage in areas that had received direct spray, possibly due to the scarcity of earthworms. In British Columbia orchards, robin eggs contained 18-3,500 times more DDT and 4-100 times more DDE than eggs of other species. Orchard-nesting robins had significantly higher concentrations of trans-monochlor, heptachlor epoxide, and PCBs than robins nesting in other habitats. Earthworms appeared to be the major source of contamination. Contaminant levels in the Niagara Peninsula of Ontario are lower than those in British Columbia, probably due to the species of earthworms that are present. One of the dominant

earthworms in Ontario is the common earthworm which burrows as deep as 1 m and thereby dilutes contaminant burdens. Despite high levels of contaminants in British Columbia orchard-dwelling robins, they were capable of surviving and successfully rearing broods. DDT was sprayed on a Wisconsin university campus from 1959 to 1961. More than 340 dead birds were collected during this period, and at least 232 were robins. Mortality occurred mostly in birds with a minimum of body fat and those that ate highly contaminated food. Birds collected later in spring had higher fat reserves and tolerated higher levels of contamination before succumbing. In Maine where DDT was used to kill spruce budworms, arriving birds contained burdens of DDT accumulated on the wintering grounds and most also carried mirex which was used to control fire ants in the south. Of 20 birds sampled in sprayed areas, only 2 did not carry higher burdens of DDT than those in unsprayed areas. Females transferred a significant amount of their contaminant burden to the eggs. Contaminated food in sprayed areas maintained residue levels in females but residue levels declined in females in unsprayed areas. Residues in eggs (14.8 µg) were passed on to nestlings (9.6 µg) and fledglings (7.7 µg) in unsprayed areas. In sprayed areas, residues accumulated significantly from eggs (23.9 µg) to nestlings (29.5 µg) to fledglings (110.4 µg). No influence of pesticides on reproduction was noticed. Adults collected in August from the sprayed area had about the same amount of residues as spring migrants. The rapidity at which pesticides were eliminated when uncontaminated food was available was important. DDT was sprayed on the Iowa State University campus in an attempt to control Dutch elm disease. This resulted in a gradual loss of breeding robins. Annual production declined to a total of 1-3 fledglings, although there were originally as many as 47 nests on campus. Following a switch from DDT to methoxychlor, a significant increase in number of nests and young was observed, although some mortality continued. In Illinois, 85-90% of a population was eliminated following an application of heptachlor. The following year, the population had only recovered by 5% but was back to 75% the second year. Spraying of dieldrin in Illinois resulted in high mortality, probably due to consumption of dead earthworms. Robins in urban areas tend to accumulate higher levels of lead than those in rural areas, but at levels lower than those considered toxic. This difference may not be so great since leaded fuel has been banned. In 1972, 10,000 robins were killed in a field that had been treated with Azodrin® near Homestead, Florida. Treatment of Quebec lawns with insecticides (chloropyrifos) resulted in decreased productivity. Other chemicals known to cause robin mortality are carbofuran, hydrogen sulphide, furadan, famphur, nemacur, cyanide, dursban, fenthion, chlordane, and carbamate and organophosphate pesticides (Elliott et al. 1994; Graber et al. 1971; Hunt 1969; Johnson et al. 1976; Knupp et al. 1976; Tardif and Lanoue in Gauthier and Aubry 1996; Vanderhoff et al. 2020; Weller 1971).

Late spring storms may cause mortality of robins, even when there is sufficient food available. A late storm in the spring of 1933 in the Mackenzie Delta killed virtually all robins, and it was still scarce 2 years later. Snowstorms early in spring may cause mortality even in more southern locations, such as Illinois. Periods of prolonged or heavy rain may kill nestlings. During a severe Michigan cold front in March, robins fed on frozen earthworms stuck to concrete and on a moribund luna moth (Graber et al. 1971; Johnson et al. 1976; Porsild 1943; Royall 1995).

First nests are only about half as successful as second nests. In New York, 32% of first nests fledged young compared with 55% for second nests. There are a number of inter-related factors

that lead to lower success early in the season. The robin selects coniferous trees over deciduous trees early in spring, but nesting success is much lower in conifers: 18% in conifers compared with 52% in deciduous trees in Maine. Coniferous trees are more likely to attract red squirrels, a nest predator. In Minnesota shelterbelts, nest success was 40% where squirrels were present and 67% where they were absent. Other factors that may contribute to low success rates of early nests are relative scarcity of food and weather that may result in nests falling or mortality of nestlings. Many early nests are conspicuous prior to leaf-out and may be more susceptible to predation. In Iowa and Illinois, nest success was 69.0% in rural areas and 32.7% in urban areas with the difference apparently due to predation by cats (Graber et al. 1971; Howell 1942; Klimstra and Stieglitz 1957; Knupp et al. 1977; Yahner 1983).

Habitat loss is currently not a limiting factor for the robin. Forest fragmentation, selective logging, clear-cutting, fires, and urbanization are all beneficial. It is one of few species that thrives in urban areas where it may occur at higher densities than in natural habitats. In North Carolina, its abundance increased significantly with increasing numbers of houses and buildings within 200 m of the centre of the forest patch (Lumpkin and Pearson 2013). Along the Michigan shoreline of Lake Superior, it was significantly more abundant on developed cottage lots than in contiguous forest on the other side of the road (Ford and Flaspohler 2010). Although the robin thrives in urban areas, modern subdivisions may be marginal habitat or even unsuitable for it. Houses are built at very high densities with tiny lawns and few trees, so nest sites and foraging areas are limited.

In deciduous forests in southeastern Ontario, robin density, pairing success, and nest success were unaffected by habitat characteristics within 100 m of nests. The amount of forest cover within 2 km was positively associated with its productivity and the amount of intensive agriculture within 2 km was positively correlated with its density and productivity. Early in spring, it was often observed foraging for earthworms and other arthropods in bare soils in agricultural land. The amount of intensive agricultural land surrounding forest fragments could influence where males establish territories by providing them with an early spring source of food (Richmond et al. 2012).

In many studies on the effects of selective timber harvesting, there were no significant differences in abundance of the robin in uncut areas and where varying degrees of harvesting had taken place. In Vermont, the robin occurred equally in forests and adjacent clear-cuts. In Newfoundland, it was insensitive to the effects of clear-cutting; 63% of robin captures were in clear-cuts. In the Boreal Forest Region, a 50% increase in its abundance resulted when as many as 70% of trees were removed. In northern hardwoods near Sault Ste. Marie, it was more abundant in forests that had been selectively thinned than in uncut forests. In the Carolinian Forest Region, it preferred recent cuts in forests over old cuts, with heavier cuts most preferred. In British Columbia, it often increases after clear-cutting or fires, with numbers increasing once tree heights reach 1 m and declining once trees become 10 m tall. In South Dakota, density of breeding robins was 6.0-19.8 times higher in very small fragments of woodlands than in large riparian forests and there were no differences in survival rates in fragmented and contiguous forests (Campbell et al. 1997; Gentry et al. 2006; Hanowski et al. 2003, 2005; Holmes and Pitt 2007; Holmes et al. 2004; Howell 1942; Lent and Capen 1995; Medin and Booth 1989; Vanderwel et al. 2007; Whitaker et al. 2008). In the Ontario Canadian Shield, there was no difference in its abundance in early and mid-successional clear-cuts

compared with similarly aged stands after fire. It was equally abundant in mid-successional and mature stands but significantly more abundant in early successional than mature stands (Zimmerling et al. 2017).

Forest fragmentation is generally beneficial to the robin, but it may promote invasion by nonnative shrubs. Nests built in common buckthorn and nonnative honeysuckles experienced higher predation rates than those in native shrubs (hawthorns and viburnums) and in native trees. Increased predation rates in nonnative shrubs may be due to a combination of lower nest heights, absence of sharp thorns, and perhaps a branch architecture that facilitates predators. Invasion by nonnative shrubs may result in a decrease in nest success (Schmidt and Whelan 2000). In Chicago, its abundance was positively correlated with litter and negatively correlated with cover by nonnative honeysuckle species and invasive shrub stem density (Schneider and Miller 2014).

In Pennsylvania and New Jersey over a 15-year period, hemlock declined from 56% of the total basal area to 46% due to the hemlock woolly adelgid, and the coverage by deciduous shrubs increased. The robin increased in these woodlots, probably due to the increased shrub coverage and more open canopy (Toenies et al. 2018).

The common house mosquito preferentially feeds on robins. This mosquito is the vector for the West Nile virus. Robins are a key reservoir for the disease and are responsible for spreading it in the summer months. Regional declines in the robin in Massachusetts, Maryland, and Minnesota may be due to the West Nile virus.

The robin responds to light pollution by initiating singing earlier in the morning, as early as 255 minutes before civil twilight in the brightest areas. The consequences of earlier singing in brightly lit areas were uncertain. The longer period of singing could potentially reduce survival if energy demands or predation risks were elevated. Conversely, light pollution might increase productivity if robins can forage or seek mates during longer periods of time. Nestling growth rates might also be enhanced due to the longer feeding period (Miller 2006).

In Alberta, the robin was equally abundant at noisy compressor stations and quiet well pads. It exhibited no response to chronic noise (Bayne et al. 2008). It was significantly more abundant along pipelines and at well pads than in adjacent forest interior; it was equally abundant along seismic lines and in adjacent forest interior (Bayne et al. 2016). In West Virginia, it was significantly more abundant at well pads, access roads, and pipelines than distant from these features (Farwell et al. 2019).

The robin is vulnerable to being killed on roads by vehicles. In British Columbia, it is one of the most road-killed species. It is also vulnerable to flying into windows when flocks feed in vegetation near windows (Campbell et al. 1997; Vanderhoff et al. 2020).

Bird feeders that are maintained during the breeding season have the potential to reduce the reproductive success of the robin. Ohio neighbourhoods with at least 15 feeders had 2.7 times more American Crows and 3.2 times more Brown-headed Cowbirds than neighbourhoods with 3 or fewer feeders. In neighbourhoods with the most feeders, fewer than 1% of nests were expected to survive until fledging compared with 34% in neighbourhoods with few feeders (Malpass et al. 2017).

Becker and Weisberg (2015) studied the effects of spring temperatures on the robin in Nevada. Nest success was significantly correlated with temperature, with nestling survival increasing by 12% for every 1°C above baseline temperatures. Moderate warming of spring temperatures as a result of climate change may be beneficial to the robin.

Status

The robin has always been abundant in Ontario. McIlwraith (1894) reported that great numbers nested throughout the province. Baillie and Harrington (1937) considered it one of the most common and widely distributed bird species in Ontario. It nested everywhere in the province north to at least Moose Factory and the Severn River but was uncommon between latitudes 53-54º N along the Manitoba border. It was most common near habitation and comparatively scarce in large areas of northern Ontario. During the first atlas, it was found in virtually every square in southern Ontario and in most blocks in the north (James and Long in Cadman et al. 1987). James (1991) considered the robin abundant in residential and agricultural areas and uncommon in forested areas throughout the province.

The second atlas demonstrated that the distribution of the robin had not changed since the first atlas; in essence, it inhabits the entire province. It was confirmed as a breeder in every square in the Carolinian Forest Region and most squares in the Great Lakes–St. Lawrence Forest Region. Probable or confirmed breeding was reported from every block in the Boreal Forest Region and the Hudson Bay Lowland. Its probability of observation did not change province-wide between atlases, but significant increases were recorded in the Boreal Forest Region and Hudson Bay Lowland. It was most abundant south of the Canadian Shield. Densities were much lower in the remainder of the province, with localized areas of higher density associated with towns, cities, and agricultural areas (Burke in Cadman et al. 2007).

The robin is probably many times more abundant in Ontario and North America now than it was prior to European settlement. Forest clearing, fragmentation, and urbanization created better habitat. In addition to modifying habitat to the benefit of the robin, settlers inadvertently introduced earthworms and a new food supply (Graber et al. 1971; Pitts 1984; Tyler in Bent 1949; Vanderhoff et al. 2020).

Breeding Bird Survey data indicate that the robin increased at an annual rate of 0.051% in Canada and decreased at an annual rate of 0.503% in Ontario 1970-2021. From 2011 to 2021, it decreased at annual rates of 0.569% in Canada and 3.07% in Ontario. All results were highly reliable, except for the long-term Canadian results which were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Usually young cannot fly when they leave the nest, but are able to fly about 2 days later. Fledged young are dependent on the adults for 3-4 weeks after leaving the nest. In Maryland, young first attempted to feed themselves 20 days after fledging, but remained partially dependent until 28-31 days after fledging (Brackbill 1947b; Howell 1942; Young 1955). Near Kingston, adults commonly cared for some young more than others. Males were associated with fledglings more than females because the female typically initiated another clutch. By 3 weeks after nest departure, both adults were largely free of caring for the young, although some young were fed 26 days after fledging. The

female provides care to the young until she starts incubating the next clutch (Weatherhead and McRae 1990).

In Wisconsin, maximum distances from the nest by time after fledging were: 0 days, 46 m; 1 day, 69 m; 2 days, 73 m; 3 days, 119 m; 10 days, 160 m; 14 days, 389 m; 28 days, 1.46 km; and 31 days, 1.65 km. One young was seen near the study area 89 days after leaving the nest (Young 1955). Near Kingston, some young flew in excess of 50 m 2 days after fledging, but most only showed a gradual expansion of their range (Weatherhead and McRae 1990). In Massachusetts, most juveniles were still near their parents' territory or within 160 m of the nest 3 weeks after fledging. Between 4 and 6 weeks, most had moved only 320 m from the nest. After 8 weeks, 27% remained within 320 m of the nest; 33% had moved 800 m or further away. Young stayed an average of 14.5 days near the nest (range 5-32 days). Time spent near the nest may vary by individuals within a brood. In 1 brood, 2 young left after 13 days and the third remained 32 days. In another brood, 3 young remained 8, 11, and 22 days. In this area, 63% of robins captured in a cherry orchard were juveniles; 90% were juveniles in an area of blueberry plantings. Juveniles concentrated in orchards where there were cultivated cherries, blueberries, and wild blackberries; and a tree nursery with cultivated blueberries and wild tartarian honeysuckle and black cherry. The presence of these food sources may have limited dispersal distances of birds. The 2 feeding areas were 1.1 km apart; only 7.1% of fledglings were observed at both sites. Foraging sites each had an area adjacent to them that was suitable for loafing during hot days. Loafing sites were in small stands of coniferous or deciduous trees with a closed canopy and very little undergrowth. Flocks of fledglings remained intact as long as the food source persisted. There was very little interchange of individuals among flocks. After the fruit was depleted, some young remained, others disappeared entirely, and a few were seen 1.6 km away. Seven of 106 fledglings (6.6%) were seen more than 1.6 km from the nest during the summer. One traveled 9.0 km but the remainder moved less than 4 km. Only 6% of 93 juveniles and adults were seen at more than 1 roost. The average distance from the nest travelled by 9 juveniles in October was 500 m. Two were within 160 m and 1 moved 3.7 km (Hirth et al. 1969). In Washington State, juveniles consistently used heavy- to medium-developed urban and residential areas more than expected by availability. Forest cover was used less than expected. Areas with high road densities were used significantly less than expected by fledglings and more than expected by juveniles. High use of urban habitats was most pronounced in landscapes where urban cover was least common. Urban habitat may be preferred because of the abundance of worms in lawns. Of the species studied, the robin had the largest home range of 259 ha, the highest proportion of urban cover (46%), and the highest road density (0.4 m/m^2) in its home range (Whittaker and Marzluff 2009). In Michigan, Akresh et al. (2009) captured 100% of juveniles in riparian forest and none in upland forests. In Ohio, Vitz and Rodewald (2007) captured 32 juvenile robins in regenerating clear-cuts suggesting that they may seek out dense cover in the postbreeding period. In Minnesota, Streby et al. (2011b) captured only a single robin in regenerating clear-cuts during the breeding season, but captured 9 adults and 9 fledglings during the postbreeding period.

In the postbreeding period, adults may seek denser cover. On a Tennessee university campus, birds moved out of the study area in mid-August to moult in more heavily wooded areas (Pitts 1984). In Ohio, Vitz and Rodewald (2006, 2007) reported adult robins in regenerating clear-cuts. Home

ranges of adults increased in the postbreeding period near Kingston. Adults foraged in an average area of 1,472 m² during the nestling period and 8,080 m² during the fledgling stage. Adults and their fledglings had broadly overlapping home ranges during the fledgling stage even though fledglings from the same nest were seen together on only 23% of observations (Weatherhead and McRae 1990).

MIGRATION

The robin is predominantly a diurnal migrant but some nocturnal migration occurs. In spring, there are more morning than evening flights; the reverse is true in autumn. Of 533 recoveries of Ontario and Quebec robins, 85% were re-encountered within these provinces, with nearly all recoveries between March and October and 76% between April and July. Birds banded or encountered from December to February were nearly all found in the Carolinas and Gulf Coast states east of Texas. A single record from Mexico and 2 from Texas indicate that a few Ontario and Quebec birds winter further west. Recoveries in the Detroit to Chicago area suggest that robins may cross in the Sarnia area (Brewer et al. 2018; Graber et al. 1971; Speirs 1953; Vanderhoff et al. 2020). Since the 1990s, more robins have adapted a nonmigratory strategy and travel less than 100 km from their breeding areas, possibly in response to climate change (Vanderhoff et al. 2020).

In spring, the robin tends to follow the advance of the isotherm of average daily temperature of 2.8ºC. Males arrive before females who may join the males within a week (Graber et al. 1971; Howe 1898; Howell 1942; Tyler in Bent 1949). In the south, the first spring migrants usually appear in late February or early March with a few arrivals in mid-February. Migrants continue to move through in late April and early May, even after local birds have been nesting for some time. In the southern Shield, average arrival is around the third week of March. By early to mid-September, robins are migrating south in the Hudson Bay Lowland. Most pass through central Ontario in late September and the first half of October, but it is often seen into mid-November; some occasionally persist into December or beyond. In the south, migration peaks in October and most are gone by 15 November except for those that overwinter. Autumn migration is conspicuous along the Lake Erie shoreline at Elgin County hawk watches, where peaks occur near the end of October (Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008; Wilson and McRae 1993).

During migration, the American Robin occurs in a wide variety of habitats and is more likely to be detected in fragmented than contiguous habitat. In spring, it forages mostly in grasses; it inhabits woody areas much more in autumn. During spring migration in Pennsylvania, it was 4 times more likely to be observed in shrubs than in forest. During migration in the Yukon, it is especially common in wetlands. Spring migrants there forage on mudflats alongside flocks of shorebirds and waterfowl. In British Columbia, migrants occur primarily in fields, open woodlands, edges, and rural and suburban areas. Flocks occur in almost any open, grassy, or bare-soil area that provides foraging opportunities. It also forages on intertidal mudflats during low tide. Favoured habitats include pastures, fields, park lawns, golf courses, open swamps, meadows, school yards, beaches, agricultural areas, suburbs, logged and burned areas, along open riverbanks, and in open forests along lakeshores and marshes. During spring migration in Minnesota and Wisconsin, it was observed more frequently in floodplain forests than in upland forests, but the difference was not significant. In Kansas, where it is warm in autumn, robins congregated on cooler, moister, northern slopes where

grapevines were more abundant. While the weather was warm and deciduous trees still retained leaves, it tended to stay in well-shaded areas in thick woods (Campbell et al. 1997; Fitch 1958; Graber et al. 1971; Keller and Yahner 2007; Kirsch et al. 2013; Sinclair et al. 2003; Smith and Hatch 2008).

Food preferences during migration typically dictate what habitats are used. In spring, lawns and short grassy areas are selected because they provide earthworms and a variety of other arthropods. In New York, robins foraged on rotten apples in an orchard during spring migration. In autumn, areas supporting large amounts of fruit are selected such as orchards, open fields and edges with pokeweed and grapes, vineyards, commercial blueberry farms, and residential areas with fruit-bearing ornamental shrubs. In British Columbia and the Yukon, important fruits during autumn migration include mountain-ash, juneberry, balsam poplar buds, holly, arbutus, and crabapples. In Algonquin Park, fruits of wild raisin and winterberry holly are important. During autumn migration in New York, approximately 13% of fecal samples contained bella honeysuckle fruits; 37% contained common buckthorn fruits. Fruits of red-osier and gray dogwood were available but apparently not consumed. It has been documented eating sunflower seeds and grubs in a household compost pile (Campbell et al. 1997; Fitch 1958; Johnson et al. 1976; Mudrzynski and Norment 2013; Sinclair et al. 2003; Tozer 2012).

McClure et al. (2013b) created a phantom road by playing traffic noise in an undisturbed forest during autumn migration. Abundance of the robin declined with noise intensity. Eight robins were present on average when the noise level was about 36 dB(A) compared with 1 at 57 dB(A). Robins appeared to be avoiding the noise, and it was assumed that they would be less frequent near roads than in quieter areas. In Alberta, robins exhibited no response to noise (Bayne et al. 2008).

The robin is an abundant migrant in Ontario, with many daily counts of 1,000-10,000 (Curry 2006; James 1991; LaForest 1993; Lancaster et al. 2004; Weir 2008).

WINTER

Speirs (1953) examined the winter distribution of the robin east of the Rocky Mountains. Recoveries of Ontario birds in winter were predominantly south of latitude 37ºN. Its greatest abundance occurred between latitudes 30-35ºN, with extensions into eastern North Carolina and central Tennessee, and south into the Florida peninsula and wooded regions of southeastern Texas. Most occurred between the 4.4ºC and 15.6ºC isotherms with only about 6% of the population north or south of this area. The 4.4ºC isotherm corresponds well with the northern boundary of the region in which fewer than 15 days per winter have continuously freezing weather. In this area, it can probably find unfrozen ground and animal food. Robins from all latitudes of the breeding range winter in the same average latitude of 32ºN. Root (1988) stated that it avoids areas where the average minimum January temperature drops below –15ºC and areas that receive less than 20 cm of precipitation annually.

During winter, the robin inhabits areas with more trees and denser cover than at other times of the year, and presence of abundant fruit is a requirement. In Presqu'ile, it favours dense brush in winter, such as stands of white cedar or where fruits of common juniper or red cedar are abundant (LaForest 1993). Smith (2003) analyzed Ontario Winter Bird-Population Study results. Densities of robins per km^2 by habitat were 6.9 in urban natural areas with water, 2.1 in urban natural areas

without water, and 0.1 in small urban natural areas. It was not documented on counts in farm or rural habitats. Doherty and Grubb (2000) studied winter use of forest fragments (0.05-6.01 ha) by robins in Ohio. Density decreased from early to mid-winter and as woodlot edge increased, as shrub coverage increased, and with increasing connectivity to other woodlots. In 1906-07, the primary habitats used by wintering robins in Illinois were picked cornfields (with the stalks remaining), forests, and orchards. In 1956-58, the habitats used most frequently were shrubby areas, forests, and pastures (Graber and Graber 1963). In Arkansas, Kentucky, and Mississippi, it was less common in row-crop fields with buffers of native grasses and forbs than in fields without buffers, but not significantly (Evans et al. 2015).

Winter roosts are important and are often in evergreens such as junipers, small pines, cedars, and magnolias (Speirs 1953). Tyler (in Bent 1949) reported winter roosts in common reed in marshes in Missouri. Curry (2006) reported an early winter or late autumn roost on the south shore of Cootes Paradise (supporting 614 birds), but did not specify the habitat.

The robin may be territorial in winter, but food resources are defended rather than a fixed area. Flocks of robins may defend fruit supplies against other species such as Northern Mockingbird and Cedar Waxwing. The robin is nomadic in winter; once a supply of fruit has been depleted it moves elsewhere (Vanderhoff et al. 2020).

The winter diet is comprised almost entirely of fruit, especially grapes in Illinois, but berries of cedars and junipers may be important. Fruits of common hawthorn are a staple in the western United States. In Maryland, hundreds of robins were observed feeding on holly berries in late winter. It uses a number of cues in foraging, in descending order of importance: fruit crop size, fruit size, and fruit pulpiness. Once a plant has been selected, larger fruits are selected over smaller ones. Fruit abundance defines the local abundance of robins. When fruit is abundant, robins may be common, but they may be absent in the same location during poor crop years (Chavez-Ramirez and Slack 1996; Graber et al. 1971; Petrides 1942; Vanderhoff et al. 2020). Riverbank grape and common buckthorn berries are staples of the winter diet in the Cambridge area (personal observation).

The robin occasionally visits winter bird feeders. Favourite feeder foods are fresh and dried fruit and water. Infrequent choices are mixed seeds, millet, black oil and striped sunflowers, safflower, cracked corn, milo, hulled peanuts and hearts, suet, peanut butter mixes, bird puddings, and baked goods. Occasionally, it eats pet food, meat scraps, and popped corn (Dunn and Tessaglia-Hymes 1979). One bird overwintering in the Yukon ate raisins at a feeder (Sinclair et al. 2003).

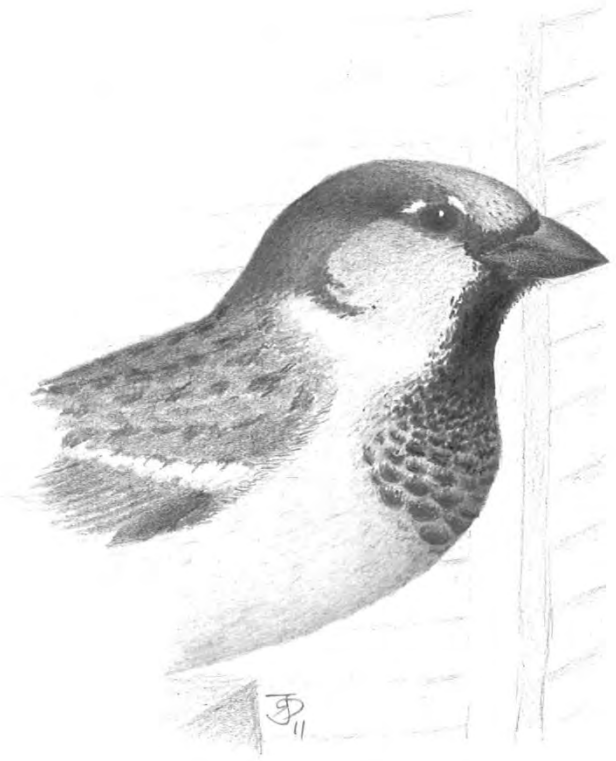
In winter in Colorado, the robin was positively influenced by the density of housing within 100 m and the height of understorey vegetation, but was negatively affected by percent canopy cover and percent cover of understorey vegetation (Miller et al. 2017).

The robin may die in winter during extreme cold coupled with precipitation even if ample food is available. After severe winter weather in Illinois, robins moved from upland to bottomland forests. The number of birds per km² before and after the storm were 26.2 and 36.5 in bottomland forest (a 40.0% increase), 151.4 and 14.8 in upland forest (a decline of 90.2%), and 0 and 35.1 in urban residential. A few dead birds were observed (Graber and Graber 1963; Vanderhoff et al. 2020).

The robin has always occurred in winter in Ontario. McIlwraith (1894) stated that it occasionally spent the winter in sheltered hollows. James (1991) considered it a rare to locally uncommon winter resident in the south and occasional and rare north to Thunder Bay and Kirkland Lake. Speirs (1953) reported that the most northerly winter locations for robins in Ontario at that time were Thunder Bay and Ottawa, and that fewer than 10 per party were recorded on Ontario Christmas Bird Counts (CBCs). Freedman and Riley (1980) analyzed CBC data for southern Ontario. Numbers remained stable from 1929 to about 1961 after which an irregular but large increase occurred, with peaks in 1972 and 1976. They speculated that increases might have been due to increased winter food supplies such as plantings of fruit-bearing shrubs. CBC trends for Ontario were annual increases of 6.17% 1970-2021 and 3.17% 2009-21 (National Audubon Society 2022).

House Sparrow

Passer domesticus



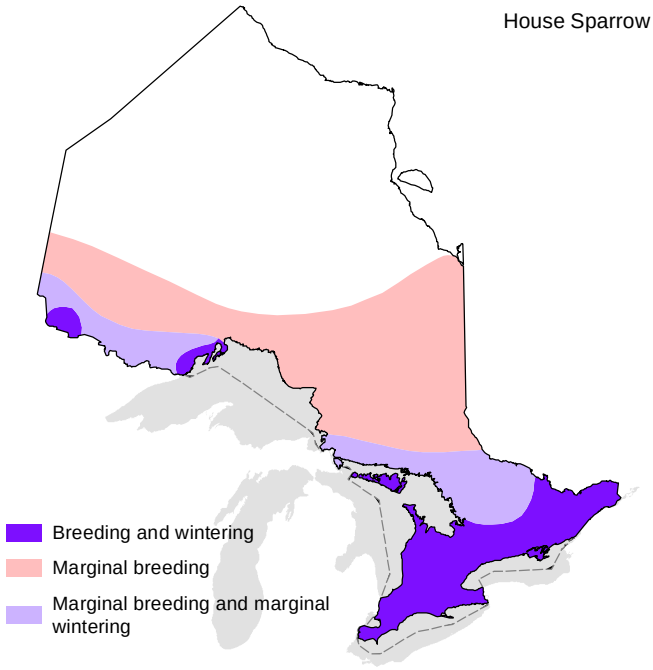
BREEDING SEASON

Habitat Requirements

Ontario House Sparrow nests were typically associated with human buildings and structures, with much less use of natural habitats. Of 1,234 nests, 56.4% were in urban and rural residential and commercial areas, including buildings, gardens, and cemeteries; 30.5% were in farmland, including farmyards, roadsides, hedgerows, fields, and pastures; 3.5% were in wooded areas including mixed and deciduous woods, orchards, and plantations; 3.2% were in river courses; 3.1% were in cottage and camping areas; 2.0% were in treed sand dunes; 0.9% were in wetlands, including swamps, meadow marshes, and dykes; and 0.4% were on railway rights-of-way. Wooded areas that were used were usually open, or nests were at clearings. Wet habitats were apparently chosen only because of the presence of suitable nest sites (Peck and James 1987). Even in natural habitats, it often nests in nest boxes or other artificial sites.

In Ontario, the House Sparrow is restricted to areas where there is human habitation such as urban centres, suburbs, villages, and scattered countryside dwellings. In rural areas, it favours areas with livestock and small grains and is rarely found in natural areas (Lancaster et al. 2004; MacLulich

1938; Mills 1981). It was equally abundant on southern Ontario organic and conventional farms. Its abundance was significantly correlated with the presence of farmsteads. It was also positively correlated with pastures and negatively with hedgerows and spring grain, but these relationships were not significant (Kirk et al. 2011).



In North America, the House Sparrow is associated with human settlements and agricultural lands with grain crops. It is absent in extensive woodlands, grasslands, and deserts. In the far north and arid west, it is present only in the immediate vicinity of human habitation. In large areas of desert, small colonies are present at every isolated ranch, gas station, and roadside rest areas, but none occur away from human-made structures (Lowther and Cink 2020). MacGregor-Fors et al. (2017) investigated its density relative to land use and location relative to an urban centre and urban intensity in Mexico and California. They studied its usage of 5 land uses: intra-urban areas with high urbanization (average of 77.3% built cover), intra-urban areas with low urbanization (average of 13.4% built cover), periurban areas with high urbanization, periurban areas with low urbanization, and agricultural areas. In Los Angeles and Mexico City, it was significantly more abundant in the intra-urban high urbanization habitat than in other land use classes. In Mexico City, there were also high densities in the periurban high urbanization class with only a few or 0 in the remaining classes; no birds occurred in agricultural areas. In Los Angeles, its abundance was positively correlated with maximum building height and high urbanization in urban areas. In Mexico City, its abundance was correlated with high urbanization and pedestrians. In all areas, its abundance was negatively correlated with trees. In urban areas, it can take advantage of a wide range of resources because most other species are absent due to lack of habitat or urban-related hazards. Its density and abundance are determined by variables unique to different cities and urbanization densities. In Illinois, densities were highest in high-density urban areas followed by low-density urban areas, with densities in developed open space dropping to less than 30% of densities in developed urban areas. Densities dropped another 50% in wheat and another 50% in grazed grass with very low densities in corn, soybeans, oats, alfalfa, savannahs, and grass mowed for hay. It was not detected in upland forests, floodplain forests, shrubs, idle grasslands, or marshes (Walk et al. 2011). In Manitoba, it used nest boxes in sites that had the highest percentage of long grass and the lowest percentage of forest and wooded pasture of the secondary cavity-nesters that were studied. Used sites had 8.0% wooded pasture and 41.4% long grass compared with 12.7% and 30.9% for unused sites, respectively; these differences were significant. It was significantly more likely to use nest boxes in disturbed areas and where utility lines were present. It was strongly associated with sites less than 400 m from buildings

but used boxes as far as 800 m from buildings (Munro and Rounds 1985). In Quebec, nests are usually near a food source in an open area such as a park, garden, or greenspace, or near a dwelling or building (Aubry in Gauthier and Aubry 1996). In Alberta, it nested in rows of blue spruce on a farmstead (McGillivray 1980a). In British Columbia, the House Sparrow is a resident of most human settlements and farmland areas where it concentrates near buildings and anthropogenic food sources. It occurs in highly urbanized commercial and industrial sites to sparsely settled rural and farmland areas. It is most abundant in residential areas followed by apartment residential areas, commercial areas, older residential areas, woody residential areas, and industrial areas; it is absent in mixed woodlands. It occurs regularly around railway yards, grain elevators and grain-shipping facilities, livestock barns and feedlots, poultry pens, and landfill sites. In cities, it often frequents fast-food restaurants, sidewalk cafes, bakeries, concession stands, and parks. Its distribution within residential areas is strongly influenced by the location of feeding sites. In Vancouver, numbers drop sharply when total vegetative cover reaches 60%. Nests are almost always close to buildings (Campbell et al. 2001). On a university campus in Mississippi, it nested in a group of 4 magnolia trees, a horse barn, an equipment shed and orchard, and a cluster of buildings associated with a pig feedlot (Sappington 1977). In rural areas of Oklahoma, it nested in boxes in open fields with scattered trees (Pogue and Carter 1995). In Iowa, it nested naturally in trees in riparian habitats, including herbaceous meadows, savannahs, scrub, wooded edges, and floodplain and upland woodlands (Stauffer and Best 1982). In suburban areas of Massachusetts, its abundance was positively associated with 4 variables: volume of structures, building density, cats, and humans. It was positively associated with distance to fallow fields and woodlots, indicating a preference for built-up areas. It was negatively associated with low volume of both conifers and deciduous trees and shrubs. It was positively correlated with high canopy, particularly coniferous volume 17-21 m from the ground, but was probably responding to the presence of nest sites in buildings rather than vegetative features. Suburban areas are ideal habitat because they provide buildings for nesting and grassy cover and open ground for feeding, dusting, and gathering nest material. It was observed on 61.7% of plots in suburban areas. In Florida suburban areas, it comprises more than 50% of the total breeding bird population (Thomas et al. 1977).

Nocturnal roosts are an important component of the House Sparrow's habitat year-round. In spring and summer, communal roosts in urban areas may support thousands of birds. In Oklahoma, roosts consisted of 1 or several trees, with roosts distributed throughout the city but not close to each other. Roosts were in maples, oaks, elms, sycamores, and cottonwoods. The main factors determining suitability for a roost were tree height and foliage density, with tree species probably not important. Trees at least 6 m tall with dense foliage were preferred. It seldom roosted closer than 3 m to the ground. There often was a congregating site near the roost where birds gathered 30-60 minutes before entering the roost. In 1 case, this was a clump of shrubs about 45 m from the roost. At another site, birds congregated on telephone wires, then flew down into shrubs, then to the roost which consisted of 3 large cottonwoods. The largest roosts in Stillwater, Oklahoma supported about 1,000 birds. In Iowa, birds roosted in Boston ivy on the walls of a hospital. In Philadelphia, thousands roosted in a single 12-m tall tree, with birds huddling as close together as possible. Additional birds roosted on an adjacent store covered with Boston ivy and Virginia creeper. In Boston, 3,000 birds roosted in 5 trees; 2 adjacent trees were devoid of sparrows. Roosts are occasionally shared with

other species, particularly the European Starling (Bent 1958; Bergtold 1921; McAtee 1950; North 1973). It is probable that rural birds roost in barns and other outbuildings but this does not appear to have been documented. While nesting, the female spends the night on the nest.

In Ontario, 44.2% of 1,198 nests were in bird boxes; 35.1% were on or in buildings; 10.4% were in trees; 5.1% were on hydro poles, traffic lights, or signs; 4.5% were on bridges; and 0.8% were in fence posts and other posts. One nest was near the ground in a fallen fence post. Nests were either concealed in cavities or recesses of trees and human-made structures or exposed in trees and vines on human-made structures. Concealed nests were in both single- and multiple-unit bird houses, with many in Purple Martin and Eastern Bluebird houses; in or on buildings in eaves and eavestroughs, holes, beams, roofs, canopies, ledges, fixtures, walls, and air conditioners; in trees in natural cavities and old woodpecker and chickadee holes; in or on signs, traffic lights, and hydro and telephone poles; on beams or in holes of bridges and culverts; in holes in posts; and in mail boxes. Exposed nests were in tree crotches, on beams of bridges and buildings, on hydro transformers and lines, in ivy on building walls, on silo ladders, on top of pillars, and on light and other outdoor fixtures. Of 109 nests in trees, 56.0% were in 12 species of deciduous trees and 44.0% were in 5 species of conifers. Species selected most frequently for nesting were spruce (29 nests), white cedar (16), maple (11), and willow (11). The House Sparrow sometimes built on top of or otherwise used old nests of Barn Swallows (25 nests), Cliff Swallows (24), American Robins (4), and Common Grackles (1). Nest boxes intended for Purple Martins, Tree Swallows, Northern House Wrens, and Eastern Bluebirds were usurped or used. Nests were occasionally built into the sides of occupied raptor nests, including 2 of the Red-tailed Hawk and 1 of the Bald Eagle. Nests were often close together with groups of 2-12 nests occurring together. Three nests between 2 billboards were 0.3 m apart and there were 6 occupied nests on the same bridge railing. Heights of nests in trees ranged from 1.2 to 23 m, with most 3.7-7.6 m up. Heights of nests in human-made structures, excluding nest boxes, were 0.9-15 m, with most 2.7-5.5 m up. Nests may be reused for as long as 4 years (Peck and James 1987). In Toronto, Savard and Falls (1981) characterized House Sparrow nest heights in 8 neighbourhoods representing the main types of residential development. House density ranged from 6.2 to 27.3 per ha; 4 plots contained 1-storey houses and 4 plots contained 2-storey houses. The average nest height was 5.29 m (range 1.5-11.9 m). Nests were equally abundant in 1- and 2-storey houses. Nest height depended on the height of the eavestroughs which was determined by the number of storeys; 6.5 m at 2-storey buildings and 3.86 m at 1-storey buildings. Fifty-one percent of nests were in openings around eaves and eavestroughs. It also nested in vent holes of attics, behind window shutters, and in decorative boxes over drain pipes. In plots with 1-storey houses where human-made structures were scarce, it frequently nested in conifers. Nests in trees were significantly higher than those on buildings in the same plot. In 2 plots, average nest heights in trees were 6.29 m and 5.65 m from the ground compared with 2.97 m and 4.13 m for nests on buildings. Where they were abundant, human-made structures were preferred. In 1 plot, tall conifers were present but all nests were on buildings. All tree nests were in dense foliage indicating a preference for cover. Height was also selected for in conifers. Coniferous shrubs were abundant in both plots but were not used for nesting. Nests in conifers averaged 5.95 m from the ground (range 3.05-9.14 m).

Throughout its range, the House Sparrow prefers to nest in cavities such as nest boxes and openings and crevices in buildings and other human-made structures. Occasionally, it nests in natural cavities in trees or old woodpecker holes. Less frequently, nests may be exposed and placed in trees or vines on buildings. Nests in trees may either be in forks of branches or among dense branching. Nests are always elevated and have been reported at heights of 0.2-32.2 m. Occasionally it uses old nests of other species as a platform or cavity for nests, including those of the Eastern Phoebe, Bank Swallow, Cliff Swallow, Barn Swallow, Northern House Wren, American Robin, and European Starling. In Bank Swallow colonies, it occupies the lower rows of nests. It readily uses nest boxes built for it and those intended for Tree Swallows and bluebirds. Similar to Ontario, nests have been reported in active raptor nests, including those of the Osprey, Bald Eagle, Swainson's Hawk, and other hawks. Unusual nest sites include tunnels into hay bales that were accessed from cracks in the boards below them and on oil pumps that were in constant motion, moving up and down approximately 60 cm every 3 or 4 seconds. One pair nested in an old hornet's nest. In British Columbia, 93% of nests were in cavities or crevices or on partially enclosed ledges and 7% were non-enclosed globe-shaped nests in trees, vines, hedges, or shrubs. Only 4 of 620 nests (0.6%) were in natural or excavated tree cavities. Forty-six percent of nests were in nest boxes, 35% were in building structures (houses, garages, sheds, barns, roof shelters, commercial or industrial buildings, and grain elevators), and 6% were in other human-made structures, including utility poles, street lights, signs, traffic lights, marine pilings, and bridges. Most non-cavity nests were in thick ornamental spruce or in vines on walls sheltered by a roof overhang (Bent 1958; Campbell et al. 2001; Kalmbach 1940; Leighton et al. 2002; Lowther and Cink 2020; Morejohn 1953; Rand and Rand 1952; Tatschl 1968; Werler and Franks 1975). In Vancouver, nest height ranged from 1.5 to more than 9 m (mean 5.1 m); most were 3-4.6 m from the ground. Of 56 nests, 51 were in buildings, 3 were in bird boxes, 2 were in deciduous trees and vines, and 0 were in conifers. The habitat included high- and low-density residential areas and apartment buildings. Of 44 nests in Hope, British Columbia, 38 were in buildings, 5 were in bird boxes, and 1 was in an old Cliff Swallow nest (Weber 1975). In Iowa riparian habitat, 46% of nests were in snags, 23% were in dead limbs, and 31% were in live trees. In snags, the House Sparrow nested predominantly in soft and intermediate-density snags with lesser numbers in hard snags. Nest height averaged 10.7 m in trees averaging 16.4 m tall with a diameter of 18.5 cm at the cavity; it nested high in small structures (Stauffer and Best 1980, 1982). In Alberta, McGillivray (1980b) studied clumping of nests in 2 rows of blue spruce 80 m apart. Ninety-seven percent of nests were against the tree trunk. Nests in 1 row were spaced evenly with only 2 trees with more than 2 nests. Nests in the other row were clumped with a maximum of 14 nests in 1 tree and 10 nests within a 1-m radius. In the row with dispersed nests, the mean number of nests within 1 m was 0.76 and the mean distance between nests was 1.52 m. In the row with clumped nests, the mean number of nests within 1 m was 3.43 and the mean distance between nests was 0.66 m. Dispersed nests had significantly more clutches and number of young hatching than clumped nests but fledging success was nonsignificantly higher in clumped nests. Grouping of nests may be associated with synchronous clutch initiation that may increase postfledging survivorship by providing flock mates. Clumping of nests may minimize the detrimental effects of adverse weather. Nests may be very close together; as many as 4 nests may be joined together into a communal structure. Birds may steal nesting materials from other nests, but not from their immediate

neighbours. Nests may be reused within and between seasons, but not necessarily by the same birds (Lowther and Cink 2020; McGillivray 1980a). In Kansas, nestlings did not imprint on their natal nest type, with the nest type they selected for nesting unrelated to their natal nest type. Males showed no preference for cavity nests or tree nests, but females showed a preference for cavity nests. Males advertising from tree nest sites may be at a disadvantage in attracting a mate (Cink 1976).

In Purple Martin houses, the House Sparrow was significantly less abundant in colonies with gourds only than in colonies with houses only or with both houses and gourds. There was higher occupancy of wooden than aluminum houses, but not significantly. Presence of some shrubs at the base of the pole appeared to favour occupancy and it preferred houses that received some sun, but not in the afternoon. On average, it occupied 20.4% of apartments in house colonies. Several factors had no influence on whether a Purple Martin house was occupied by the House Sparrow: type of house, its exterior and interior colour, whether it was cleaned out in spring, habitat (urban business, urban residential, suburban, rural), whether water was nearby, whether there was a neighbouring Purple Martin house, whether there were nearby utility wires, the amount of time that the house was in shade, and how many years the structure had been present (Jackson and Tate 1974). Other studies examined factors affecting nest box use. In Manitoba, used boxes had the largest internal area, the smallest entrance hole, and were higher above ground and closer to buildings than those used by other species. Four parameters differed significantly for boxes that were used and unused, respectively: box area, 263 and 259 cm^2; hole diameter, 39.3 and 41.7 mm; height above ground, 138.6 and 130.1 cm; and distance from building, 467.0 and 1,040.8 m. It selected boxes less than 800 m from buildings with box entrances of 30-38 cm. Boxes facing roads were used significantly less than expected. It did not select for exterior colour of nest boxes (Munro and Rounds 1985). In Tennessee, it preferred boxes with white interiors, but used boxes with dark interiors. White interiors may allow adults to detect predators (snakes) in the box easier and see the nestlings easier (Pitts 1977). In Ohio, there was a significant positive relationship between box usage and distance to the nearest tree. The mean distance of used boxes from a tree was 9.17 m compared with 3.07 m for unused nests (Horn et al. 1996). Lowther (2012) determined that there was a significant correlation between clutch size and area of the bottom of the nest box. The mean clutch size was 4.49 eggs in small boxes (112 cm^2) compared with 4.77 eggs in large boxes (221 cm^2). Nest-box size did not influence hatching or fledging success, egg mass, or nestling condition. There was no evidence that adults selected either large or small nest boxes.

The House Sparrow defends a small area around the nest. Experienced males may remain in the vicinity of the nest site year round, but it is defended strongly only during the breeding season. In Alberta, there were agonistic encounters between birds nesting in boxes 3 m apart, but birds nesting in blue spruce were more tolerant of each other. The foliage may have screened visibility, but birds nesting in trees were still more tolerant of each other than those nesting in boxes. Pairs of birds with nests in the same tree perched side by side without antagonism. Birds nesting within 1 metre were accepted, but strangers were attacked aggressively. A male that constructed a nest within another active nest was initially chased by a neighbouring male. Once the intruder attracted a mate and they began to nest, they were accepted by their neighbours (Lowther and Cink 2020;

McGillivray 1980a; Morrison et al. 2008). Breeding birds tend to remain within 1-2 km of the nesting area (Lowther and Cink 2020).

The House Sparrow is a highly sedentary species that does not migrate. Only 3 banded birds in Canada were recovered more than 25 km from the banding site: 33, 43, and 175 km. All these records were in southwestern Ontario (Brewer et al. 2018). Despite its sedentary nature, natal philopatry rates may be low due to dispersal during the postfledging period and high mortality. In Michigan, 7 of 187 fledglings (3.7%) from artificially enlarged broods returned; 7 of 99 control fledglings (8.1%) returned. There was no difference in the return rates of fledglings of second broods of females that laid 3 clutches (5.7%) and those that did not attempt a third brood (2.7%; Anderson 1998). In Kansas, Fleischer et al. (1984) studied colonies at 7 farms and checked for banded birds at 9 other farms, all within an area of 12 km^2. Only 63 of 3,360 nestlings (1.9%) were recaptured and 23 of these (36.5%) dispersed: 47.8% of females and 30.0% of males. Dispersal rates of females were significantly higher than for males. For both sexes, dispersers came more frequently from nests that had greater fledging success. Breeding success and population size may affect philopatry. On the farm with the lowest productivity per female and lowest population, 0 of 13 nestlings subsequently captured there had hatched there. All 5 recoveries of birds hatched there occurred at surrounding farms. Another farm about 1 km distant had the second highest breeding success and population. Of 90 birds captured there, 28 (31.1%) had been banded there as nestlings and only 8 (8.9%) were recovered at other farms, a highly significant difference. Brood size and hatch date had no effect on dispersal rates. Sixty-two percent of first-year autumn birds dispersed compared with 32% of adults; this difference was significant. Most or all dispersal occurred in late summer and early autumn. In Ohio, Dexter (1949) banded 668 House Sparrows; only 2 juveniles (0.3%) returned. In Kansas, 24.7% of treatment fledglings that had been moved to another nest box and 30.7% of control fledglings returned the following year (Cink 1976). In Illinois, 89 of 1,785 birds of unspecified age (5.0%) returned; 2 were banded as nestlings and 15 as fledglings. Random movements as far as 700 km have been reported and these represent dispersal by juveniles. Such movements are undertaken by a very small proportion of the population (Will 1973). North (1973) concluded that juveniles do not necessarily return to their original home range, but become dispersed over a large area. Few juveniles returned to the area in the Oklahoma town where they had hatched; instead they dispersed into new home ranges. Lowther and Cink (2020) reported that 1 bird banded as a nestling travelled approximately 26 km.

The House Sparrow is wary of traps and difficult to catch. Adults in particular are likely to avoid traps if they have been caught previously. Consequently, rates of natal philopatry and especially adult site fidelity may be underestimated. In Kentucky, 109 of 244 males (44.7%) that used nest boxes returned to nest in the subsequent year. Seventy of the returning males (64.2%) returned to the same nest box, 17 (15.6%) returned to a different box on the same barn, 4 (3.7%) returned to a box on a different barn, and 18 (16.5%) did not defend a box in the following year. Forty-two males lost their nesting box in the middle of the season and only 2 (4.8%) were seen at a box later in the season. Both defended a box on the same barn. Nine of the 42 males (21.4%) were seen in subsequent years: 3 returned to defend a nest box and 3 did not occupy a box. Sixty percent of males that were box owners for 2 or more years used the same box and 76% returned either to the same box or same

barn (Morrison et al. 2008). Another Kentucky study determined that fewer than 25% of birds survived long enough to breed in more than 1 season (Stewart et al. 2006). At a Michigan site, overwinter returns of females were less than 40%. There was no difference in return rates of females that raised 3 broods (36.0%) and those that raised 2 broods (28.3%; Anderson 1998). In Mississippi, 125 of 156 birds (80.1%) nested at the location where they were banded, but not necessarily in the same nest box where they bred the previous year. Eighty-six percent of males occupied the same box for the entire season, significantly more than those that used multiple boxes. There was no difference in the number of females using a single box (45%) or multiple boxes (55%) within a season. In subsequent breeding seasons, only 6 of 60 breeding males (10.0%) returned to their previous nest sites. Nest-site tenacity may have been affected by humans tearing down old nests and others deteriorating due to weather (Sappington 1977). In Kansas, adults dispersed significantly less than juveniles, with only 1 of 15 adult recoveries (6.7%) occurring at another farm. Adult males that dispersed were significantly larger than those that did not disperse, suggesting that smaller dispersing males had lower survival rates. Nineteen percent of males recovered as adults dispersed compared with 50% of yearling males; females of both age classes dispersed at equal rates (Fleischer et al. 1984). In Ohio, 11 of 668 birds (1.6%) were recovered and 9 were adults (the number of adults banded was not specified). Two recoveries were 1.2 and 1.6 km from the banding location (Dexter 1949). In Illinois of 1,785 banded birds of unspecified age, 4 adults returned. The longest movement was 3.2 km; only 3 birds moved as far as 1.6 km. One was an adult male that moved 2.4 km daily between its autumn feeding and roosting areas. Most movements occurred in late summer, autumn, and winter; many movements may have been within the daily flight range. Only 23.6% of birds were recaptured more than 30 m from where they were banded (Will 1973). In Oklahoma, most birds spent their entire lifetime within a very small area. Fifteen percent of birds (721 of 4,805) were subsequently recovered. Movement generally occurred in autumn. At 1 barn where no birds were collared, 1.0% of birds there in September were collared and this increased to 3.1% in October and 5.2% in November. Some birds were found 6.4 km distant and 2 were recaptured 11.3 and 109 km away, all in a northwesterly direction (North 1973).

Limiting Factors

Peck and James (1987) reported eggs in Ontario nests from the beginning of April until mid-August, with most present from mid-May to mid-June. Peck and James (1998b) reported nestlings on 3 November which would indicate a later egg date. They also reported nest building on 3 February and 4 March which may indicate earlier nesting. Early nests may take more than a month to construct, and adults may continue nesting most of the year (Weaver 1943), so it is difficult to predict when these nests might have held eggs. An egg was found in an Ottawa nest on 18 January (Kalmbach 1940). Young were found in a Utah nest on 1 January when temperatures averaged around −17°C and dropped to as low as −25°C. The young fledged successfully, but 1 or both adults were on the nest at all times and both spent the night in the nest box (Bent 1958; Weaver 1943). Although the House Sparrow may rarely nest very early or very late in the year, nesting typically occurs from April to August or early September, or slightly earlier further south. Murphy (1978) compared the timing of nesting initiation and termination in Kansas and Alberta. Breeding began later but at cooler temperatures in Calgary, so breeding initiation was not strongly tied to photoperiod or temperature; breeding continued longer in Calgary. Cessation of egg laying was

related to cooler temperatures in late summer in Calgary and high temperatures and dry weather in midsummer in Kansas. At both sites, cessation of egg laying was probably due to decreased insect abundance.

Nests built early in the season are constructed very leisurely. One British Columbia nest initiated in late February took 42 days to build. No information is available on how long it typically takes to build a nest. Peak periods of nest building tend to be followed by intensive egg laying within a week. One egg is laid per day and incubation usually begins with the laying of either the third or penultimate egg; occasionally incubation begins with the laying of the final egg. The incubation period of 15 Ontario nests was 9-14 days. Elsewhere incubation periods of 10-17 days have been reported, with most eggs hatching in 11-13 days. The longest-reported incubation period of 17 days was at a nest where a Barn Owl near the nest site inhibited nest attentiveness. Hatching may be synchronous in small clutches and those where incubation did not start until the last egg was laid. Hatching may take place over 2-3 days in broods where incubation started before the clutch was complete. The nestling period has been reported as 9-23 days but most nestlings fledge at age 14-17 days. Earlier departures are often associated with nest disturbance and the longest period was associated with the presence of the Barn Owl (Anderson 1994, 1997, 1998; Bartlett et al. 2005; Campbell et al. 2001; Cink 1976; Hegner and Wingfield 1987; Kalmbach 1940; Lowther 1990; Lowther and Cink 2020; Peck and James 1987; Sappington 1977; Weaver 1943).

The House Sparrow typically raises 2 or 3 broods in the northern portion of its range and as many as 4 in the south. Triple brooding has been confirmed in Ontario and British Columbia and was common in Michigan. There are reports of more than 4 broods per year but these may be erroneous. Individual nest boxes may be used by as many as 3 different females within a season; researchers that assume the same birds are using a nest may report an inflated number of broods. Yearling females are capable of rearing 3 broods, but significantly fewer (43.8%) did so compared with adult females (68.8%) in Michigan. Females raising large second broods of 7 or 8 young were significantly less likely (42.9%) to raise a third brood than those with normally sized second broods (72.7%). Thirty percent of females moved to a different nest box to raise their next brood. The distance between successive nests was 2-89 m, but 66.7% of females had their next brood within 10 m of the previous nest; the median internest distance was 5.9 m. The interval between fledging of the previous brood and laying the first egg of the next clutch is usually about a week, but ranges from −8 to 49 days. Females may lay eggs in nests still containing young of the previous brood and sometimes initiate egg laying in another nest before young leave the previous nest. In New York, the interbrood interval increased significantly with the number of fledglings in the previous brood. The interbrood interval averaged 7.0 days for broods that were experimentally reduced, 7.1 days for control broods, and 11.3 days for experimentally enlarged broods. The House Sparrow is a persistent renester if nests are lost and may lay as many as 8 clutches in an attempt to raise a brood (Anderson 1994, 1998; Campbell et al. 2001; Hegner and Wingfield 1987; Kalmbach 1940; Lowther 1979; Lowther and Cink 2020; Mitchell et al. 1973; Peck and James 1987; Peck and Peck 2010; Sappington 1977; Weaver 1943). Clutches of 3-7 eggs have been reported in Ontario (average 4.66 eggs). Four- and 5-egg clutches were most frequent, with more nests containing 5 than 4 eggs (Peck and James 1998b). Elsewhere, clutches of 1-9 eggs have been reported, but the normal range is 3-7 eggs.

Clutches of 5 eggs are most abundant, followed by 4 and 6 eggs. Clutch size is strongly correlated with latitude, with mean clutch sizes of 2.0-3.3 in Central America to more than 5 eggs in Alberta. The size of subsequent clutches in a season is negatively correlated with the size of the previous clutch. In New York, mean size of second clutches was 5.4 eggs for females whose first clutch had been experimentally reduced, 4.3 eggs for control females, and 3.6 eggs for females whose clutches had been experimentally enlarged. Some studies observed no seasonal decline in clutch size; others reported that clutch size declines with season. In Kansas, clutch sizes increased to a maximum in midseason, the only time when 7-egg clutches were present. In Illinois, clutches initiated in March and April averaged 4.46 eggs, significantly larger than 4.17 eggs for clutches initiated in July and August (Anderson 1994, 1998; Baker 1995; Bartlett et al. 2005; Bent 1958; Campbell et al. 2001; Hegner and Wingfield 1987; Kalmbach 1940; Lowther 1990; Lowther and Cink 2020; Mitchell et al. 1973; Sappington 1977; Weaver 1943; Will 1973).

Both sexes are capable of breeding when they are 1 year old. In many populations, some birds of each age and sex class do not breed, possibly because of limited nest sites. In Kentucky, male nest-box holders were more likely to be older birds. Those that were nest-box owners in previous years and yearlings that had hatched in a box at the site were more likely to become nest-box owners. Sixteen of 51 males (31.4%) that were hatched in on-site boxes became a box owner compared with 10 of 100 yearlings (10.0%) that had hatched elsewhere (Morrison et al. 2008). In Mississippi, 82.6% of adults bred, including 78.4% of males and 86.7% of females (Sappington 1972).

The House Sparrow is monogamous with no cases of polygyny reported. Mate fidelity is variable. In Missouri, only 60.5% of pairs remained together for the entire season, although the number of males having a single mate was significantly higher than those having multiple mates in a season. There was no evidence of pairs remaining together for more than 1 season (Sappington 1977). In Missouri, females that were removed were replaced within 1-20 days, with most replacement females appearing in an average of 12.2 days (mode 5-8 days). Replacement females began to lay eggs as soon as 1 day after arrival. Replacement birds were mostly yearlings that had not bred previously and older females that had not been at the colony the previous year (Anderson 1990).

In Kentucky, 45 of 419 nestlings (10.7%) were extra-pair and 33 of 126 broods (26.2%) contained extra-pair young. Yearlings were as likely as adults to be sires; size had no influence on whether a male was a sire of extra-pair young. Sires included neighbours, males breeding at the same barn, and some that may have been breeding some distance away. Adult males tended to have more extra-pair young in their broods than yearlings. Yearling females had more extra-pair young in their broods than adults. Later broods were more likely to contain extra-pair young, probably because some females stop breeding after the second or third clutch, freeing their mates to seek extra-pair copulations. There was no relationship between nesting density or breeding synchrony and the rate of extra-pair copulations, but significantly fewer extra-pair young occurred in larger broods (Stewart et al. 2008). Rates of extra-pair young reported elsewhere include 1%, 7%, 10%, 14, and 20% (Stewart et al. 2006; Wetton et al. 1987).

In Delaware, 8 of 94 clutches (8.5%) showed evidence of intraspecific parasitism. Parasitism was confirmed by electrophoresis. Other signs of parasitism were unusually large clutches, odd-coloured eggs, and 2 eggs appearing in the nest in a single day. Kendra et al. (1988) artificially parasitized

some nests and hosts had 3 different responses. One female removed 3 eggs that had been inserted after she laid her first 3 eggs, 2 of the 17 manipulated nests (11.8%) were abandoned after an egg was added, and at 3 of the manipulated nests (17.6%) the host female failed to lay an egg on the day following egg addition. Eggs were removed from some nests, demonstrating that the House Sparrow was an indeterminant egg layer until the clutch size reached 3 eggs after which total egg production appeared to be limited to 4-6 eggs. Females could increase their fecundity by laying parasitic eggs before they laid 3 eggs in their own nests. Parasitism may be detrimental to the host, suffering reduced fecundity and diluted resources for her own clutch. If an egg is inserted before the host lays 3 eggs, the parasitic egg may halt egg production, reducing the host clutch size by 1 egg. If parasitism occurs after the third egg, the host may have an oversized clutch that can result in decreased food deliveries to each young and decreased survival. It was uncertain what occurred when the host female skipped a day in egg laying after parasitism. It is possible that she laid her egg parasitically in another nest.

The House Sparrow forages mostly on the ground for seeds. In grain fields, it alights on the stalks and plucks the seeds from the fruiting heads, or shakes them to the ground to be picked up later. It pursues low-flying beetles through the air and captures them on the wing; it is one of the heaviest predators of the Japanese beetle. It catches insects by flycatching and hover pouncing, follows lawnmowers to catch moths, kleptoparasitizes earthworms from robins, pierces flowers to obtain nectar, and picks insects out of grills of stopped cars. It flushes prey from trees and shrubs by shaking the leaves or twigs with its feet while vigorously flapping the wings. Moths and other prey flushed by this method were captured in flight. In Connecticut, it captured larvae of the elm leaf beetle by creeping around trees in nuthatch fashion as high as the first limbs to intercept descending larvae. It captures black locust leafminers by systematically searching the curled-up edges of leaves. It responds to outbreaks of geometer moth caterpillars, crickets, and locusts. It has eaten salt from salt blocks in barnyards and foraged at night on insects at floodlights (Bent 1958; Brooke 1973; Brooks 1951; Brown 1971; Calhoun 1945; Campbell et al. 2001; Guillory and Deshotels 1981; Lowther and Cink 2020; Wilmot 1917). The House Sparrow is highly vigilant while foraging, with flocks frequently flying from the food source to adjacent cover. Food resources in locations where sparrows cannot adequately detect predators may not be used. In Wisconsin, Popp (1988a) studied their selection of horse pats for foraging. Pats were in grassy pasture grazed to within 5 cm of the ground and weedy areas where many of the plants were taller than 0.5 m. Visibility for the House Sparrow was good and bad in these habitats respectively. Over 2 years, 88.7% and 92.2% of foraging visits to horse pats were in the grassy area. Birds preferred to forage at pats where 2-4 birds were already present. These pats were approached more than expected by chance; pats with no birds present were approached less than expected. Pats with 1 or 5 or more sparrows already present were approached with the expected frequency. Foraging in taller vegetation would put sparrows at risk of predation, especially by cats, due to low visibility. Joining a small flock at a pat could provide benefits from the selfish-herd effect and from reduced vigilance rates. Presence of other sparrows might also be indicative of a good foraging location. At a Saskatchewan site, House Sparrows comprised about 65% of the breeding season diet of the Merlin, which increasingly took juveniles rather than adults from May to July. Approximately 70% of adults and 80% of juveniles foraged within 1 m of cover. In June, all juveniles were in or near cover. In July, juveniles occurred at almost every distance from cover, but

more juveniles were close to cover than adults. As juveniles aged, they became more proficient at detecting predators and ventured further from cover (Sodhi 1992). In Pennsylvania, sparrows feeding on a flat roof initially congregated on the wall prior to descending to feed. When alarmed, they retreated to 2 adjacent trees, but mostly to a hemlock that offered better cover than a red oak. Each sex was equally likely to initiate a feeding flock, but 71.6% of birds remaining after a disturbance were males, significantly more than expected. Males are subordinate to females and may be excluded from the best foraging areas so they may risk predation to get better access to food (Breitwisch and Hudak 1989). Other studies demonstrated that females are dominant to males (Jawor 2000; Johnston 1969), but males in northern latitudes may be dominant in certain seasons.

Young House Sparrows subsist predominantly on insects but switch to a diet of seeds as they age. At age 11 days, nestlings ate live flies and puppy food when it was offered but showed no interest in millet and canary seeds. At age 16-17 days, they abruptly switched from a strong preference for insects to a complete refusal of insect offerings. By age 25-30 days, they fed on seeds almost exclusively and ignored the puppy food (Mueller 1986). Kalmbach (1940) analyzed the stomach contents of 2,819 nestlings from all months. The diet consisted of 68.13% animal food and 31.87% vegetable matter. Nestlings consumed significantly more animal food than adults (3.39%). The animal food consisted of 15.17% weevils, 4.01% scarab beetles, 0.46% click beetles, 2.65% ground beetles, 0.29% leaf beetles, 1.43% other beetles, 25.24% orthopterans, 11.16% caterpillars and moths, 1.34% bugs, 2.88% flies, 1.34% hymenopterans, 0.16% other insects, 1.79% spiders and other arachnids, and 0.21% other animal material. Vegetable matter consisted of 29.76% agricultural feed, 0.19% oats, 0.95% wheat, 0.03% corn, 0.01% other grain, 0.17% grass and weed seeds, 0.11% mast and wild fruit, 0.11% cultivated fruits and vegetables, and 0.54% other vegetable matter. The amount of animal food consumed declined as nestlings aged, with a decrease in the amount of weevils, caterpillars, fly larvae, and spiders. The percentage of animal food in the diet was 90.15% for nestlings 1-3 days old, 65.1% for nestlings 4-6 days old, and 49.13% for nestlings older than 7 days. Other animal foods in nestlings' diet included lacewings, mayflies, dragonflies, millipedes, earthworm cocoons, snails, and fragments of hens' eggs. Judd (1901) reported that 50 nestlings had consumed 65% insects, 2% weed seeds, and 33% grains. The insect food consisted of 49% grasshoppers, 8% beetles (mostly weevils), 4% lepidopterans (armyworms, cutworms, fall webworms, and tussock moth caterpillars), 3% ants and other hymenopterans, and 1% bugs. Almost all the grasshoppers were short-horned grasshoppers, but nestlings also ate crickets and long-horned grasshoppers.

In Ontario, adults have been observed eating cicadas (Luft 2000). In Hamilton, McIlwraith (1894) reported that they depredated the grapes in his yard by eating the fruit buds. Judd (1901) examined 82 stomachs collected throughout the year in eastern and Midwestern states. The diet consisted of 2% animal matter and 98% vegetation, which consisted almost entirely of seeds. Insects were consumed mostly in May and June when they comprised 10% and 8% of the diet respectively. It has been observed capturing nymphs of twelve-spotted skimmers (a dragonfly) that had just emerged from the water. Other animals consumed included small bees, ichneumonid wasps, parasitic wasps, weevils, dung beetles, June beetles, leaf beetles, soldier bugs, leafhoppers, aphids, scale insects, and cicadas. The vegetable matter consisted of 7% grass seeds (wild rice, panic grass, foxtails, and

crabgrass), 17% weed seeds, and 74% grain, which comprised 90% of the diet from June to August. Seeds consumed included those of lamb's-quarters, black bindweed, sweet clover, knotweed, field mustard, smartweed, climbing false buckwheat, dandelion, sunflower, and ragweed. Kalmbach (1940) analyzed the contents of 4,848 adult stomachs. The diet consisted of 3.39% animal matter and 96.61% vegetation. Most animal food was consumed in May, with a decrease through summer and autumn. The animal food consisted of 3.32% insects and 0.07% arachnids, crustaceans, and miscellaneous invertebrates. Weevils were an important component of the insect diet, with most eaten in May and June. It regularly visited alfalfa fields to feed on alfalfa weevils. Other beetles commonly consumed included bark beetles, which were also fed to young, and June beetles and other scarab beetles. Urban birds ate more beetles than rural birds. Other beetles that occurred in the diet included click, ground, leaf, lady, long-horned, tiger, darkling, rove, and clown beetles. Orthopterans were eaten from April to September with a peak in August, but comprised only 0.57% of the annual diet. These were predominantly short-horned grasshoppers, but it also ate crickets, locusts, and long-horned grasshoppers. Lepidopterans comprised 0.23% of the diet; only in July did they comprise more than 1% of the diet. It most frequently ate owlet and geometer moth caterpillars and adults and occasionally consumed cabbage white butterflies, fall webworm caterpillars, forest tent caterpillars, and gypsy moths. Bugs were insignificant in the diet and were consumed from April to September with a peak in April. It ate ebony bugs, stink bugs, lace bugs, treehoppers, leafhoppers, planthoppers, aphids, scale insects, and cicadas. Flies were consumed from March to September but mostly in April; overall they comprised 0.10% of the diet. These were predominantly crane flies and house flies taken chiefly from manure. Hymenopterans comprised 0.31% of the diet and were eaten every month except February and December with a peak in September. They were mostly ants but some ichneumonid and parasitic wasps were consumed. The amount of other insects consumed was trivial and included termites, lacewings, mayflies, odonates, and stoneflies. In addition to spiders, it ate millipedes, earthworms and their cocoons, snails, and fat and meat fibres that were human garbage. One pecked out the eyes and fed on the brains of a dead House Sparrow that was in the same trap. Vegetation comprised 96.61% of the diet and constituted less than 90% of the diet in only May. It ate feed picked up in chicken coops and yards and barnyards and it was the dominant food, representing 59.5% of the annual diet. Grains were important in the diet, including 14.37% oats, 2.70% wheat, 0.43% corn, and 0.58% other grains. Other vegetation consumed included 16.97% grass and weed seeds, 1.39% mast and wild fruits, 0.2% cultivated fruits and vegetables, and 0.58% other vegetable matter. Those consuming the greatest amounts of feed were collected in the vicinity of poultry runs, with maximum consumption in February. Oats were eaten in sheaves, stubble, and from granaries and horse manure, but mostly from village streets and barnyards. Other grains consumed included sorghum, rice, barley, and millet. Grass and weed seeds were eaten every month with greatest consumption in October and the least in June. Dominant seeds consumed were those of ragweed and crabgrasses, and smartweed seeds were also prevalent in the diet. Other seeds included those of lamb's-quarters, amaranths, foxtails, panic grasses, paspalum, barnyard grass, Johnson grass, annual bluegrass, timothy, flatsedges, common chickweed, plantains, sheep sorrel, catnip, bedstraws, white clover, and sunflowers. Mast and wild fruits were eaten every month but mostly in June and July. Elm seeds were most prevalent, but it also ate mulberries, blackberries, strawberries, and fragments of rose hips. Cultivated fruits and vegetables it consumed included

cherries, peas, and beans. It also eats cultivated strawberries, raspberries, blueberries, gooseberries, currants, grapes, mulberries, plums, peaches, apples, pears, and tomatoes. It feeds on buds of fruiting trees. In spring and early summer, it feeds on the tender sprouting leaves of peas, beans, lettuce, peppers, cabbage, beets, asparagus, and other vegetables and on those of certain flowering plants such as pansies and carnations. It feeds on the flowers of vegetables such as peas and beans. From April to August, it fed on the foliage of clover obtained from lawns. Gavett and Wakely (1986) compared the diets of 218 urban and 267 rural House Sparrows in Pennsylvania. In the country, 97.3% of birds consumed cereal grains and 94.3% ate insects that were mostly beetles. These 2 food items were the most important for rural birds. In the city, 93.1% of birds ate insects, 81.2% ate seeds, and 82.6% ate commercial bird foods. By volume, cereal grains were most important for rural birds and bird seed was the most important for urban birds. The most important grains in the diet of rural birds were corn (eaten by 49.4% of birds), oats (4.1%), and wheat (3.7%). The most important seeds for urban birds in bird seed included milo (consumed by 14.7% of birds), millet (9.6%), and sunflowers (1.4%). Urban birds consumed elm seeds (18.3% of birds) but these were not eaten by rural birds. Urban adults ate significantly more bird food than rural birds and urban juvenile birds. Urban birds consumed other seeds significantly more frequently than rural birds. Rural birds tended to eat more plant fragments than urban birds; urban birds were more likely to eat spiders and other arachnids than rural birds. Other miscellaneous foods consumed by House Sparrows included seeds of wood-sorrel and panic grasses, springtails, flies, bugs, aphids, insect eggs, cestodes, bird lice, fleas, and mites. The significant differences in the diets of urban and rural birds probably reflect differences in food availability. Beetles were the most important insects in the diet of both urban and rural birds. The significant difference in the amount of other seeds consumed by urban and rural birds was due to the preponderance of elm seeds in the diet of urban birds; these trees were common along city streets. In urban areas, it was often seen feeding on discarded food and other refuse, but this was probably digested too quickly to show up in the results. Most food consumed by both urban and rural birds came from humans. Urban birds have been documented feeding on chicken drumsticks and other human waste food (MacGregor-Fors et al. 2020). Howell and Clements (2019) documented it depredating brown anoles in Florida. Both sexes caught the lizards, bashed them against the ground, and pecked off and consumed small pieces.

The House Sparrow is a rare host of the Brown-headed Cowbird. This is probably because the House Sparrow either nests in cavities or builds a globular nest with a side entrance whereas the cowbird prefers open-cup nests. No parasitized nests have been reported in Ontario. There are fewer than 20 records of cowbird parasitism of House Sparrows, but they include 2 cases where they successfully fledged a young cowbird. In British Columbia, 1 of 359 nests (0.3%) was parasitized and there is a single record of a House Sparrow feeding a fledgling cowbird. A 1951 report of a parasitized nest in Maryland was the fourth known case of parasitism at that time (Brackbill 1951; Campbell et al. 2001; Lowther and Cink 2020; Peck and James 1998b).

Food availability is probably the greatest limiting factor for the House Sparrow. It has declined significantly in response to reductions in the amount of available food. The invention of the internal combustion engine had an indirect but highly significant impact. Prior to then, horses were used for transportation and harvesting crops and sparrows fed heavily on grain in horse droppings. Horses

were widely replaced by tractors and automobiles. Bergtold (1921) provided evidence of a decline in House Sparrows in Denver, Colorado, and attributed it to the decline of horses in the city. Previously, hundreds of sparrows were present in the business section but they were absent by that time. In the downtown area, it fed almost exclusively on grain in horse manure. There was a 66% decrease in horse droppings from 1911 to 1919. By 1919, there were enough tractors in Colorado to displace 16,000 horses. Immediately following World War 2, cars became abundant and horses essentially disappeared from urban areas, resulting in further declines in the House Sparrow. In urban areas, food from garbage decreased due to better sanitation methods (Bent 1958; Erskine 2006; Holder 2003; Lowther and Cink 2020). Although there has been an increase in bird feeding in urban areas, this occurs predominantly in winter and many people do not offer the oats, cracked corn, and feed mixes that it prefers. Urban areas also support more predators than they did previously, especially domestic cats, but also raptors such as Sharp-shinned Hawks and Merlins. In the Maritime Provinces, urban areas no longer provide a favourable habitat for the House Sparrow and it may disappear from cities there within a few decades (Erskine 2006).

Several factors have contributed to less food availability for the House Sparrow in rural areas, resulting in lower populations. The number of farms has decreased, livestock numbers have declined and they are managed differently now, methods of harvesting crops have changed, and the crops that are grown have changed. Beginning around the 1950s, marginal farmlands were retired and often reforested or allowed to undergo natural succession. This resulted in less habitat for the House Sparrow due to fewer barns and outbuildings and less land in agricultural production.

The number of cattle declined in Ontario. This decline continues, with 2.141 million cattle in Ontario in 2001 and 1.624 million in 2016 (Statistics Canada 2018), a decrease of almost 25%. Until the mid-20th century, each farm typically had a few cattle that grazed outside in pastures. Now, fewer farms have cattle and they are often kept and fed within barns where their feed and manure is unavailable to sparrows. Manure was formerly stored outside in barnyards and spread on fields as fertilizer. Farmers are now required to have manure management systems that often consist of sewage lagoons that offer no food for sparrows. Earlier most farms had a small flock of chickens that was kept in a coop and fed in an enclosure outside the coop. Sparrows were able to feed on the food that was intended for the chickens. Most chickens are now raised and fed inside barns where sparrows cannot access their food.

Prior to the 1950s and 1960s, grain was harvested using a binder that tied the grain into sheaves. Sheaves were stooked together in the field to dry for a few days before they were taken to the barn to be threshed. This method of harvesting left considerable waste grain in the fields, and sparrows could also feed on the grain heads while they were drying. Now almost all grain is harvested with combines that leave little waste grain, and the harvested grain is transported immediately into barns.

The crops that are grown in Ontario have changed significantly and these changes have been detrimental to the House Sparrow. Originally, most crops were designed to support livestock and included pastures and hayfields for forage and small grains to supplement their diet, particularly oats but also wheat and some barley. The pastures with their livestock and the extensive fields of small grains provided abundant food for the House Sparrow. As the number of livestock declined, pastures were converted to croplands and corn and soybeans began to be the dominant crops.

Wheat became the dominant small grain grown rather than oats. In Ontario, corn production increased over 3,000% from 1947 to 1987, mostly at the expense of oats and mixed grains. The area of cropland planted to corn and soybeans continues to increase. In 2001, there were 909,922 ha planted to soybeans compared with 1,126,419 ha in 2016; there were 810,595 ha planted to corn in 2001 and 874,932 ha in 2016. During the same period, the area planted to oats declined from 41,144 ha to 33,268 ha (Statistics Canada 2018). The changes in crops are significant because oats are the preferred grain food of the House Sparrow. Full-sized corn kernels are too large for it to handle efficiently although it readily consumes cracked corn. It is unknown whether it eats soybeans at all. Erskine (2006) identified many of these same factors as contributing to the decline of the House Sparrow in the Maritime Provinces. In Illinois, Graber and Graber (1963) reported that populations declined in the southern portion of the state but increased in the north from 1907-09 to 1957-58. They attributed this to changes in crops. The amount of land planted to oats increased in the north where sparrow populations also increased, whereas the area planted to wheat increased in the south.

The number of available nest sites has declined in both urban and rural areas. In cities, most of the ornate architectural fashions on eaves that provided abundant nest sites have disappeared. More significantly, most modern buildings have eaves constructed of aluminum and many older structures are being retrofitted with aluminum eaves. Eaves of houses were formerly an abundant source of nest sites, but these sites are largely gone. In rural areas, the number of wooden barns and outbuildings has decreased significantly and continues to decline. Modern barns are typically built of steel and provide no nest sites.

Researchers had varying opinions on whether the House Finch had an adverse effect on the House Sparrow in eastern North America. It is agreed that House Sparrows were declining before the introduction of the House Finch so it was not fully responsible for the decline, with changes in urban and agricultural practices being more important. Most studies conducted at large scales determined that the decline of the House Sparrow was accelerated in the northeast where the House Finch was abundant. In the southeast and in Indiana where the House Finch population is not as great, presence of House Finches did not influence House Sparrow population trends. This suggests that competition influences are not manifested unless the House Finch density is high. Beginning in 1994, disease significantly reduced House Finch populations. In the northeast, the House Sparrow declined significantly in winter when the House Finch was increasing, but no longer declined after the House Finch decreased. Trends in summer were similar but nonsignificant. It appears as though high densities of House Finches can depress House Sparrow populations, but this may no longer be a significant limiting factor now that the House Finch is declining (Bennett 1990; Cooper et al. 2007; Hamilton and Wise 1991; Holder 2003; Kalinowski 1975; Kritcher 1983; McClure et al. 2011; Wootton 1987).

The House Sparrow is host to a variety of parasites, viruses, and bacteria that can have adverse effects on individuals or populations. It is occasionally infested by gapeworms and adults with severe symptoms such as gasping for air have a reduced probability of survival (Holand et al. 2014). Nestlings are involved in the amplification of the western encephalitis virus. They circulate the virus for several days in their bloodstream at concentrations high enough to infect vector mosquitoes

(Mitchell et al. 1973). Sparrows nesting in Cliff Swallow colonies may become infected with the Buggy Creek virus (BCRV). This virus was typically associated only with the Cliff Swallow and is transmitted by the ectoparasitic swallow bug. BCRV has little effect on adult House Sparrows but only 9% of infected nestlings fledged in Nebraska. The bugs prefer Cliff Swallows as hosts, so the closer a House Sparrow nest is to a Cliff Swallow nest, the more likely it is to fledge young. Cliff Swallows have become immune to BCRV and rarely show any symptoms of infection. It was considered unlikely that House Sparrows would develop immunity due to low site fidelity, lack of imprinting on nest sites by young, and limited maternal transmission of antibodies (O'Brien and Brown 2012). Die-offs of House Sparrows due to salmonellosis have occurred in Prince Edward Island and transmittal of it may have been aided by increased transportation between urban centres (Erskine 2006).

Severe weather may have adverse effects on the House Sparrow. High mortality may occur when sudden storms arise at night while birds are roosting (Kalmbach 1940). High winds may cause extensive damage to nests in trees (Mitchell et al. 1973) and nests may be deserted late in the season due to hot dry weather (Will 1973).

Traffic noise does not appear to have significant effects on the House Sparrow. Brischoux et al. (2017) played recordings of traffic noise at nest boxes. Noise did not influence nestling growth. Those chronically exposed had a reduced resting metabolic rate, the opposite of the expected effect.

Status

Originally native to Europe, Asia, North Africa, the Middle East, India, and Burma (Myanmar), the House Sparrow was introduced widely so that it now has a cosmopolitan range. With the exception of Antarctica, it may occur almost everywhere that humans reside. Where it was introduced, densities initially increased in urban areas and spread to suburban areas and then rural areas, especially where small grain crops were grown or where there was livestock. In North America, its spread was hastened by the network of railway tracks. Birds travelling in grain cars established colonies at most settlements along railway corridors. A small population in Churchill is associated with the railway and grain elevator, but there are no other populations within several hundred kilometres (Erskine 2006; Jehl and Smith 1970; Kalmbach 1940; Lowther and Cink 2020).

The House Sparrow was introduced to New York City predominantly from England but some German birds were also introduced. The rationale for its introduction was three-fold: it was believed that it would control larvae of the elm spanworm moth, some European immigrants wanted to see familiar birds from their homeland, and others wished to introduce to North America all bird species that were mentioned in Shakespeare's works. Its initial successful establishment in New York was met with enthusiasm. People were paid to feed them, nest boxes were erected for them, legislation was enacted to protect it, and bounties were put on shrikes and hawks that might prey upon them. It spread rapidly and the enthusiasm quickly turned to annoyance. The legislation protecting it was repealed and bounties were placed on House Sparrows and removed from the predatory species. In a few days in 1899 in Boston, 6 men filled 5,000 nest holes, destroyed 4,000 nests, and broke 1,000 eggs. A sparrow shooting contest was held in Streetsville, Ontario in 1902 with the successful team

bagging approximately 3,000 (Curry 2006; Judd 1901; Lowther and Cink 2020; Robbins 1973; Walk et al. 2011).

The first introduction of the House Sparrow to North America consisted of 6 pairs that were released in Brooklyn, New York in the spring of 1851. These birds did not survive. In 1852, approximately 100 were brought from England. Fifty were released upon arrival and 50 were released the following year. These became successfully established and the rate of spread from the release site was a radius of 40 km in 5 years, 80 km in 10 years, and more than 160 km in 15 years. The public clamored for more releases and at least 19 shipments were released in the next year and liberated from New England to Utah. Numerous undocumented releases were made throughout the continent from stock that had already become established. It spread further by travelling in train boxcars and established populations at most settlements along railways. By 1886, its range included most of the eastern United States, southern Ontario, southwestern Quebec, and New Brunswick, with extensive thriving colonies in major cities in the western states. The eastern population peaked around 1890 and has been declining since (Bennett 1990; Kalmbach 1990; Robbins 1973).

The first successful introduction in Canada was in Quebec City. The House Sparrow appeared in Montreal around 1870 and was abundant by 1896 (Aubry in Gauthier and Aubry 1996). It was established in the Maritime Provinces in the 1880s (Erskine 2006). Around 1870, 10 pairs were released in Ottawa and an unknown number were released in Hamilton in 1872. It was first observed on the streets of Hamilton in 1875 and 2,000 were observed on a single day in 1943 (Curry 2006; McIlwraith 1894). Its early distribution and abundance is difficult to trace because it was held in such contempt that many people refused to acknowledge its presence. It was not included in the annotated checklists of the birds of Elgin County in 1891 or 1954, but would certainly have been abundant during both periods (Lancaster et al. 2004). Sheppard et al. (1936) reported that it was very abundant in Niagara Region. Populations appeared to be stable in rural areas but declining in cities and villages. In the Toronto area, its numbers increased or decreased depending upon the severity of the winter but the general trend was an increase in population (Fleming 1907). It was first reported during the breeding season in Algonquin Park in 1912 and bred sparingly in small settlements, particularly those along the railroad. The last confirmed nesting in the park was in 1967; by the 1970s, most villages had been abandoned and dismantled (MacLulich 1938; Tozer 2012). By the late 1880s, it was established at North Bay (Mills 1981). It was not reported in Sudbury in 1889 but occurred there in great numbers in 1901 (Baillie and Hope 1947). It has variously been reported in small numbers or absent in Moosonee and Moose Factory and first appeared there in 1911. It is likely that birds do not survive the winter but that new colonists occasionally arrive on the train (Barlow 1966; Manning 1952; Schueler et al. 1974; Weaver 1943). The most northern record for Ontario was a female collected in June 1940 at Fort Severn; it appeared to be the only House Sparrow that was present (Barlow 1966). Baillie and Harrington (1937) concluded that the House Sparrow was very common in suitable habitat throughout the province, and that it probably nested wherever it occurred. They had no breeding records for areas north of Lake of the Woods or Kapuskasing, where it was a common breeder in 1928. R.L. Weaver (1939) described its distribution in Ontario and concluded that it extended northward regularly as far as there was systematic cultivation. In northern areas, it was restricted to areas near railways, roads, and cultivated crops. The northern

boundary of successful establishment appeared to be the Great Lakes–St. Lawrence Forest Region from Lake Nipissing to Lake of the Woods. At that time, it was considerably less abundant in Toronto than it had been 30 years previously. The first atlas revealed a slightly more extensive northern range. It occurred in the Moosonee area, in the Lake Nipigon area eastward to the Quebec border at the same latitude, and north to Red Lake north of Lake of the Woods. It was absent in heavily forested landscapes of the southern Canadian Shield. It was reported in every square south of the Shield except for the extreme tip of the Bruce Peninsula and portions of Manitoulin Island; these areas are predominantly forested. It was a common to abundant resident south of the Shield. In the north, it was absent or rare to locally common depending upon remoteness, winter severity, food abundance, and winter shelter (Barlow in Cadman et al. 1987). James (1991) considered the House Sparrow a common to locally abundant permanent resident north to Georgian Bay and Ottawa, becoming increasingly uncommon and local to Red Lake and Moosonee, and a vagrant to the north coast.

The second atlas revealed no significant change in the breeding distribution of the House Sparrow since the first atlas. There were some contractions in the northern extent of its range, but many of these probably represented populations in isolated settlements. Its probability of observation declined significantly province-wide and in the Carolinian and Great Lakes–St. Lawrence forest regions. It also declined in the Boreal Forest Region and the Hudson Bay Lowlands but not significantly. The decline was most evident in the Shield portion of the Great Lakes–St. Lawrence Forest Region, probably due to an increase in forest cover. It was common only south of the Shield. It was most abundant in areas of intense agricultural operations and high human population. These included Ottawa and farmlands to its southeast, the Toronto and Hamilton area, the Niagara Peninsula and Haldimand County, and the farmlands and urban centres in Perth, Waterloo, Wellington, Oxford, Lambton, Essex, and Chatham-Kent (Lang in Cadman et al. 2007).

Breeding Bird Survey (BBS) results may underestimate declines of the House Sparrow because routes typically avoid urban areas. It is also possible that some surveyors did not include it in their counts in earlier years. BBS data for 1970-2021 indicate that it decreased at annual rates of 3.08% in Canada and 3.32% in Ontario. For 2011-21, the annual rates of decrease were 2.38% in Canada and 2.47% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young are capable of more or less sustained flight when they leave the nest, unless they are disturbed and fledge prematurely. Fledglings are typically cared for by the male and remain with him 7-10 days after leaving the nest. After this, juveniles congregate together into foraging and roosting flocks (Lowther and Cink 2020; McGillivray 1984).

Both juveniles and adults are most mobile during the postbreeding period, which extends into late autumn. Fledglings are being produced by May and by June they begin to gather in flocks. By then, food may be scarce in urban areas. These flocks move into rural areas where they feed on small grain crops. Flocks of juveniles are joined later by adults when they cease to breed. These flocks may number in the thousands of birds, but start to break up in October. In Oklahoma, birds returned to urban areas in October and remained there until the following June (Kalmbach 1940; Lowther and Cink 2020; North 1973).

Communal nocturnal roosts are important during the postfledging period. The House Sparrow establishes flyways between roosts and feeding areas and there is a general movement out of urban centres as the season progresses, especially by juveniles. In Oklahoma, 7.5% of birds in fields were adults compared with 48.8% in the urban centre. Birds left the roost in the morning in small flocks of 2-25 birds, but returning flocks may contain more than 100 birds. Specific flight lines were used. Early in the season, routes were more indirect, becoming increasingly direct with continued use. In early May, flocks foraged in pastures and cut hayfields close to the city and began feeding in standing and harvested grain in June. At this time, few birds fed more than 800 m from the city. In late July, sorghum fields were visited and were used into October. Few birds travelled further than 3.2 km between roosts and feeding areas, but some moved as far as 4.8 km. When returning to the roost, birds often stopped in feeding and staging areas at the edge of the city. These had a supply of food and trees and shrubs for cover. Communal roosts tended to be in areas of the city where buildings protected trees from the wind. There were no roosts in or near the field where birds fed daily. Roosts were abandoned late in autumn once the leaves dropped. At this time, birds moved to more numerous, smaller, and more sheltered roosts for the winter (Kalmbach 1940; North 1973).

M. Brown (1972) described what appeared to be migratory behaviour in October on an island in New Jersey. He observed numerous flocks of 10-30 House Sparrows flying at a height of about 30 m. He estimated 400 in 30 flocks within a half hour, but more could have passed through. They appeared to be doing a reverse migration to the mainland. The birds that were moving may have come from densely populated areas further north. When the tourists leave, there is a critical shortage of food and the House Sparrow must move or perish. This is the only report of possible migration in North America, but it appeared to be a local response to food shortage rather than true migration.

WINTER

Winter habitat for the House Sparrow is the same as the breeding habitat, consisting of urban areas and rural sites where there are livestock or small grains. Most birds remain in the same area year round, but some may move from urban areas to rural areas for the winter or vice versa depending on which areas provide the most food (Root 1988). In Toronto, it was least abundant in January and started increasing in February to a peak in September, falling to winter levels in October (R.L. Weaver 1939). In Muskoka and Parry Sound districts, it is found only locally and mostly in larger cities in winter but occasionally occurs around active farms (Mills 1981). In southern Ontario, Smith (2003) used results of Winter Bird-Population Studies to characterize its habitat. It was recorded exclusively in cities and urban natural areas. Densities per km^2 were 150.3 in city commercial or residential areas, 46.2 in urban natural areas smaller than 10 ha, 8.4 in urban natural areas with water, and 0 in cultivated fields with hedgerows and mixed rural areas. Nonetheless, it does occur in rural areas near farms or feeders (personal observation). In Kansas, large flocks frequented almost every farmyard and it was common wherever grain was grown or livestock was kept. Flocks often occurred in thorny trees and shrubs that bordered grain fields or were close to farm buildings (Fitch 1958). Along an urban gradient in California, it was significantly correlated with structures and negatively correlated with trees (Kalinowski and Johnson 2010). In Illinois, it was absent in bottomland and upland forest and occurred solely in urban residential areas; agricultural lands were not surveyed (Graber and Graber 1979).

Roosts are even more important in winter because they help the House Sparrow conserve energy. In more temperate areas, individuals may roost in nest boxes or other nest sites. Where winters are more severe, it constructs feather-lined structures in nest boxes and crevices in buildings. Birds may huddle together in cold temperatures and huddle closer as the temperature drops. Near the northern extent of its range, it may select heated areas for nocturnal roosts including inside grain elevators, attics, soffits, livestock barns, and structures such as light fixtures, street lights, and electric signs. In Missouri, it roosted in a subterranean transformer vault. Birds entered through a grate and roosted under the concrete roof about 1 m underground (Anderson 1998; Burns et al. 2013; Campbell et al. 2001; Jehl 2004; Jehl and Smith 1970; Kalmbach 1940; Marti 1974).

Adults may defend their former nest sites during the winter and also use them as roosts. In winter, juveniles visit multiple nest boxes or other potential nest sites to prospect for nest sites (Lowther and Cink 2020; Sánchez-Tójar et al. 2017).

The House Sparrow is highly vigilant and skittish when feeding in winter. As the number of birds in a flock increases, the amount of time spent scanning for predators decreases and the amount of time feeding increases (Studd et al. 1983). Dominant males with larger bibs spend less time being vigilant and more time feeding (Boujja-Miljour et al. 2018). Of 305,087 House Sparrows foraging events at feeders, white proso millet was the dominant seed consumed (by 70% of birds), followed by black oil sunflowers (5%), cracked corn (5%), 0.3-mm sunflower chips (3%), and 0.5-mm sunflower chips (2%). It did not eat niger seed, red milo, safflower, striped sunflowers, or whole peanuts. Factors such as presence of a hull on the seed, protein content, fat and fibre content, seed volume, and ratio of bill to seed volume were not good predicators of food choice (Johansen et al. 2014). It preferred tube feeders over platform and hopper feeders (Horn et al. 2014). The House Sparrow is a common and consistent visitor to feeders all winter. It is less likely to visit rural feeders but is equally abundant at rural and urban feeders. Flock size declines steadily as winter progresses. Favourite feeder foods include mixed seeds, millet, black oil and hulled sunflowers, cracked corn, milo, baked goods, popped corn, and barley. Infrequent choices include canary seed, striped sunflowers, whole corn, wheat, niger seed, hulled peanuts and hearts, canola, pet food, peanut butter mixes, bird puddings, dried fruit, and sugar water (Dunn and Tessaglia-Hymes 1999).

Severe winters may result in extensive mortality. Heavy snow cover in rural areas may cover food and result in widespread starvation. Cold weather may cause mortality even when there are sufficient food resources. From the Sudbury and Algonquin Park areas northward, local populations may be extirpated in winter and this has been documented in numerous other northern locations (Campbell et al. 2001; Erskine 1977, 2006; Jehl and Smith 1970; Kalmbach 1940; MacLulich 1938; Root 1988; R.L. Weaver 1939). Large females and small males have lower survival fitness and are less likely to survive the winter (Johnston and Fleischer 1981).

Most surveys conducted in winter demonstrated that the House Sparrow population is declining in Ontario. Freedman and Riley (1980) analyzed results from Christmas Bird Counts (CBC) in southern Ontario 1929-77. Numbers were relatively stable over this period. Both the CBC and Project Feeder Watch (PFW) results for Ontario 1977-97 indicated a significant decline. The PFW abundance index averaged about 9 1977-89, dropped to 3-4 in 1990 and 1991, and was down to 1 by 1997. Over the same period, the CBC abundance index dropped from 40 to less than 5 (Lepage

and Francis 2002). Curry (2006) reported that the Hamilton CBC peaked at 3,900 in 1966 followed by a sharp drop to 1,717 in 2005 with a 10-year average of 2,064. CBC results for Ontario indicate that it decreased by 6.15% annually 1970-2021 and 3.54% 2009-21 (National Audubon Society 2022).

American Pipit

Anthus rubescens

BREEDING SEASON

Habitat Requirements

Ontario American Pipit nests were on dry tundra areas on raised gravel ridges or beside tundra ponds (Peck and James 1987). In Ontario, it breeds only in the Tundra Region and Hudson Bay Lowland, predominantly on coastal tundra. Preferred habitat is relict gravel and boulder-strewn beach ridges within 20 km of the Hudson Bay coast. It also occurs locally inland on extensive, open palsa plateaus (Sutherland in Cadman et al. 2007). Manning (1952) reported that it bred at Little Cape where it was observed most frequently among driftwood and boulders near the top of the coastal storm beach.

The American Pipit typically nests in arctic or alpine tundra which differ from each other and the gravel ridges that are inhabited in Ontario. In the arctic, it usually avoids flat areas, although flat areas are occasionally used. Nesting has occurred on the Iqaluit airport on Baffin Island. Preferred habitats in the arctic are moss-grown slopes with southern exposures, sunny ravines cut into bluffs, rocky slopes near streams, sheltered meadows on south-facing slopes, high rocky ridges along Hudson Bay near Churchill, and granite ridges. It is very common in rocky habitat and absent in wet tundra with no granite outcrops. The extensive lowlands of Baffin Island are less suitable than the rugged slopes and support a much smaller population; it was infrequent in the high plateau-like interior. Favoured areas were completely free of wind even in adverse weather and warm when the sun was

out. Insects and spiders tend to be common in these areas even when it is windy. Mosquitoes were often a good indicator of suitable pipit habitat. The pipit is closely correlated with the most mesophytic vegetation and areas with the highest diversity of plant species. Many nesting areas are slowly watered by melting snow from above, contributing to development of mesic plant communities, often dominated by mosses, lichens, heather, and horsetails, and creating habitat suitable for mosquito breeding (Bray 1943; Drury 1961; Freeman 1970; Jehl and Smith 1970; Manning et al. 1956; Parmelee et al. 1967; Soper 1946; Sutton and Parmelee 1954; Wynne-Edwards 1952).

In alpine habitats above the treeline, the pipit breeds in the Rocky Mountains as far south as New Mexico. In these areas, it nests in mesic meadows, barren lava flows with scattered dead or dying trees and minor amounts of herbaceous vegetation growing in cracks and crevices, sparsely vegetated alpine tundra, heath meadows, more richly vegetated meadows, boulder fields, scree slopes with scattered vegetation between rocks, cliff ledges, and gravelly streambeds. Territories in Wyoming alpine areas included fell-fields (at least 40-50% rock and soil with most vegetation shorter than 2 cm, but with scattered plants as tall as 15 cm) and wet meadows, on level to steeply sloping ground, and on bare to well vegetated surfaces. The 2 main habitat requirements were that a site must become ice-free soon enough for nesting and it must have some rough features such as tussocks, tilted rocks, or eroded spots for nest sites. In British Columbia, most nests were in well vegetated sites, usually on sloping hillsides where there were overhanging clumps of vegetation, sod, and stones for nest sites. In California, nesting occurred in exposed gravel shorelines around alpine lakes (Anderson 1989; Campbell et al. 1997; Hendricks and Verbeek 2020; Miller and Green 1987; Norris and Morgenson 1982; Sinclair et al. 2003; Verbeek 1970).

Pipits typically arrive at the breeding area before all the snow has melted. The first birds occupied snow-free areas in Wyoming, but frequently abandoned these areas before the good weather set in (Verbeek 1970). In Washington, territories consistently had snow in them. As the snow melted, these areas became more hydric and supported taller vegetation than other areas. Territories may not be selected for the snowfields themselves, but for the vegetation that the melting snow provides (Norvell and Creighton 1990).

Ontario nests were cups sunken into the sides of heath and lichen hummocks. One had a short tunnel entrance overhung by a heath plant, and this appears to be the only reported nest with a tunnel. Another nest was overhung by a clump of earth (Peck and James 1987).

Throughout its range, the pipit always nests on the ground and the nest typically has a recognizable entrance. Nests are rarely exposed from above, but most are under overhanging rocks, sod, or vegetation. Nests are frequently built into the side of a tussock with vegetation overhanging the nest, but they may be under rocks or in fissures in rocks. The female scrapes out a small depression in the ground prior to building the nest, or rarely builds the nest over the entrance of a small mammal burrow. In alpine areas south of Canada, most nests are oriented northwest to northeast. In these areas, temperatures may become very hot so nests are orientated to avoid direct sunlight and prevent discomfort to the incubating female. Nests in the arctic, including areas as far south as the Belcher Islands, face southward, presumably to take advantage of the warm sun in colder climates. Old nests are occasionally reused. When this occurs the female may remove the old nesting material or simply add to it (Bent 1950; Campbell et al. 1997; Drury 1961; Freeman 1970; Hendricks and Verbeek 2020; Johnson 1933; Norris and Morgenson 1982; Pickwell 1947; Sinclair et al. 2003; Soper 1946; Sutton and Parmelee 1954; Verbeek 1970, 1981; Wynne-Edwards 1952).

The American Pipit defends a territory and may be aggressive to Horned Larks, Pine Siskins, and Brewer's Blackbirds. Silent pipits that are feeding may sometimes intrude into neighbours' territories without fights. At other times, intruders may be attacked. Almost everywhere throughout its range, large areas of suitable habitat are unoccupied. This allows pipits to feed outside their territory without being accosted. Most foraging occurs within 150 m of the nest, but some birds travel as far as 300 m to forage. In Wyoming, 5 territories averaged 0.18 ha (range 0.16-0.36 ha). Larger territories have been reported elsewhere, but the foraging area outside the defended area may have been considered part of the territory. In California, the territory of 1 bird was several 100 m in diameter, but consisted mostly of snow with small meadows of heather and grass. The average territory size in Utah was 0.7 ha; territories were 1.7-2.1 ha in the Rocky Mountains in Colorado (Drury 1961; Hendricks 1987a; Hendricks and Verbeek 2020; Pickwell 1947; Verbeek 1970).

Natal philopatry rates appear to be very low, although there are limited data. In Wyoming, 1 of 222 nestlings (0.5%) returned to breed the following year (Verbeek 1970).

Hendricks (1991a) banded 32 nesting females in Wyoming and 4 (12.5%) returned the following year; 1 returned a second year. Two returning birds nested 34 m and 37 m from their previous year's nest. The female that returned in 2 years had her final nest 24 m and 38 m from her earlier nests. It was uncertain whether the low return rate of females was due to dispersal or mortality. Also in Wyoming, 1 of 9 adult females (11%) returned and nested about 400 m from her previous nest (Verbeek 1970).

Limiting Factors

Eggs are most likely to be present in Ontario nests during the first 3 weeks of June (Peck and James 1987). An average of 5.1 days elapse from when the female excavates the nest hollow until the first egg is laid. The interval between nest completion and laying of the first egg is 1-3 days. Initiation of egg laying appears to be related to air temperature. Initiation of egg laying in Wyoming occurred after 4 days with an average temperature of 7.3-8.2°C. It takes 4 days for the female to develop an egg and once she has, she is committed to laying. Eggs are normally laid at the rate of 1 per day, but occasionally a day is skipped. Size variation in broods of 6 suggests that incubation may begin before the clutch is complete, at least in large clutches. On Baffin Island, the incubation period was just a

few minutes less than 12 days. In Wyoming, the average incubation period was 14 days 10 hours (range 13 days 18 hours to 15 days 19 hours). It has been suggested that reported incubation periods of less than 13 days were likely in error, but it is possible that arctic-breeding birds have shorter incubation periods. On Baffin Island, the nestling period was 12-14 days; the mean nestling period in Wyoming was 14.0 and 14.2 days (range 12-15 days). The entire breeding cycle takes about 50 days from nest building until independence of the young (Hendricks and Verbeek 2020; Johnson 1933; Sutton and Parmelee 1954; Verbeek 1970; Wynne-Edwards 1952).

A single brood is raised annually. In the arctic and alpine habitats where the American Pipit breeds, the breeding season is too short to raise a second brood. Renesting may occur if a clutch is lost, but renesting often does not occur, particularly if losses occur late in the season. The female may continue laying in a nest if an egg is lost, but not if the first egg is lost. After nest loss, many females abandon the territory and general area. Those that renest build a new nest, usually within the same territory or in undefended areas adjacent to the original territory. Four replacement nests were an average of 36.8 m from the first nest. The first egg in replacement clutches appeared an average of 5.5 days after the first nest was lost. Two replacement clutches had the same number of eggs as the first, 1 had 1 less egg, and 1 had 1 more egg. Clutches or broods of 4-6 have been reported from Ontario. The overall clutch size is 3-7 eggs with 5 or 6 eggs most frequent. In Wyoming, the mean clutch size remained stable in June but declined around mid-July. The mean clutch size increases significantly with latitude. In Wyoming, 5 eggs was the most frequent clutch size and 6- and 7-egg clutches were rare. On Baffin Island, all clutches contained 5-7 eggs. The larger clutch sizes in the north are unrelated to daylength and are because birds in arctic areas initiate nesting earlier than those in more southern alpine areas (Bent 1950; Campbell et al. 1997; Hendricks 1991a, 1991b, 1997; Hendricks and Norment 1992, 1994; Hendricks and Verbeek 2020; Peck and James 1987; Verbeek 1970, 1981; Wynne-Edwards 1952).

The age at first breeding is 1 year. It is likely that most birds are monogamous, but 1 Wyoming male attended 2 nests concurrently that were 120 m apart (Hendricks 1987a; Hendricks and Verbeek 2020). Intraspecific parasitism appears to be rare. Four Wyoming nests were apparently parasitized by other female pipits, with 2 fresh eggs occurring within them in a single day (Hendricks and Verbeek 2020).

Most foraging occurs by walking through thick moist vegetation, often along stream banks, in meadows at the crests of bluffs, on frost-heaved barrens on slopes, on south-facing slopes, on mud and pebble shorelines of lakes, on snowfields, on drifted sea wrack along the coast, and in salt or brackish marshes along tidal streams. The American Pipit tends to forage at the edge of vegetation, weaving in and out of open and vegetated areas. It forages mostly by walking often simply walking from the nest to forage, but it may run to capture food. It occasionally makes short flights from the ground or boulders to pursue prey. Less frequent foraging techniques include wading in shallow water to capture aquatic invertebrates and perching in branches of tall plants growing in shallow water and reaching for insects among heads of plants. Birds in a flock were observed flying 0.9-1.2 m above ground capturing moderately sized flying beetles then dropping back to the ground. In Ungava Bay, birds fed on maggots at whale carcasses. During the breeding season, birds forage alone. Members of a pair leave the nest in different directions and forage in different areas to avoid

competition for resources. In Wyoming, the area used for foraging by 6 pairs averaged 6.7 ha (range 3.3-10.1 ha); 5.3 ha (range 1.8-10.1 ha) for males and 3.6 ha (range 2.2-6.6 ha) for females. Each foraging area contained portions of all 4 major habitats that were present. Males tended to visit tundra meadows and snowfields more than females. Females tended to visit fell-fields and stony areas more than males. In alpine areas, snowfields offer a unique foraging substrate. Thermal winds carry insects up from lower altitudes and deposit them on snow where they are abundant, easily detected, and often moribund and easy to capture. Despite the abundance of suitably sized prey, snowfields are used considerably less than their availability for foraging. In Washington, 89.9% of birds were seen on snow-free surfaces. In Wyoming, 19.6% of time was spent foraging on snowfields, 19.6% on fell-fields, 17.7% in rocky meadows, 31.4% in grassy meadows, 6.5% in shrub growth, and 1.3% in treed areas. During summer snowstorms, the pipit feeds in snow-free pockets on the leeside of rocks, hummocks, and shrubs. Peak visitation to snowfields corresponds with the maximum density of arthropods in this habitat which is in mid-July and in mid- to late afternoon when updrafts are most likely to be depositing invertebrates. Avoidance of snowfields may be because foraging pipits are conspicuous on snow and may be more vulnerable to predation (Bent 1950; Drury 1961; Hendricks 1987a, 1987b; Hendricks and Verbeek 2020; Norris and Morgenson 1982; Norwell and Creighton 1990; Pickwell 1947; Verbeek 1970).

In Wyoming, most food supplied to nestlings was 5-10 mm long. In California, the mean length of food provided to nestlings was 8.05 mm (range 2-22 mm). Two percent of nestling food items were less than 3 mm in length, 86% were 3-6 mm, and 12% were longer than 6 mm. In Wyoming, stomach contents of 25 nestlings 4-14 days old consisted of insects and grit; grit was absent in stomachs of nestlings younger than 4-5 days. Vole and squirrel molars were found in nestlings' stomachs. The mammal teeth were probably picked up from the ground and do not indicate that these animals had been eaten. In another Wyoming study, of 62 prey loads delivered to nestlings, lepidopterans were identified in 71.0% of deliveries, flies in 19.4%, spiders in 6.5%, grasshoppers in 1.6%, and flying ants in 1%. In Labrador, nestlings ate mostly flies and small larvae, including 1 large grub. In California, 95% of nestlings' diet consisted of flies plus aphids, seed bugs, and jumping plant lice. During the breeding season, adults eat almost 100% insects plus a few seeds, small snails and crustaceans, and wild berries. In Wyoming, the diet of adults consisted of 58.3% flies, 11.1% bugs, 11.1% moths, 2.1% millipedes, and 0.7% snails. Other arthropods eaten during the breeding season included emerging stoneflies, crane flies, mayflies, lacewings, dragonflies, caddisflies, and spiders. The diet in Colorado consisted of 10.0% orthopterans, 9.7% bugs, 6.0% beetles, 25.1% lepidopterans, 25.1% flies (10.7% crane flies, 7.5% stilleto flies), 1.9% ants, 14.7% mites and spiders, and 8.2% miscellaneous. Along marine shores, the American Pipit may forage in tidewater pools where it feeds on marine worms and crustaceans (Bent 1950; Hendricks 1987a, 1987b; Hendricks and Verbeek 2020; Johnson 1933; Pickwell 1947; Verbeek 1970; Wynne-Edwards 1952).

The most significant limiting factor to the American Pipit is snowstorms and other adverse weather during the breeding season. A severe thunderstorm on Baffin Island killed at least 1 adult and most nestlings perished from exposure, starvation, or both. A July snowstorm in Wyoming covered nests with 15-30 cm of snow. The researchers dug out all the nests, but a high percentage of young still perished. Without human intervention, probably all young would have been lost.

Nestlings younger than 11 days probably died of exposure; older birds died of starvation. Prolonged periods of wet, windy, or foggy weather may reduce insect availability and result in death of nestlings due to starvation or exposure (Drury 1961; Hendricks and Norment 1992; Hendricks and Verbeek 2020; Sutton and Parmelee 1954).

High temperatures are injurious to developing embryos. Exposure of eggs to direct sunlight when the female is off the nest can kill embryos even if temperatures are fairly low. In Wyoming, there was a correlation between the incidence of addled eggs and unusually warm weather at a subalpine site (Hendricks and Norment 1994).

Status

Breeding evidence for the American Pipit in Ontario was first established when Manning (1952) collected recently fledged young near the mouth of the Sutton River in 1947. He concluded that it nested in small numbers in a few locations along the Hudson Bay coast. The first nest was found at Cape Henrietta Maria on 29 June 1948. Other early breeding and nest records were from Fort Severn and radar sites 415 and 416. It was concluded that it probably nested all along the Hudson Bay coast (Baillie 1962; Peck 1972; Peck and James 1987). Wilson and McRae (1993) concluded that it nested at Shagamu. During the first atlas, 16 breeding records were obtained, all from coastal tundra from the Manitoba border east to Cape Henrietta Maria, again indicating that it nests in suitable habitat all along the Hudson Bay coast (Peck in Cadman et al. 1987). James (1991) considered it a common summer resident along the Hudson Bay coast.

The second atlas revealed that there had been no significant changes in the distribution or probability of observation of the pipit since the first atlas. Prior to this atlas, all breeding records had been within 20 km of the Hudson Bay coast, but breeding evidence was found in 4 squares 38, 38, 53, and 65 km inland. It is likely that it breeds all along the Hudson Bay coast and along the northern James Bay coast as far south as latitude 54°N. Highest density appears to be in the vicinity of Cape Henrietta Maria where there are more extensive areas of suitable beach ridge habitat (Sutherland in Cadman et al. 2007).

Breeding Bird Survey data indicate that the American Pipit declined in Canada at annual rates of 3.16% 1970-2021 and 1.58% 2011-21, but results were of low reliability. No population trends are available for Ontario (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Some young are not capable of flying when they leave the nest but others may be able to fly short distances. The young appear to make no effort to feed themselves the first 2 weeks after fledging and are highly dependent upon the adults during this period. Young may be partially dependent for 6 weeks after fledging (Hendricks and Verbeek 2020).

In Wyoming, postfledging young were most likely to inhabit rock slides or strips of rock (Vermeer 1970). In Labrador, 3 young with 1 or both their parents frequented an area about a woodpile and house approximately 300 m from the nest. They were seen there for 2.5 weeks after fledging. Another family was frequently seen in this area, but no brood mixing occurred (Johnson 1933).

MIGRATION

The American Pipit migrates during the day, usually in loose, straggling flocks of a few to several hundred. Single birds may also occur during migration. Autumn flocks are typically much larger than spring flocks. The timing of initiation of autumn migration is uncertain. In late summer, at least part of the local population moves and is replaced by other birds. Adults moult in mid-August and flocks at this time are comprised mainly of juveniles. By the end of August, adults flock with juveniles and flocking behaviour becomes stronger toward early September (Bent 1950; Hendricks and Verbeek 2020; Verbeek 1970).

In southern Ontario, spring migrants pass through from late March until the end of May (Speirs 1985). Wilson and McRae (1993) saw spring migrants at Longridge on 8 and 9 June, at Ekwan on 19 June, and at Shagamu from 28 May to 9 June. Manning (1952) reported that the pipit occurred all along the western James Bay coast during autumn migration and observed a large flock on 29 September several kilometres inland on the Hayes River above York Factory. Wilson and McRae (1993) saw migrants at Shagamu 20-30 August, at Ekwan on 12 September, and migrants were common at Longridge 4-13 September. In the southern Shield, most pass through between mid-September and mid-October with early arrivals in mid-August and stragglers until mid-November (Mills 1981; Tozer 2012). In southern Ontario, autumn migration is from mid-September until mid-November (Speirs 1985). There is often a noticeable peak in numbers at the end of October or early November. If there is no snow cover, some birds may linger into late December or January (Black and Roy 2010; Curry 2006; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Weir 2008).

During migration, the pipit inhabits open areas that are often unvegetated. In Ontario, it is most often observed in freshly plowed fields, along the shorelines of Lake Ontario and Lake Erie, on rocky shores of islands in the Kingston area, in stubble fields in autumn, in forest clearings, in gravel pits, in moist meadows in open country, and on shores of ponds, creeks, and inland lakes (Curry 2006; LaForest 1993; Lancaster et al. 2004; McIlwraith 1894; Tozer 2012; Weir 2008). Similar migration habitat requirements have been reported elsewhere. It may prefer mudflats and river banks during migration, but significant numbers are found on beaches and plowed and stubble fields, and it has been recorded in gravel pits, landfills, short-grass pastures, along roadsides in forested areas, on river gravel bars, at airports, and on playgrounds. At Churchill, birds congregated around grain elevators to feed on waste grain (Bent 1950; Campbell et al. 1997; Falardeau in Gauthier and Aubry 1996; Hendricks and Verbeek 2020; Jehl and Smith 1970; Leighton et al. 2002; Sinclair et al. 2003).

The pipit usually feeds in loose flocks during migration and winter (Hendricks and Verbeek 2020). In Utah, Knowlton (1944) collected 103 birds that were foraging in alfalfa and wheat stubble fields and along roadsides. Of 3,450 food items, 56.3% were true bugs (47.5% seed bugs and 1.6% plant bugs), 16.3% beetles (12.2% weevils, 2.2% scarab beetles, and 1.0% rove beetles), 14.0% weed seeds, 6.0% soft-winged bugs (2.7% leafhoppers and 2.6% aphids), 3.1% lepidopterans, 1.7% hymenopterans (0.6% ants), 0.9% orthopterans (0.8% crickets), 0.9% flies, 0.6% springtails, 0.3% spiders, 0.1% thrips, and 0.1% bristletails. Two birds collected during autumn migration had eaten 10% vegetable matter (violet seeds) and 90% animal material: 37% beetles (ground beetles and weevils), 33.5% caterpillars, 8% plant bugs, 7.5% spiders, 2.5% flies, and 1.5% hymenopterans (Bent 1950).

Hendricks and Verbeek (2020) concluded that forest clearing probably improved habitat for migrating pipits, but that wetland drainage had the opposite effect. Less habitat is available as marginal farmland reverts back to forest or is converted to other uses.

The American Pipit is a rare to locally common spring migrant in Ontario and a common autumn migrant (James 1991).

WINTER

Root (1988) concluded that wintering pipits were most abundant where there is moist habitat along streams and ponds and also numerous irrigated fields. Wintering areas in the east are generally where the minimum January temperature is higher than −1°C, but it occurs in areas as cold as −7°C in the west. It is often found in fields containing very little vegetation. When snow covers fields, it often forages along plowed roads. Hendricks and Verbeek (2020) concluded that it avoided regions that had persistent snow on the ground, and that it used similar habitat in winter as during migration. Ontario is north of the typical wintering range of the pipit and is marginal winter habitat because of the snow cover. Keyser et al. (2023) considered it an avoider of snow that selected areas where there were frequent temporal changes between snow cover and bare ground.

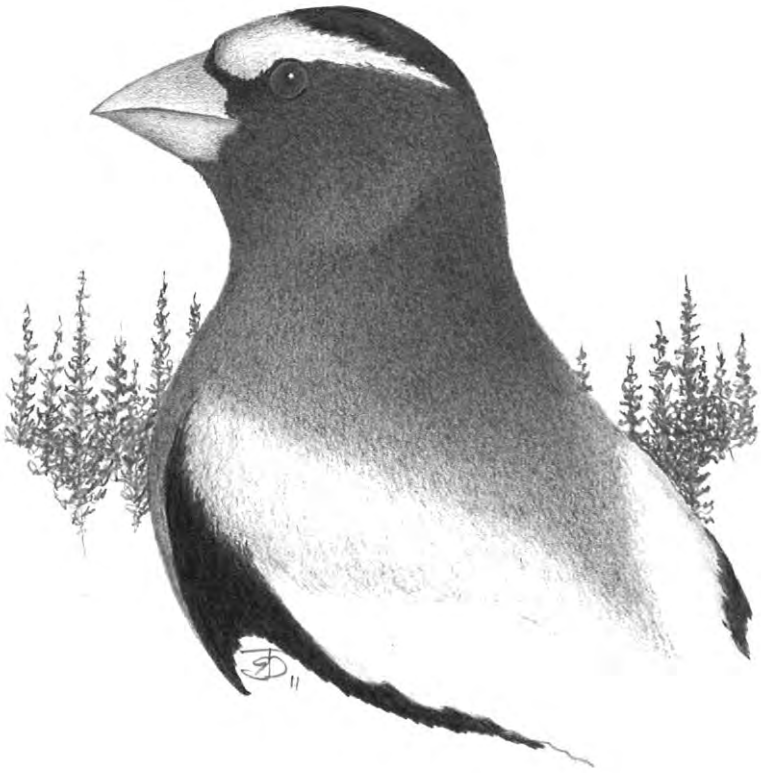
In winter in North Carolina, the pipit was seen only in the largest hayfields, in winter-wheat fields, and in old cornfields where the corn stalks were all down. It was not observed in plowed fields. In Florida, it occurred in prairies, old fields, and marshes, and occasionally on sand dunes and sea beaches (Bent 1950). Campbell et al. (1997) reported usage of similar habitats by the pipit in winter in British Columbia. In addition, it occurred on golf courses and playing fields, at sewage lagoons and airports, and on tidal flats and river estuaries.

James (1991) reported that the American Pipit was an occasional and rare winter resident in the south, north to Peterborough. In the Hamilton area, there are only 3 records of birds overwintering, all single birds (Curry 2006).

CBC data for Ontario for 1970-2009 indicate that the American Pipit is rare in winter and that observations of it increased during that time. It was not recorded on any counts in the province in the 1970s. The 2000s were the first decade in which the pipit was recorded every year, but numbers observed were quite low. Ontario trends determined by CBC data indicated an annual increase of 7.28% 1970-21 and an annual decrease of 14.88% 2009-2021 (National Audubon Society 2022). It is probable that many birds observed on CBCs are late migrants rather than wintering birds.

Evening Grosbeak

Coccothraustes vespertinus



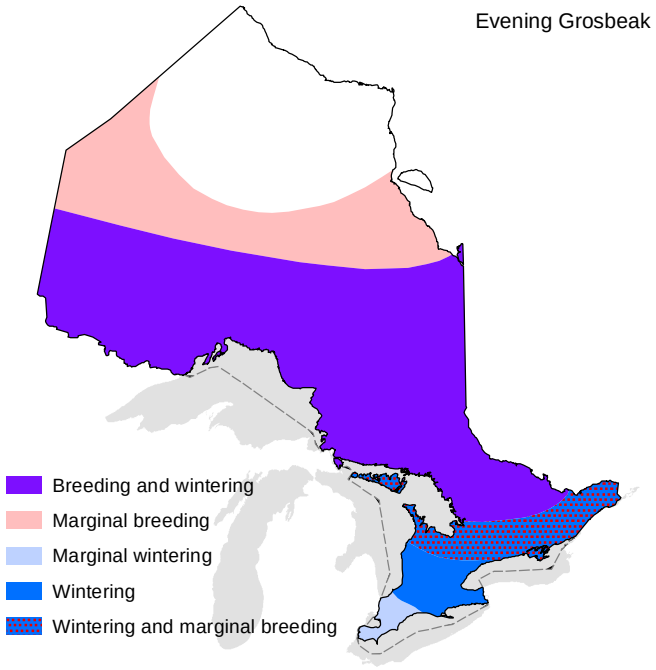
BREEDING SEASON

Habitat Requirements

Ontario Evening Grosbeaks breed in second-growth and mature forests. Five nests were in mixed-wood forests, 1 was in an open coniferous forest, and 3 were in unspecified forest types (Peck and James 1987).

In the Hudson Bay Lowland, Schueler et al. (1974) reported the Evening Grosbeak nesting near Moosonee in a spruce stand, the most northern record at that time.

In the Clay Belt in the Boreal Forest Region, the Evening Grosbeak was most frequent in white spruce stands followed by stands dominated by white spruce–balsam poplar, black spruce, jack pine, and tamarack–white cedar. It was absent in stands dominated by trembling aspen. It occurred in mesic to wet stands, but not in dry stands. It was present along the entire nutrient-richness gradient (Welsh and Lougheed 1996). Near Hearst, it occurred in upland mixed stands, including an unharvested stand and clear-cuts 3 and 17 years old (Welsh and Fillman 1980). Those detected in clear-cuts may have been foraging rather than nesting. Near Manitouwadge, it was absent in stands



1-21 years old, occurred in low density in stands 24-36 years old, and was 6.7 times more abundant in stands 60-223 years old (Venier et al. 2009).

In jack pine stands near Gogama in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, most observations of Evening Grosbeaks were of birds simply flying over. James and Peck (1995a) concluded that it could feed in any pine or mixed forest more than 10 years old, but would likely nest only in areas with mature trees. In Algonquin Park, it nested in a second-growth mixed forest of white pine, black spruce, white spruce, balsam fir, and white birch (Hope 1947). It was associated with coniferous forests in Algonquin Park, but not those dominated by white pine. Kingsley and Nol (1999) found it in all age classes of white pine forests, but many observations may have represented birds foraging distant from their nests. In white pine stands throughout the Shield portion of the Great Lakes–St. Lawrence Forest Region, it was 2.5 times more abundant in old-growth than mature stands. It was positively correlated with the mean patch size of pines (Kirk et al. 2012). Results from the Ontario Forest Bird Monitoring Program suggested that it was sensitive to the amount of habitat available at the 3.2- and 24-km scales (Savignac 2016).

At the landscape level, the Evening Grosbeak selects habitat based upon food availability. Its presence is highly correlated with outbreaks of spruce budworms or other tree defoliators. It is strongly associated with coniferous and mixed forests, particularly those dominated by white spruce and balsam fir because these are the main species attacked by the spruce budworm. In Quebec, it occurs at low frequency in northern, more boreal forests dominated by black spruce because spruce budworms are much less likely to be attracted to this species. The spruce budworm typically attacks only older stands and thus the Evening Grosbeak is associated mostly with mature and old-growth stands (Erskine 1977; Gillihan and Byers 2020; Vincent in Gauthier and Aubry 1996).

The Evening Grosbeak nests predominantly in mature mixed and coniferous stands throughout its range, and much less frequently in deciduous woods (mostly in the west). Most forests it nests in have a diverse structure and a fairly open canopy. In the east, these forests have a high proportion of balsam fir, white spruce, and trembling aspen. In the west, it may be common in mature and old-growth trembling aspen stands and mixed conifer–trembling aspen stands. In the Upper Peninsula of Michigan, it breeds in hardwood forests but moves to jack pine stands during spruce budworm outbreaks (Campbell et al. 2001; Flack 1976; Gillihan and Byers 2020; Savignac 2016; Scott and Bekoff 1991). In Quebec, Falardeau et al. (1999) detected it in low densities in strip-cuts, but it is most likely that it was feeding in this habitat rather than breeding. Dawson (1979) considered it locally common

in northeastern lowland conifers. It was absent in open bogs and shrubs with scattered conifers, uncommon in young or low black spruce, common in intermediate-aged to mature black spruce stands, and occurred in moderate densities in tamarack and white cedar stands. In the Prairie Provinces, it was in a guild associated with coniferous trees. It occurred on sites that were dry and rich in nutrients (Kirk et al. 1996). In Saskatchewan, it was most common in white spruce stands and mixed stands, and least common in trembling aspen stands, although the differences were not significant. It was more common than expected in contiguous forest (Hobson and Bayne 2000). In British Columbia, Campbell et al. (2001) considered it a habitat generalist that nested in a variety of coniferous, mixed, and deciduous forests. It made little use of black spruce–tamarack bogs or pine stands. In the south, presence of the western spruce budworm was an important predictor of its breeding patterns and densities. In the Yukon, it was most common in or at edges of old-growth white spruce stands. It inhabited stands that were structurally complex, with a lush shrubby understorey, standing dead trees, downed woody debris, and scattered old trembling aspens and balsam poplars (Sinclair et al. 2003). There is 1 record of a nest in an orchard (Speirs in Austin 1968).

In Oregon, nesting sites were significantly more open than unused areas, with fewer deciduous stem intersects, lower deciduous canopy cover, fewer large clumps of shrubs, and less shrub dispersion. Vegetation at nesting sites was less dense and more dispersed than in non-nesting areas. Open areas allow high visibility for detecting predators, allow easier departure and arrival at the nest, and allow better thermoregulation (Bekoff et al. 1987). Another Oregon study determined that this grosbeak's distribution was associated with beaked hazel. Forest openings where hazel and other deciduous species' buds occur may provide a food source (Gillihan and Byers 2020).

The Evening Grosbeak is typically associated with mature or old-growth forests. In boreal mixed-wood forests in Saskatchewan, its probability of detection was 0% in stands 50-60 and 80-90 years old, 20-49% in stands 100-110 years old, and 50-79% in stands older than 140 years; these differences were significant (Cumming and Diamond 2002). In the Prairie Provinces, it occurred only in stands 80 or more years old. It was 1 of only 4 species that was detected exclusively in old stands (Kirk et al. 1996).

Ontario nests were in living trees, with coniferous trees selected more than deciduous trees. Nest-tree species included white pine (2 nests), white birch (2 nests), and 1 nest each in white cedar, balsam fir, black spruce, and white spruce. Nests were in crotches of trees or forks of branches, often within 2 m or less of the top of the tree. An equal number of nests were against the tree trunk or 1-3 m distant from it. Nests were 7.5-16.8 m from the ground, with most 9.3-15 m up. Many were very well concealed and invisible from the ground (Devitt 1944; Hope 1947; Kendeigh 1947; Peck 1973; Peck and James 1987; Speirs in Austin 1968).

Nests reported elsewhere are similar to those described from Ontario, except that in the west it occasionally nests in shrubs and nests in deciduous trees are more frequent. Nests are typically well concealed and extremely difficult to find, but nests in trembling aspen near Edmonton were exposed because tent caterpillars had denuded the forest canopy. Two California nests were fully exposed in dead fir trees. Nests tend to be near the top of the nest tree or shrub; in Colorado, nest height averaged 60-80% of tree height. Tall willows appear to be the only shrubs that have been used for nesting. Nests have been found in trembling aspen, balsam poplar, white pine, red pine,

Douglas-fir, lodgepole pine, sugar maple, red spruce, Norway spruce, jack pine, balsam fir, black spruce, white cedar, white birch, elm, juneberry, silver maple, black oak, and tamarack. Nests may be either near the trunk or on a horizontal limb. In Colorado, nests averaged 1.5 m from the tree trunk at a height of 9.7 m. A Michigan nest was 7.6 m up in a red pine near the drooping end of one of the lowest branches. Nests have been reported 2.1-18.2 m from the ground, with many above 10 m (Bekoff et al. 1989; Campbell et al. 2001; Flack 1976; Gillihan and Byers 2020; Hoffman and Pletz 1988; Ligon 1923; Shaub 1954; Speirs in Austin 1968). In Colorado, there was no correlation between the relative abundance of tree species and the percentage of nests built in that species. Nests were predominantly in Douglas-fir and lodgepole pine with none in trembling aspen or fir. Nests were higher in trees and closer to the trunk than expected, and were nonrandomly oriented to the south. No nests were built between 271° and 360°; 60.9% were built between 91° and 180°. Placing nests on the south side of the tree may protect them from the prevailing winds. Placing them close to the trunk would shelter them from wind and rain and increase their stability (Bekoff et al. 1987, 1989). Of 64 nests in Colorado, none were used in subsequent years but 2 (3.1%) were used again in the same year for a replacement clutch (Bekoff et al. 1989; Gillihan and Byers 2020; Scott and Bekoff 1991).

The Evening Grosbeak is nonterritorial and tolerates other grosbeaks close to the nest. Avian predators, such as Canada Jay and Common Grackle, are chased away as are Hermit Thrush and American Robin. Because it is nonterritorial, loose groups of 10-12 pairs may occur in small areas, although pairs may be widely dispersed. North of Lake Nipigon, the closest other pair to a nest was 2.4 km distant. During nesting, adults may wander widely to obtain food, particularly males. In Algonquin Park, 1 bird routinely flew 3.2 km to obtain salt. In New York, birds travelled long distances in flocks to feed on pin cherries in clearings. During the incubation phase in Colorado, males often foraged within sight of the nest tree but also travelled as far as 1 km during foraging excursions. Unmated males are locally nomadic, wandering widely during the breeding season (Bekoff et al. 1987; Devitt 1944; Gillihan and Byers 2020; Hope 1947; Kendeigh 1947; Scott and Bekoff 1991; Shaub 1956; Speirs in Austin 1968). The facts that it is nonterritorial and may travel considerable distances to feed make it difficult to determine its breeding habitat. Most records of it in clear-cuts and younger forest stands probably represent foraging rather than breeding birds.

No information is available on natal philopatry. Because of the species' high nomodic tendencies, natal philopatry is probably very low or nonexistent.

Adult site fidelity is very low because the Evening Grosbeak nests wherever food is most abundant. In New York, 1 of 54 adults (1.9%) banded in summer returned to breed in the same general locality (Shaub and Shaub 1953). In Quebec, 0 of 500 adults returned (Blais and Parks 1964). Savignac (2016) reported that 8 of 10 birds banded during the breeding season dispersed as far as 950 km from the previous year's breeding site.

Limiting Factors

Eggs are most likely to be present in Ontario nests in the last 3 weeks of June (Peck and James 1987). In Algonquin Park, nests are under construction from mid-May to mid-June, eggs are present from late May to late June, nestlings are present from mid-June to mid-July, and dependent fledglings are present from early July to mid-August (Tozer 2012).

The large bisexual winter flocks break up in spring and form smaller groups of 4-10 birds; pair bonds are established within them. Where the Evening Grosbeak is absent in winter, birds are often paired when they arrive on the breeding grounds. Nest building occurs almost immediately and is timed to be synchronous with leaf-out of deciduous trees. In Colorado, nest building and egg laying took an average of 6.3 days, suggesting that it took 2-3 days to build the nest. One egg is laid per day. Incubation may start with the laying of the second egg. The incubation period averaged 13.4 days in Colorado (range 12-14 days). Because incubation begins before the clutch is complete, hatching may take place over 1-4 days (average 2.5 days in Colorado). The nestling period is 13-15 days (average 14.1 days in Colorado). It is well adapted to nesting in areas that often have severe weather, short growing seasons, and patchy food resources by devoting little or no time to prenesting activities, not establishing breeding territories, spending only a short time building nests, and producing fledglings that remain in the nesting area for only a short time (Bekoff et al. 1987, 1989; Gillihan and Byers 2020; Scott and Bekoff 1991; Speirs in Austin 1968).

The Evening Grosbeak raises a single brood in a year but may renest if the first clutch is lost. Clutches of 3-4 eggs have been reported in Ontario (mean 3.6 eggs). Elsewhere, clutches of 2-5 eggs have been reported but most contain 3 or 4 eggs. The mean clutch size in Colorado was 3.0 eggs (Peck and James 1987; Scott and Bekoff 1991; Speirs in Austin 1968).

The age at first breeding is unknown (Gillihan and Byers 2020), but is probably 1 year. The Evening Grosbeak is typically monogamous, with 63 of 64 mated pairs (98.4%) being monogamous in Colorado (Scott and Bekoff 1991). The other male was polygynous and attended 2 females nesting approximately 1.6 km apart; both nests were successful. Nest B lagged behind nest A by about 8 days. Polygyny may be facilitated when food is unusually plentiful (Fee and Bekoff 1986). Because nests are difficult to find and nests of females mated to polygynous males may be distant from each other, it is possible that polygyny is more common than has been documented.

During the breeding season, the Evening Grosbeak gleans insects from foliage, especially caterpillars and other larvae and pupae. Early in the season before insects are abundant, it feeds on buds and is particularly fond of sugar maple sap. It rummages among leaves on the ground to find fallen maple seeds, especially those of sugar, Manitoba, and mountain maples. It occasionally captures insects by aerial pursuit. From July into autumn, it feeds extensively on cherries, particularly those of the pin cherry. It discards the outer pulp, cracks open the pit with its bill, and eats the seeds within the pit. It may take cherries that have already had their flesh removed by Cedar Waxwings and seek out pits that have been voided by other vertebrates. When transporting food back to the nestlings or incubating female, it is stored in the back part of the throat or mouth so that a considerable quantity can be carried. It is strongly attracted to salt and ingests salty water and salt-impregnated earth. In northern Ontario near Wawa, many pools beside the Trans-Canada Highway have sodium concentrations as high as 100-160 ppm even in summer. Grosbeaks were attracted to these pools in June and the first week of July but were never observed at natural mineral licks, even though they had higher sodium concentrations. It is also attracted to roads where calcium chloride is used for dust suppression, so it is the chloride that it seeks. It eats ashes and soot from campfires and other sources, and presumably is attracted to recent wildfires. The soot and ashes are another source of minerals for it. It drinks copious amounts of water and eats much snow in winter (Brunton

1994; Campbell et al. 2001; Devitt 1944; Downs 1956; Fraser 1985; Gillihan and Byers 2020; Shaub 1956; Shaub and Shaub 1954; Speirs in Austin 1968). Benkman and Pulliam (1988) reported that the handling efficiency of the Evening Grosbeak increased as seed size increased. It needs to encounter a seed every 200-500 seconds to meet its midwinter energy requirements compared with 1-5 seconds for sparrows. Of the 6 species studied, only the Evening Grosbeak can survive on seed sizes larger than 90 mg. Its ability to feed on large seeds enables it to exist at low seed densities. It can also store seeds in its mouth and throat, allowing it to use seed resources that are patchily distributed.

The male brings the female most of her food while she is incubating. In Vermont, males initially offered females sugar maple buds followed by elm and cherry buds. Later, they provided salt-impregnated soil and sunflower seeds (Downs 1956). The most important food items provided to nestlings include masticated spruce budworm larvae and the contents of pin cherry pits. In British Columbia, a female fed 4 nestlings for 4 days on the aphid contents of galls on cottonwoods; they were also fed fruits of viburnums and buckthorns. In Winnipeg, nestlings were initially fed semi-digested food. After they were a week old, they were fed caterpillars and small soft green seeds (Bekoff et al. 1987; Brunton 1994; Hope 1947; Scott and Bekoff 1991; Shaub 1956; Speirs in Austin 1968).

Vegetation is important in the adults' diet in the early and late portions of the breeding season and in the nonbreeding season. Invertebrates are important during the peak of the breeding season. Buds are the most common food item upon arrival on the breeding grounds, and the Evening Grosbeak also eats tree flowers. It has eaten buds of maples, elm, willows, oaks, poplars, and lilac. Once insects become available, they dominate the diet. Where the spruce budworm occurs, this is the preferred prey. Several birds in New Brunswick had eaten large numbers of sixth instar larvae and pupae of the spruce budworm. In Quebec, it was present from 15 June to the end of the month once budworm larvae were large enough to eat. Prior to that, few grosbeaks were seen when the larvae were too small. It decreased after 15 July when spruce budworms were in the moth stage. Numbers of grosbeaks at this site were sufficient to effectively decrease the budworm population. It may eat larvae and pupae of other insects that may reach epidemic populations, such as cankerworms, western spruce budworms, jack pine budworms, larch sawflies, and aspen leafrollers. Other insects it may consume include beetles and aphids. As numbers of larvae decline, it switches back to a vegetable diet dominated by seeds and fruits. The most important of these is the seeds and pulp within pin cherry pits; it eats chokecherry and black cherry pits where they are available. Other fruits it eats include those of Russian olive, ash, crabapple, hawthorn, and juniper. Seeds are important in the diet, particularly those of sugar maple and Manitoba maple. Other seeds it consumes include those of ashes, apples (often while they are still on the tree), tulip tree, elm, pine, baldcypress, hawthorn, blackberry, blueberry, birch catkins, black locust, hickory, buffaloberry, snowberry, beech, sumac, and cotoneaster. It eats variety of seeds from nonwoody plants including those of sunflowers, docks, bindweeds, goosefoots, sedges, spotted geranium, buttercups, and violets (Bekoff et al. 1987; Blais and Parks 1964; Brunswig et al. 1983; Brunton 1994; Curry 2006; Fee and Bekoff 1986; Gillihan and Byers 2020; Ligon 1923; McIlwraith 1894; Mills 1981; Mitchell 1952; Savignac 2016; Shaub 1954, 1956; Speirs in Austin 1968). Gabrielson (1924) analyzed the contents of

127 stomachs collected in 14 states and Canada throughout the year. In winter, the diet consisted entirely of seeds and fruit. The summer diet consisted of 20.82% animal matter and 79.18% vegetation. In winter, the diet was comprised of 37.63% seeds of wild fruits, 37.96% winged seeds (maples and ashes), 14.5% conifer seeds, and miscellaneous seeds, mast, and rubbish. The most important wild fruits were cherries (17.48%), dogwoods (13.77%), mountain-ash (3.82%), and snowberry (1.77%). Fourteen birds had eaten juniper berries and 13 had eaten seeds of other conifers. In summer, the vegetation consumed was 37.87% seeds of wild fruits, 2.79% winged seeds, 28.45% conifer seeds, and miscellaneous weed seeds and rubbish. Additional wild fruits that were consumed included those of blackberry, apple, juneberry, sumac, New Jersey tea, mallows, nightshade, and elderberries. Beetles and caterpillars were the main animal foods, but it also ate small numbers of wasps, ants, bugs (chinch bugs), and spiders. The beetles consumed included ground, click, stag, darkling, and June beetles and weevils. June beetles that ate leaves of pine, willow, hickory, and other trees were the most abundant beetles consumed. Caterpillars comprised 11.49% of the overall diet.

Presence of the Evening Grosbeak is strongly correlated with outbreaks of the spruce budworm. Its highest frequencies during the first Quebec breeding bird atlas corresponded with the principal areas of spruce budworm infestations (Vincent in Gauthier and Aubry 1996). The same was true in Ontario during the second atlas (Hoar in Cadman et al. 2007) and probably during the first atlas although this analysis was not undertaken. Near Manitouwadge, the number of Evening Grosbeak territories per year mirrored those of the spruce-budworm specialists but with a steeper response to budworm populations. It was absent until the budworm outbreak occurred (Venier et al. 2009). In 1962 during a spruce budworm outbreak in Quebec, large flocks were seen daily and groups of 30-50 occurred daily at a feeder. In 1963 when budworms were absent or very scarce, a single flock of 7 was seen once (Blais and Parks 1964). In New Brunswick, numbers of grosbeaks responded directly but weakly to budworm numbers. Before the budworm outbreak, it was rarely seen in northern New Brunswick in summer, but large flocks were common throughout the infested area (Morris et al. 1958). Campbell et al. (2001) attributed high concentrations of Evening Grosbeaks in British Columbia to high populations of spruce budworms coupled with salty roadsides. Similar to the warblers that are considered spruce-budworm specialists, the population of the Evening Grosbeak is closely tied to the abundance of the spruce budworm and declines when the area affected by budworms decreases. Scarcity of spruce budworms can be a major limiting factor to the Evening Grosbeak.

The Evening Grosbeak is a rare host of the Brown-headed Cowbird, probably because the 2 species have different habitat preferences. There are no reports of parasitism in Ontario. An Edmonton nest contained 2 cowbird nestlings, 1 Minnesota nest was parasitized, there is 1 record of adults feeding a cowbird fledgling in New York, and 2 such records in British Columbia (Campbell et al. 2001; Gillihan and Byers 2020; Hoffman and Pletz 1988).

Selective thinning in mature and old-growth forests may be beneficial for the Evening Grosbeak because it prefers stands with open canopies. In Oregon, it was more common in thinned than unharvested stands but in Montana there was no difference in its abundance in selectively logged, mature second-growth, and old-growth stands (Gillihan and Byers 2020).

Forest management typically conducted within the range of the Evening Grosbeak in Ontario and Canada may be a significant limiting factor that affects the abundance of its habitat and food. The magnitude of the impacts of forestry does not appear to have been fully recognized. In the Committee on the Status of Endangered Wildlife in Canada status report it was concluded that threats from forestry were either low or negligible (Savignac 2016). Management practices such as fire suppression, clear-cutting, reforestation, and spruce budworm control all have negative impacts on its habitat and food availability.

Wildfires are routinely suppressed to protect forest resources. Areas that are burned provide an abundance of favoured food for the Evening Grosbeak. Most important of these are the pits of pin cherries, and chokecherries are also common in burns. The pin cherry does best after fire and is often called fire cherry; it disappears once the canopy closes over it. In Ontario, it was less abundant in early successional clear-cuts than in recent burns, but the difference was not significant. It was significantly more abundant in mid-successional burns than similarly aged clear-cuts. Regeneration rates may be slower in burns than clear-cuts due to removal of the litter layer and burning of organic soils, thus early successional species such as pin cherry and chokecherry may persist longer in burns. It was significantly less abundant in early- and mid-successional stands than mature stands (Zimmerling et al. 2017). Although younger stands may provide food resources, nesting typically occurs in mature stands. This study suggests that clear-cuts and younger stands resulting from harvest provide inferior habitat to burns and unharvested mature forests.

More than 20 million ha of boreal forest, mainly mature and old-growth stands, were harvested in Canada 1975-2010, and an additional 6 million ha were predicted to be harvested by 2020. Almost all this timber is harvested by clear-cutting with short rotation periods of 40-70 years. This does not allow forests enough time to become mature and develop a diversified structure (Savignac 2016). These perpetually young stands are suboptimal habitat for the Evening Grosbeak. In Saskatchewan, it was found significantly more frequently in stands older than 140 years old, but the rotation period was only 80-90 years. Cumming and Diamond (2002) concluded that some stands older than 120 years should be maintained to sustain species characteristic of older forests.

In eastern Canada, balsam fir stands are often harvested and replanted with faster-growing species such as black spruce and jack pine. These species are much less susceptible to spruce budworm outbreaks. Balsam fir stands are a preferred habitat by the Evening Grosbeak. Black spruce and jack pine stands are suboptimal habitat due to the lower numbers of spruce budworms they support. In northwestern Canada, mature mixed-wood stands are managed to reduce tree species diversity in favour of trembling aspen, thus decreasing habitat suitability for the Evening Grosbeak (Savignac 2016).

In eastern Canada, the spruce budworm has a population cycle of 25-40 years and this has a direct effect upon the abundance of the Evening Grosbeak. During the first atlas, the area in Ontario affected by spruce budworm outbreaks was 8,000,000-18,000,000 ha annually. By 1997, the area of outbreaks had declined to 53,000 ha but there were 2 moderate outbreaks of 200,000+ ha in 2003 and 2004 (Hoar in Cadman et al. 2007). Forest management is undertaken to reduce the extent and severity of spruce budworm outbreaks to the detriment of the Evening Grosbeak. Applications of Bt target caterpillars and a reduction in their population can have adverse effects on the development

and survival of nestlings. More importantly, remote sensing is being used to detect mature and old-growth balsam fir stands that are most likely to host spruce budworm outbreaks. Preventative logging will be undertaken before outbreaks occur. This will decrease the density of fir forests in the landscape and forest composition will be changed to produce habitat that is unsuitable for budworms. This will also reduce the amount and quality of habitat and food resources for the Evening Grosbeak (Savignac 2016).

In Colorado, Bekoff et al. (1989) compared characteristics of nest sites that were successful and unsuccessful in fledging young. Successful nests were started later in the season in the last 3 quarters of the building period, were in more open areas with less dense vegetation and a higher canopy, were 2 m or closer to the trunk, were oriented in a more southerly direction (average 179° for successful nests and 137° for unsuccessful nests), were in taller trees, and were further from the closest neighbouring nest (77.6 m for successful nests and 24.7 m for unsuccessful nests). This was a high-altitude site, so later nests were probably more successful due to weather influences. Areas with less dense vegetation could increase visibility from the nest, which could enhance predator detection. Nests nearer the trunk were better camouflaged, more stable, and more difficult to approach for avian predators. Large trees are more stable than smaller ones and provide more cover for the nest.

In eastern Canada, overbrowsing by moose and white-tailed deer may limit regeneration of suitable habitat (Savignac 2016).

Price (2004) concluded that the Evening Grosbeak could disappear as a breeding species in southern Ontario if the average summer temperature increased by 2°C. It is projected that there will be a significant range contraction of balsam fir which would be a direct loss of habitat for it and would also reduce the potential extent of spruce budworm outbreaks.

Status

Originally confined to the west, the Evening Grosbeak is a fairly recent breeder in Ontario. The first evidence of breeding occurred in 1920 when an adult with young was observed near Lake of the Woods. By 1940, there were 32 breeding records for the province, with the most notable range extension occurring from 1920 to 1929. At that time, its range extended from Lake of the Woods to Thunder Bay, from Sault Ste. Marie to the Lake Nipissing and Ottawa area, and around the Gananoque area (Baillie 1940, 1967; Baillie and Harrington 1937; Devitt 1944). Although it had been seen in Algonquin Park in 1929, breeding was first recorded there in 1932 (MacLulich 1938). Breeding first occurred in Muskoka District in 1927 (Baillie 1967). de Vos (1964) noted that it previously bred in a narrow belt across Ontario, but that there had been a recent widening and spreading of this belt. The first atlas indicated a much more widespread breeding distribution than previously known. It occurred in the eastern portion of the Hudson Bay Lowland to slightly north of Moosonee, in the Boreal Forest Region to north of Lake Nipigon and to Pickle Lake, and throughout the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region. It also occurred in scattered locations south of the Shield on Manitoulin Island, the Bruce Peninsula, and a band from Lake Simcoe to the Kingston area and north of the St. Lawrence River. It was concluded that it was a fairly common breeder and that it might be extending its range further south (Peck in Cadman et al. 1987). James

(1991) considered it a common summer resident north to Pickle Lake and Moosonee, south to Simcoe County and Brockville, and occasional and rare south to Haldimand and Norfolk counties.

Widespread planting of Manitoba maple was initially believed to be the reason for the eastward breeding range extension of the Evening Grosbeak into Ontario east to the Atlantic Coast. Early observers noticed that it fed extensively on the seeds of this species during winter (Baillie 1940; de Vos 1964). Although this explanation is still occasionally provided (Gillihan and Byers 2020), it appears implausible. Manitoba maple is rare in the Canadian Shield where most of the population breeds. The Evening Grosbeak occurred only 10 years after the initial plantings of Manitoba maple, which were confined to areas near human settlement, and would not have been old enough to develop seeds (Brunton 1994). More recently, the Evening Grosbeak has declined significantly, but Manitoba maple is much more abundant now than when it first colonized Ontario. The most likely explanation for its colonization of Ontario is outbreaks of spruce budworms coupled with extensive forest fires. Massive outbreaks of budworms occurred in 1910-20 and 1945-55, coincident with the flurry of early breeding records in the province. There were also major extensive fires in northern Ontario in 1910-20, resulting in shrubby regeneration that included one of its favourite foods, the pin cherry (Brunton 1994; Savignac 2016).

The second atlas revealed that there had been no significant change in the breeding distribution of the Evening Grosbeak since the first atlas. Its probability of occurrence declined significantly province-wide and in every region where it occurred. The decline was attributed to the decline of spruce budworms and the area affected by outbreaks of this species. High densities occurred in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region and in the Red Lake and Pickle Lake areas. High concentrations in the southern Shield were probably a result of significant spruce budworm outbreaks in the Sudbury, North Bay, Bancroft, Arnprior, and Petroglyphs Provincial Park areas. During the second atlas, the Evening Grosbeak was considered an uncommon breeder in Ontario (Hoar in Cadman et al. 2007).

Cadman et al. (2016) reported that the Evening Grosbeak experienced the sixth greatest decline rate of 6.1% per year of Ontario species during 1983-2013. Declines are generally attributed to the reduction in spruce budworm numbers, although forest management may also be a factor. Breeding Bird Survey data for 1970-2021 indicate that it decreased at annual rates of 3.99% in Canada and 6.43% in Ontario. During 2011-21, it decreased at annual rates of 4.55% in Canada and 14.6% in Ontario. The long-term trends were highly reliable for Canada and of medium reliability for Ontario; the short-term trends were of low reliability (A.C. Smith et al. 2023).

A new major spruce budworm outbreak is projected to occur in eastern Canada early in the 21st century. As of 2016, the outbreak was occurring in 5 regions of Quebec and was expanding into New Brunswick and eastern Ontario. The Evening Grosbeak appears to be increasing in response to this new outbreak (Savignac 2016).

The Evening Grosbeak is designated special concern in Canada and Ontario.

POSTFLEDGING PERIOD

Fledglings remain near the nest for 2-5 days after leaving the nest. They separate when they leave the nest and often perch within 20 m of the nest tree. After 2-5 days, the young begin wandering

with their parents, visiting areas of high food concentrations, including feeders. At feeders, the adults shell sunflower seeds and feed the meat to the young. In the wild, fledglings are often fed the contents of cherry pits. It is unknown when juveniles become independent. Adults routinely feed young into August or early September and even into October (Campbell et al. 2001; Downs 1956; Gillihan and Byers 2020; Scott and Bekoff 1991; Shaub and Shaub 1953; Speirs in Austin 1968).

MIGRATION

The Evening Grosbeak migrates both nocturnally and diurnally (Gillihan and Byers 2020; Speirs in Austin 1968). In the east, it is an irruptive migrant with large flocks moving as far south as the Gulf Coast states in some years; it is scarce or even absent in other years. There is a high degree of synchrony in the irruptive pattern of boreal seed-eating birds, including the Evening Grosbeak, Red-breasted Nuthatch, Purple Finch, Redpoll, Red Crossbill, White-winged Crossbill, and Pine Siskin. Irruptions appear to be related to food availability and coincide with poor seed crops, particularly those of spruce, balsam fir, and birch. Some tree species set seeds only in alternate years or at longer intervals so irruptions are not entirely predictable but tend to occur every 2-3 years. Strongest irruptions occur when poor seed crops of all tree species coincide, including pines and white cedar. When the Evening Grosbeak was initially becoming established in Ontario, irruptions were very sporadic with as many as 35 years between irruptions. Once it became a common breeder, strong flights occurred regularly every 2-3 years, with some migrating south even in non-irruption years. Now that it is an uncommon breeder, it may be absent south of the Shield in some years but still occurs occasionally (Bock and Lepthien 1976b; Erskine 1977; Fleming 1907; Gillihan and Byers 2020; Kirchman and Van Keuren 2017; Prescott 1991; Yunick 1983a). Brewer et al. (2018) reported that birds wintering in Ontario had spent other winters in states from Michigan to the Atlantic coast as far south as North Carolina. Ontario birds have been recovered in Quebec and the Maritime Provinces.

Differential migration of the sexes occurs, with males wintering further north than females. In the east, the proportion of males in the wintering population was 65% in the north at latitude 50°N and 18% in the south at latitude 30°N. Males are larger than females. The more northern range of males is consistent with the hypothesis that larger birds are better able to withstand cold weather. Pairs become mated in early spring before reaching the breeding grounds, so males do not have to hurry to reach the breeding grounds to attract a mate or establish a territory because it is nonterritorial. The sole reason for males wintering further north appears to be that they are better adapted to colder weather. Females are subordinate to males and may migrate further south to avoid competition and colder weather (Balph and Balph 1976; Magee 1939; Mason and Shaub 1949; Prescott 1991, 1994; Shaub and Shaub 1950).

Even at the southern extent of its wintering range, the Evening Grosbeak begins its northward migration in mid-April (Prescott 1991). In Ontario, the timing of spring migration is difficult to ascertain because of the presence of wintering birds. In Elgin County, where it rarely overwinters, spring migration extends from mid-April to mid-May (Lancaster et al. 2004). In 1890 when it was rare, birds started to return to Hamilton in March and were present until mid-April (McIlwraith 1894). In the south, spring migrants may occur as late as mid- to late May, rarely into June (Black and Roy 2010; Curry 2006; LaForest 1993; Weir 2008). MacLulich (1938) reported that migrants occasionally returned to Algonquin Park before the end of February. In the south, autumn migrants may arrive in

mid-September or even August, but most arrive in mid-October (Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

During migration, the Evening Grosbeak may occur in any habitat that supports an abundant supply of food. It may be found in a variety of forest types and also anthropogenic areas with ornamental trees and shrubs and bird feeders. In spring, buds and seeds of maples are important food items and these trees may attract flocks. In autumn, conifers bearing seeds and berry-producing trees and shrubs provide important foraging habitat. Coniferous, mixed, and deciduous forests may be inhabited if the trees are bearing seeds, or there are openings or understories with maples, chokecherry, pin cherry, Saskatoon, or red-osier dogwood. In urban and rural areas, it frequents orchards and gardens where there are ornamental plants such as Manitoba maple, Chinese elm, white elm, apples, crabapples, cherries, or Russian olive. It also visits feeders, particularly those where sunflower seeds are provided (Campbell et al. 2001).

The Evening Grosbeak wanders widely during migration and exhibits no site fidelity. Once food resources are depleted at a site, flocks move in search of another food source. In New York, 0 of 1,933 banded migrants returned in a subsequent year (Gillihan and Byers 2020; Yunick 1983a).

There is a cost to migration, with increased risk to birds during this period. Survival rates are high in years with limited irruptive behaviour and low in years of major irruptions (Savignac 2016).

James (1991) considered the Evening Grosbeak a common to locally abundant migrant, although it is considerably less common now. It first appeared in southern Ontario during the irruption of 1854-55, with major irruptions in 1886-87, 1883-84, and 1889-90. Subsequent irruptions occurred with increasing frequency in 1901-02, 1903-04, 1910-11, 1915-16, 1916-17, and 1957-58 (Baillie 1940; Brunton 1994; Fleming 1907; Gillihan and Byers 2020; McIlwraith 1894). In the Kingston area, there were invasions in 30 of 60 years, but in only 3 of 17 years since 1990 (Weir 2008).

WINTER

The Evening Grosbeak is associated with snow in winter. It is least likely to occur where there are frequent changes from snow cover to bare ground and where there is frozen ground without snow (Keyser et al. 2023).

In non-irruption years, most of the Evening Grosbeak population remains in the breeding range. It tends to occur mostly in coniferous and mixed forests where conifer seeds are abundant, but may visit villages and other settlements if feeders and fruit- or seed-bearing trees and shrubs are available. South of the breeding range, it occurs in coniferous, mixed, and deciduous forests as well as urban and suburban areas and rural residential lots. Deciduous forests that are used are predominantly those that contain trees with winged seeds such as maples and ashes. In British Columbia, it appears to be highly localized in winter around human settlements, especially near feeders. In the Yukon, it is most frequent in open mixed forests around settlements with feeders. In urban areas of Massachusetts, it was most abundant in the smallest woodland size class of 1-5 ha, possibly because houses with feeders and other food sources were closer to smaller woodlots (Campbell et al. 2001; Gillihan and Byers 2020; Sinclair et al. 2003).

In winter, flocks of Evening Grosbeaks may roost together at night; birds may also roost singly. In Connecticut, flocks roosted in elms, maples, and oaks taller than 23 m. In Indiana, one roosted in small twigs in a pine in the lee of the 12.5-15 cm trunk, and one roosted on the ground where a ravine and roots of an apple tree provided protection. In Ontario, birds have roosted in a white pine at Mattawa, in white pine and white cedar in Toronto, in a large elm in a yard, and in rows of spruce trees in Mississauga (Parks 1947; Speirs in Austin 1968).

The Evening Grosbeak is not territorial in winter and occurs in gregarious flocks. These large social groups facilitate locating clumped food resources. Adult males are dominant over females and juvenile males, juvenile males are dominant over both age classes of females, and juvenile females are dominant over adult females. In Utah, females predominated at a large food tray (86 by 86 cm); males predominated at a 30-cm diameter tray. Easy recognition of status reduces agonistic interactions. This is advantageous given the large flock sizes and unstable flock membership (Balph and Balph 1976; Gillihan and Byers 2020).

Winter site fidelity is very low in the east, with typically less than 1% of Evening Grosbeaks returning to the same 10-minute block in subsequent years. In Connecticut, only 3 of 2,429 birds (0.1%) returned. It wanders extensively within winters and is unlikely to return to the same location in another year in the east. In Connecticut, 8 birds were recovered within a 24-km radius in a subsequent winter; 7 were recaptured 1 day later 8.0 km distant. In New York, 0 of 704 birds returned in a subsequent year and only 2.2% were recaptured as repeats in the same season. There were 14 recoveries of birds that had been banded elsewhere in a previous winter: from New York, Maine, Connecticut, Ontario, Pennsylvania, Ohio, Texas, North Carolina, Virginia, and Maryland. Birds banded in winter in Ontario have been recovered in subsequent years from Michigan east to the Atlantic Coast (Balph and Lindahl 1978; Gillihan and Byers 2020; Mason and Shaub 1949, 1952; Parks 1947; Savignac 2016; Yunick 1983a). Site fidelity is much higher in the west. In Utah, 15 of 107 (14.0%) returned the following winter, including 25.0% of males and 8.5% of females. This suggested that males are somewhat more site faithful than females or that females suffer higher mortality. Three returning birds were among the first to be seen at the feeders and each returned to the precise location where it had been banded. All but 1 bird remained until May whereas eastern birds appear to be constantly moving. Some returning birds did not arrive until late April or May and these tended to have been banded later in the previous season. They may have wintered elsewhere and did not return until migrating in spring, or they may have visited other feeders in the area until spring (Balph and Lindahl 1978).

Natural foods that the Evening Grosbeak eats in winter include seeds of silver maple, chokecherry pits, Norway maple fruits, catalpa seeds, mountain-ash seeds, Manitoba maple seeds, hackberry fruits, maple buds, apple buds, flowering dogwood buds, ash seeds, sumac seeds, fruits of multiflora rose, and red cedar berries (Downs 1958; Gillihan and Byers 2020; Mason and Shaub 1949, 1952; McIlwraith 1894; Parks 1947; Thompson 1890). There are 2 reports of an Evening Grosbeak killing a House Sparrow at a feeder and flying away with it (Babcock 1967; Cockwill 1986).

The Evening Grosbeak is a fairly regular feeder visitor within its breeding range, but its presence is unpredictable in other areas. It visits far more rural than urban feeders (Dunn and Tessaglia-Hymes 1999). Sunflowers are its preferred food at feeders and it eats both striped and black oil sunflowers.

It infrequently eats millet, mixed seeds, cracked corn, peanut hearts, bird puddings, suet, safflower, and milo. If water is available, it consumes great quantities and it also eats snow (Dunn and Tessaglia-Hymes 1999; Mason and Shaub 1949; Speirs in Austin 1968).

The Evening Grosbeak is strongly attracted to salt and therefore to roads and parked vehicles. Large numbers may be killed by vehicles. This may occur in all seasons because salt concentrations along roadsides remain high during the summer. In June and July of 1 year, it was estimated that more than 2,000 were killed by vehicles in a British Columbia park (Campbell et al. 2001; Parks 1947; Savignac 2016; Speirs in Austin 1968; Taylor 1997; Tozer 2012).

The Evening Grosbeak is vulnerable to diseases. In 1999, there was an outbreak of conjunctivitis in the Saguenay area and northcentral Quebec. At 14 feeding stations, 10-20% of birds were infected, which included more than 100 Evening and Pine grosbeaks. This disease affects the eyes, resulting in birds going blind (Iron 1999). In British Columbia, approximately 50 died due to salmonellosis, probably due to use of bird feeders (Campbell et al. 2001).

Occasionally, the Evening Grosbeak strikes windows at buildings that have feeders. It does not appear to be disproportionately susceptible to collisions with windows and was not listed among the more vulnerable species to building strikes in the United States. In New York, only 4 Evening Grosbeaks flew into window panes at a feeder where 2,429 were banded (Loss et al. 2014; Parks 1947; Savignac 2016; Speirs in Austin 1968).

At feeders, the Evening Grosbeak is vulnerable to being preyed upon by cats (Speirs in Austin 1968).

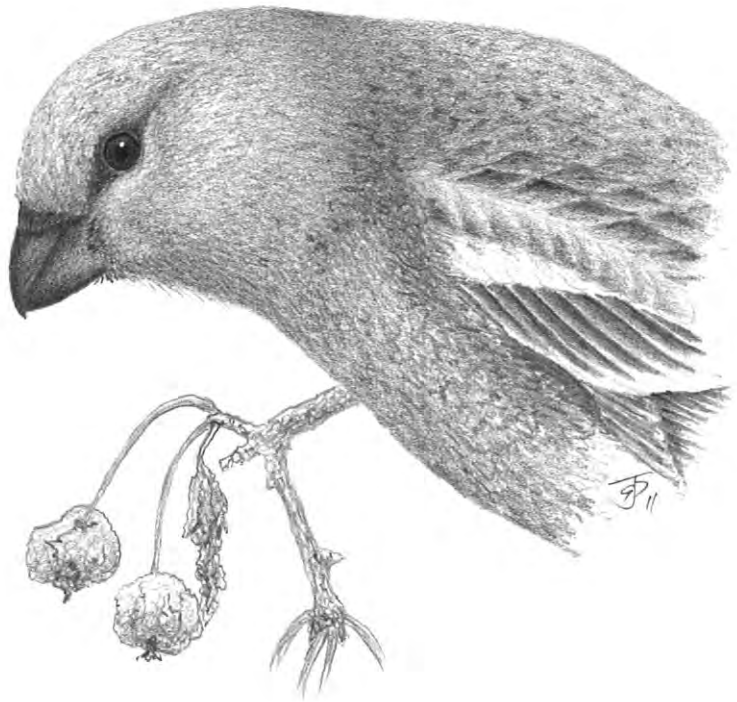
James (1991) considered the Evening Grosbeak a common winter resident in the south and uncommon in the northern breeding range, north to about northern Lake Superior. It has been detected at Moosonee in December (Schueler et al. 1974). In extreme southwestern Ontario, it has never been a common wintering species, although birds may move through during migration. There is only 1 record of an overwintering bird in Elgin County (Lancaster et al. 2004).

Winter populations of the Evening Grosbeak have mirrored those of the breeding season. Initially it was absent in the province. Periodic and intermittent winter invasions started in the mid- to late 19th century followed by a great increase in numbers and regular invasions at 2-3-year intervals, with birds present in the south even in non-invasion years. This was followed by a significant decline when few were seen in the south during winter. Freedman and Riley (1980) summarized the results of southern Ontario Christmas Bird Counts (CBC) for 1929-77. It increased greatly during that period, with erratic peaks beginning about 1960 at intervals of 2-3 years. The number of birds seen per observer was 0 to 1 in 1929-60 and peaked at 10 in 1972. The increase in the number of bird feeders during the same period probably contributed to its increase in the south (Brunton 1994; de Vos 1964). Winter numbers were high in southern Ontario until the early to mid-1980s, followed by a sharp decline. In Algonquin Park, the last time large numbers were present was in 1984-85 when 1,474 were counted on the CBC. On 6 of the last 10 counts, 0-3 were reported (Tozer 2012).

CBC results for Canada indicate a significant decrease of 1.1% per year for 1970-2012; results for Ontario indicate a significant decrease of 11.9% per year for this period (Savignac 2016). In North America, CBC results indicate a significant decrease during the period 1980-98, with the most serious decline in the Great Lakes region (Cadman et al. 2016). CBC results for 1970-2021 indicate an annual decrease of 2.84% in Ontario; there was an annual increase of 1.20% 2009-21 (National Audubon Society 2022).

Pine Grosbeak

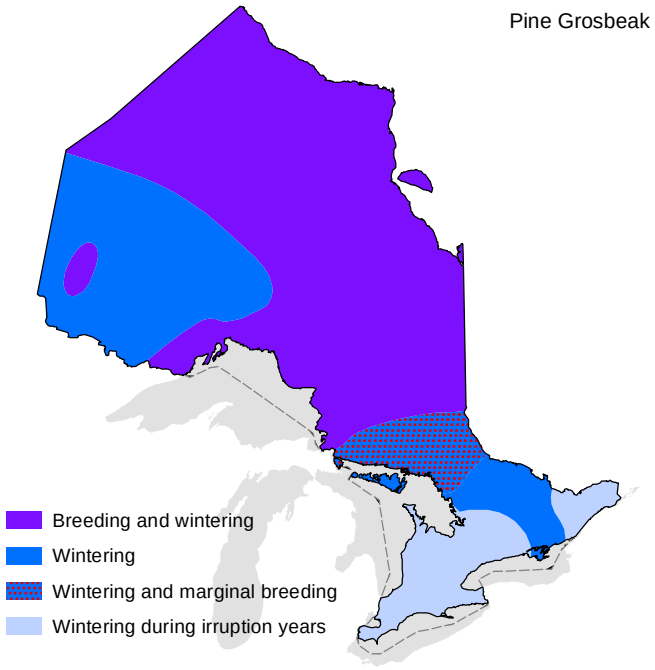
Pinicola enucleator



BREEDING SEASON

Habitat Requirements

In Ontario, the Pine Grosbeak is usually associated with open coniferous stands but may also occur in mixed stands. The first documented nest for the province was north of the Swan River on the coast of James Bay. It was in an open white spruce–tamarack forest with an understorey of willow and alder on a beach ridge. It was less than 10 m from a small stream. The ground cover consisted of a thick bed of lichens and mosses (Peck et al. 2004b). Wilson and McRae (1993) found a recently fledged young at Ekwan. This area consisted of spruce-lichen woodland and spruce forest on beach ridges. In the Clay Belt portion of the Boreal Forest Region, it was most abundant in stands dominated by white cedar–tamarack, followed by those dominated by black spruce, balsam poplar, and white birch–trembling aspen. It occurred mostly in wetter stands and those that were nutrient-poor, but to above half way on the richness scale (Welsh and Lougheed 1996). It is possible that some records in deciduous stands were of foraging rather than breeding birds, or that they contained scattered conifers. In Algonquin Park, it was extremely rare in summer, occurring in pine and spruce forests in the northern portion of the park (MacLulich 1938). The validity of these records has since been questioned and it is no longer considered a summer resident in the park (Tozer 2012).



Throughout its range, the Pine Grosbeak nests predominantly in open coniferous forests and less frequently in mixed forests. Because it prefers open stands, it is most abundant in taiga, in subalpine areas, and in forests opened up by logging. Nesting habitat may consist of widely scattered stunted conifers. Where forest is close-canopied, it nests in or near small openings and at forest edges. Within the Boreal Forest Region, it has no clear association with any particular forest type, but tends to be most common in those dominated by spruce and balsam fir (Breton in Gauthier and Aubry 1996; Campbell et al. 2001; Erskine 1977; Ray 1912; Taylor and Taylor 1979; Young and Adkisson 2020). In the Great Whale Region of Quebec, highest densities occurred in black spruce–lichen woodlands. In the Eastmain River area, highest densities were in shoreline scrub, jack pine stands, and recent burns. In northern Quebec, it occurs mainly in wooded valleys, isolated stands of conifers, and isolated patches of forest spared by fire. During the first Quebec breeding bird atlas, it was found mostly in the northeastern portion of the south, especially where balsam fir was abundant. Frequency of occurrence was very high in regions dominated by balsam fir–black spruce and also high in the balsam fir–yellow birch and balsam fir–white birch regions. At the turn of the 20th century, large numbers nested in white spruce stands on the Magdalen Islands (Breton in Gauthier and Aubry 1996). In Newfoundland balsam fir stands, Whitaker and Montevecchi (1997, 1999) considered the Pine Grosbeak a habitat generalist. It occurred in equal abundance in riparian edges and forest interior but was absent within 30 m of edges adjacent to clear-cuts or other non-forest edges. Also in Newfoundland balsam fir stands, it was significantly more abundant in stands 40 years old than those 60 or 80 years old. Younger stands were characterized by a well-developed small-tree layer that had a relatively high (6%) deciduous component of white birch and pin cherry. These species gradually disappeared as forests aged and many have provided a food source (Thompson et al. 1999). Austin (1968) reported that it nested in a spruce-tamarack swamp in Nova Scotia and in balsam fir in an open pasture in Maine. In northeastern Manitoba, it was equally abundant in coniferous forest with an understorey, coniferous scrub, and mixed scrub. It was not detected in deciduous or mixed forests, coniferous forest without an understorey, deciduous scrub, heath, or tundra (McLaren and McLaren 1981). At Churchill, it occurred most frequently in spruce forests (Jehl 2004; Jehl and Smith 1970). In northeastern Manitoba, it nested in stands dominated by white spruce–tamarack, white spruce–black spruce–tamarack, and white spruce–jack pine–tamarack. It was much less abundant in similar stands bordering on open tundra and absent in a riparian strip of willow (Gillespie and Kendeigh 1982). In British Columbia, most nesting occurs in subalpine areas, but it nests in lower hemlock-fir forests in

Haida Gwaii. It is widespread throughout the Engelmann spruce–subalpine fir forest zone and the spruce-willow-birch region of the higher elevations of the boreal white spruce–black spruce zone. It occurs in young or open subalpine coniferous forests. Habitats include older burns or clear-cuts, selectively logged areas, subalpine parkland or krummholz, and forest edges along meadows, avalanche chutes, beaver ponds, and lakeshores. The burns it used were 15-60 years old and several had a deciduous component of willow. In Engelmann spruce–subalpine forests, it avoided clear-cuts 5 years or less in age and remnant forest patches 0.4 ha or smaller within recent clear-cuts. It preferred young seral forests, edge habitats, and open subalpine areas (Campbell et al. 2001). In the Yukon, the Pine Grosbeak nests mostly in lodgepole pine forests, but also in black spruce bogs, white spruce forests, and mature black spruce forests mixed with white spruce and shrubs (Sinclair et al. 2003). In Alaska, it nested in lowlands dominated by black spruce and other spruces, on hills and bluffs dominated by deciduous forests, and in subalpine forests. It was not documented in floodplains or alpine areas (Handel et al. 2009). It breeds in alder thickets beyond the treeline in Alaska (Young and Adkisson 2020). In the Rocky Mountains in the western United States, it nests predominantly in Engelmann spruce–subalpine fir forests where there are numerous gaps in the canopy. It is absent or rare in dense coniferous forest and aspen forest (French 1954; Young and Adkisson 2020).

The first nest described for Ontario, found on 12 June 2003, was 2.36 m from the ground in a 6-m tall spruce with a diameter at breast height of 7 cm. It was not particularly well hidden and was placed atop 3 horizontal branches against the tree trunk (Peck et al. 2004b).

Very few nests of the Pine Grosbeak have been described. All were in conifers, mostly in spruce but also in fir and hemlock. Young and Adkisson (2020) stated that nests are well concealed in dense vegetation, but many were in plain view and those that were concealed were usually visible from below. Nest trees are often short or stunted but it may also nest in taller trees. Nests have been reported 0.6-10.7 m from the ground, mostly 1-4 m up. Nests may be either against the trunk or as far as 2.4 m distant from the trunk at the end of a bough. The nest is not attached to the supporting substrate and simply rests on branches (Austin 1968; Campbell et al. 2001; French 1954; Ray 1912; Young and Adkisson 2020).

Young and Adkisson (2020) stated that the Pine Grosbeak is strongly territorial during the breeding season. Although this may be the case in Eurasia, North American birds are probably nonterritorial. Young and Adkisson (2020) concluded that the facts that males approached playbacks of their songs and that captive males and occasionally females often fight with same-sex birds in adjacent cages was evidence of territoriality. Other evidence for North America suggests that the Pine Grosbeak is nonterritorial. In Utah, French (1954) stated that the diameter of 1 territory was 365 m or approximately 10.5 ha. On 2 occasions, strange Pine Grosbeaks were tolerated by a nesting pair. Another pair fed with the resident pair less than 30 m from the nest tree and another strange male joined the pair as they fed in a meadow about 45 m from the nest. This male was tolerated until it flew within 0.9 m of the female, at which time the resident male drove him away. It seems more reasonable to consider the area occupied by this pair a home range rather than a territory. At the Ontario nest, Peck et al. (2004b) saw a second singing male in a nearby tree and later a second female foraging in nearly the same location. Erskine (1977) stated that the finches were

predominantly nonterritorial. It seems most likely that the Pine Grosbeak is nonterritorial in North America.

No information is available on natal philopatry, but it is probably very low.

Information on adult site fidelity is scarce and may be different in the west and east. In the west, seasonal movements, if any, are typically short distance and altitudinal. In the east, irruptive long-distance south-north movements may be undertaken. Young and Adkisson (2020) stated that there was strong evidence of summer site fidelity, but most banding and recovery information was documented at the 10-minute-block scale. Of 28 North American recoveries, there were 5 cases of breeding season birds being captured 1-4 years later. In Colorado, 8 of 24 birds (33.3%) returned 1-3 years later and all were within 500 m of the original banding site. Near Churchill, numbers varied annually suggesting that there were regular turnovers in populations (Jehl 2004). It is possible that eastern birds are more nomadic, nesting only where food is most abundant.

Limiting Factors

At Churchill, nesting appears to start when fresh buds become available. No information is available on how long it takes to build a nest or if there is an interval between nest completion and the initiation of egg laying. Eggs are laid at the rate of 1 per day. Incubation begins with the laying of the last egg; the incubation period is 13-14 days. The eggs usually hatch within 1 day or at most 2 days. The nestling period is typically 20 days, although it has been reported to be as short as 13-14 days (Austin 1968; Campbell et al. 2001; Jehl 2004; Ray 1912; Young and Adkisson 2020).

There is no evidence that the Pine Grosbeak raises more than a single brood in a breeding season. Late clutches are presumed to be replacement clutches. Clutches of 2-5 eggs have been reported, but most contain 3 or 4 eggs. The single Ontario nest had a full clutch of 3 eggs (Austin 1968; Campbell et al. 2001; Peck et al. 2004b; Ray 1912; Young and Adkisson 2020).

Captive yearlings are capable of breeding so it is probable that first-year birds breed in the wild. Pair formation may take place in late winter when birds are still in flocks. Apparent pairs have been observed in mid-March in Michigan and Colorado. The mating system appears to be monogamous, but limited study has been conducted on this subject (Young and Adkisson 2020).

Foraging occurs on the ground and also in shrubs and trees from near the ground to the upper canopy. The Pine Grosbeak takes buds and newly grown conifer needles from the tips of branches. It spends much of its time on the ground in forest openings eating unripe seeds and developing ovaries of forbs. Fruits and seeds too high to reach by stretching are sometimes reached by biting and bending the main stalk. It captures some insects by flycatching in forest openings. On herbaceous plants, it bites flower heads open and shakes the seeds out (French 1954; Peck et al. 2004b; Young and Adkisson 2020). Both sexes develop gular sacs for a brief period during the breeding season when they are feeding young. This allows them to store food and carry large quantities back to the nest. The male feeds the female as part of the courtship ritual, during incubation, and for 3-4 days after the chicks hatch (Austin 1968; Cross 1952; French 1954; Jehl 2004; Peck et al. 2004b).

Young appear to be fed mostly insects and spiders, often mixed with vegetation. Adults eat predominantly vegetable matter. Early in spring and summer, the Pine Grosbeak eats a variety of buds and fresh growth of conifer needles; in summer, it eats insects, unripe seeds, and fruits; and buds and fruits are eaten in autumn and winter. It eats mountain-ash berries and other species with hard seeds by biting through, discarding the pulp, and crushing the seed. In late summer, unripe fruits of forbs are crushed in the beak and the flower part is discarded. It drinks water or eats snow on at least a daily basis. It eats cranberries, willow buds, moss campion seeds, salt and grit, ovaries of glacier lilies, raspberry seeds, juneberry seeds, mountain holly seeds, and terminal buds and seeds of spruce, pine, and fir (Austin 1968; Cross 1951; French 1954; Peck et al. 2004b; Ray 1912; Sinclair et al. 2003; Young and Adkisson 2020). In a Maine spruce–balsam fir stand in the first year, spruce budworms comprised 10% of the volume of the food and other insects and invertebrates comprised 79%; the remainder was vegetable matter. In the second year, spruce budworms constituted 79% of the diet compared with 11% other insects and invertebrates and 10% plant material (Mitchell 1952). Gabrielson (1924) analyzed the contents of 394 stomachs collected from 14 states and 5 provinces. He completed a literature review revealing that the Pine Grosbeak has a fondness for buds and eats mountain-ash berries, black ash seeds, maple seeds, red cedar berries, conifer seeds, frozen apples, birch and alder seeds, fruit buds of apples and pears, apple seeds, tree-of-heaven seeds, alder fruits, honeysuckle fruits, maple buds, ash buds, and Norway spruce and other coniferous buds. Nearly all these items were found in the stomachs he examined, suggesting that it feeds locally on different plants and plant parts, probably depending upon availability. It tends to eat 1 variety of seed or fruit until it is exhausted or the birds are disturbed. Stomachs from New Hampshire contained little but blackberry seeds and staminate flower buds of pines. Usually the gizzard was filled with one of these foods and the gullet with the other. The diet between April and September consisted of 83.3% vegetation and 16.17% animal matter. The vegetable matter differed from that taken in the winter chiefly in the absence of maple and ash seeds and in a higher percentage of fruit. Raspberry seeds and pine flower buds, the winter staples, were found in 7 of 29 stomachs (24.1%) and constituted only 7.0% of the summer diet. Seeds of conifers, especially spruce, accounted for 12.37% of the summer diet. Weed seeds constituted 19.97% of the diet, wild fruits contributed 32.8% to the summer diet, and deciduous tree buds, mast, and miscellaneous vegetable matter formulated the remainder of the vegetable diet. Miscellaneous seeds consumed included those of sedges, greenbriers, irises, smartweeds, docks, amaranths, mustards, currants, strawberries, juneberries, cherries, smooth sumac, buffalo-berry, wild sarsaparilla, bunchberry, nightshade, ragweeds, dandelions, hawkweeds, and Lapland rosebay. The animal food was very finely ground up; most of it could not be specifically identified. Grasshoppers, ants, spiders, and caterpillars constituted the bulk (15.08%) of the summer animal diet; small flies and beetles comprised the remainder. In New Brunswick, it exhibited no response to spruce budworm numbers (Morris et al. 1958). In Alaska, it fed on blueberries, rose hips, and cranberries until snow covered the ground. After mountain-ash berries were depleted, it ate berries of devil's club and highbush cranberry and buds of willows and alders. In June, it ate dandelion seeds and in July it fed on caterpillars on young alder buds and also ate weed seeds (Austin 1968).

The effects of forest management on the Pine Grosbeak are uncertain. Vanderwel et al. (2009) summarized the effects of partial harvesting of stands in the Boreal Forest Region in Ontario. They

stated that it should increase when 30%, 50%, or 70% of the forest cover was harvested but acknowledged that the reliability of their data was low. In British Columbia, Campbell et al. (2001) reported that 1 study found no change in its breeding abundance following selective logging that opened up the forest. Young and Adkisson (2020) and Herbers et al. (2004) concluded that large-scale clear-cutting was likely to negatively affect populations.

Status

The first breeding evidence for the Pine Grosbeak in Ontario was obtained in 1935 when an adult with young was seen on an island in the Temagami Forest. It had been observed there during the breeding season since 1922 and a nest was found in July 1940. In late August of the same year, a nest containing young was found near Sundridge. These nests were not described, so it was considered a hypothetical breeder. A female collected at Hawley Lake in 1958 had a brood patch and a fully formed egg without a shell in its oviduct. As of 1940, there were only 32 summer records, west to Sioux Lookout, north to Fort Severn, and south to Southampton in Bruce County, Mary Lake in Muskoka District, the Little Nipissing River, Combermere in Renfrew County, and Cross Lake in Frontenac County (Baillie 1960). Mills (1981) considered it sparsely distributed in Parry Sound and Muskoka districts. He was aware of only 4 or 5 breeding season records and some of these were questionable. During the first atlas, breeding records were obtained from the Lake Nipissing and Sudbury area north through the eastern Boreal Forest Region and at scattered sites throughout the Hudson Bay Lowland. No records were obtained from the western portion of the Boreal Forest Region except for 1 record north of Pickle Lake. In 1985, adults were observed feeding fledglings near the headwaters of the Black Duck River, approximately 10 km from the Manitoba border. No nests were found during the first atlas. Breeding season records were very spotty. Helleiner (in Cadman et al. 1987) concluded that it was an uncommon breeder in Ontario; it appeared to be fairly common along the north shore of Lake Superior in the Sault Ste. Marie area. James (1991) considered it a rare to uncommon summer resident across northern Ontario. Wilson and McRae (1993) concluded that it probably bred throughout the Hudson Bay Lowland in varying numbers.

The second atlas indicated limited change in the Pine Grosbeak's distribution since the first atlas. It was infrequently detected in the southern Lake Nipissing area, and records were again concentrated in the eastern portion of the Boreal Forest Region and the Hudson Bay Lowland. It was somewhat more widespread north of Lake Superior, extending westward to Thunder Bay. There were also some records in Rainy River District. There were significant declines in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region and the Boreal Forest Regions, but significant increases in the Hudson Bay Lowland resulted in a nonsignificant increase for the entire province. Greatest concentrations appeared to be in the Kapuskasing area, with low abundance and apparent absences throughout the rest of its range (Peck and Coady in Cadman et al. 2007).

Breeding Bird Survey data indicate that the Pine Grosbeak decreased at annual rates of 2.23% in Canada and 2.37% in Ontario 1970-2021. Trends 2011-21 were annual decreases of 0.182% in Canada and 1.52% in Ontario. All results were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

As soon as the fledglings are able to fly, they follow their parents, even when they forage on the ground distant from thick cover. Shortly after leaving the nest, birds gather in small flocks that may

represent family groups. In British Columbia, the earliest breeders occasionally move to lower elevations in small family groups as early as mid-May. In most years, they do not appear at lower elevations until late October or early November (Campbell et al. 2001; French 1954; Young and Adkisson 2020).

MIGRATION

In many years, the Pine Grosbeak is nonmigratory and remains within the breeding range. Even in these years, it may wander during the postbreeding and migration periods. Near Churchill, it seems to disappear in mid-October. In the Yukon, it moves out of contiguous forest habitat and occurs in human settlements from October to April. Its presence and habitat use appear to be directly related to food distribution and abundance. In western areas, it remains in subalpine habitats all winter if food is plentiful, but moves to lower altitudes when food is scarce. In the east, it makes long-distance irruptive movements far south of the breeding grounds in years when food resources are low in the breeding grounds. Migratory movements appear to occur during the day (Austin 1968; Campbell et al. 2001; Jehl 2004; Sinclair et al. 2003; Young and Adkisson 2020).

Peak numbers occurred in the Toronto area in years following maximum abundance of food in the north. Speirs (1939) concluded that there was no evidence to suggest that lack of food on the breeding grounds drove birds south. Austin (1968) noted that southward movements were unrelated to weather conditions. The Pine Grosbeak was absent in the south in some of the severest winters and present in some warm winters. Bock and Lepthien (1976b) compared the timing of irruptions of several boreal seed-eating birds and found that they were highly synchronous, although the Pine Grosbeak did not irrupt as frequently as some other species. Most trees set seeds every other year, but some do so at greater intervals. Largest irruptions occurred when seed crops of all tree species were poor. It is now generally accepted that southward irruptions are a response to low food supplies in the northern breeding grounds. When irruptions occur, the Pine Grosbeak may winter as far south as Arizona (Root 1988; Young and Adkisson 2020).

The frequency of southward irruptions is irregular. At times the Pine Grosbeak appears on a regular cycle, but then the intervals between irruptions may change or there may be long periods without any wintering birds south of the breeding grounds. McIlwraith (1894) reported that it was common in the winters of 1882-83 and 1883-84 then none were seen until the large influx in 1889-90 (Thompson 1890). Using Christmas Bird Count (CBC) data for 1929-77, Freedman and Riley (1980) concluded that irruptions in southwestern Ontario appeared to be cyclic, occurring at intervals of 3-5 years (mostly 3 years). Since 1950, peak numbers of Pine and Evening grosbeaks were highly synchronous. In the Toronto area, peaks occurred at intervals of 5-6 years, usually 6 years (Speirs 1939). In Niagara Region, influxes occurred irregularly prior to 1966, with peaks every 3 years, but occasionally with intervals of 4, 5, or 6 years (Black and Roy 2010). In the Hamilton area, it occurred at least every other year from 1950 to the late 1980s, or often every winter. Only 2 irruptions occurred during 1996-2005 (Curry 2006). In the Kingston area, irruptions occurred in 21 of 61 years 1948-2008, an average of about every third year (Weir 2008). Intervals between irruptions are irregular in other areas as well. In Massachusetts, the interval between irruptions was normally 2-6 years but with some longer intervals. In New York, intervals were as long as 18 years and 25-year intervals have been reported elsewhere (Austin 1968; Young and Adkisson 2020).

In the extensive winter invasions in the winters of 1882-83 and 1883-84, McIlwraith (1894) reported that Pine Grosbeaks first appeared in early January and remained into April. During the winter of 1889-90, when numerous birds were reported from Kingston, Toronto, southern Peel Region, and Hamilton, the first birds seen on 1 January (Thompson 1890). Parker (1973) tracked the 1971-72 irruption into southern Ontario and New York using CBC data. From 18-22 December, numbers per party-hours were more than 20 on the Canadian Shield to southern Georgian Bay, 6-20 in a very narrow band east and south of that, and 1-5 or 0 in the remainder of the south. During 23-28 December, there were more than 20 from southern Georgian Bay eastward, 6-20 from Toronto to the Port Elgin area and along the north shore of Lake Ontario, and 1-5 in the remainder of the south. During 29 December-2 January, there were more than 20 from Goderich to Toronto eastward to Quebec, a narrow band with 6-20 south of that, and 1-5 in the remainder of the south. Spring departure varies from early March to early April, with stragglers into late April. Autumn arrival is typically late October to early November (Black and Roy 2010; Curry 2006; LaForest 1993; Mills 1981; Tozer 2012; Walker 1989; Weir 2008). In Thunder Bay, it started to arrive in October or November. The population peaked around Christmas or early in January and decreased as mountain-ash fruit became depleted. A minor upsurge in numbers occurred in late February or early March (Austin 1968).

WINTER

In winter, the Pine Grosbeak is strongly associated with snow. Important predictors of its presence are length of the snow season and absence of frozen ground without snow (Keyser et al. 2023). Winter and migration habitats are essentially the same. Even in populations that do not migrate, winter habitat may differ from breeding habitat. It appears wherever food is most abundant and may use habitats in winter that are not used during the breeding season. During winter irruptions, it may occur in open coniferous forests provided that seed crops are abundant. It is more likely to occur where fruits and seeds of deciduous trees and shrubs are available and may be attracted to bird feeders, although it tends to prefer natural foods. It may occur around dwellings, in shade trees, in orchards, in deciduous woods where seeds of maple or ash are abundant, and along roadsides. Two locations where it may be abundant in winter in Ontario include Thunder Bay, where it is attracted by showy mountain-ash fruit, and the arboretum at the University of Guelph where it is attracted by crabapples. In winter in Alaska, it usually inhabits low ridges sparsely treed with birch and spruce, but retreats into willows in the severest weather (Austin 1968; Campbell et al. 2001; Earley 2009; Young and Adkisson 2020). In British Columbia, highest densities of wintering Pine Grosbeaks occurred at the highest elevations in subalpine spruce and spruce–fir forests. It was rare or absent in low-elevation ecosystems, although it occasionally moves to lower-altitude areas. It was one of few species adapted to wintering in the severe climate of subalpine areas (Herbers et al. 2004).

In winter, the Pine Grosbeak roosts in dense conifers, and birds tend to roost close to each other (Young and Adkisson 2020).

The Pine Grosbeak often occurs in small flocks of 5-10 birds suggesting that families and groups of families remain together. It may also occur singly or in much larger flocks. It may be loosely associated with other species that are attracted to the same food resources. In 1890, mixed flocks of

Pine and Evening grosbeaks were common, but each species also occurred in discrete flocks. Other species that may occur at the same food sources include Bohemian Waxwing, Evening Grosbeak, House Finch, Purple Finch, Redpoll, Red Crossbill, and Pine Siskin (Campbell et al. 2001; Thompson 1890; Young and Adkisson 2020).

Information on winter site fidelity is scarce. It is probable that western birds that tend to migrate only altitudinally have higher rates of site fidelity than eastern irruptive populations. There are 12 cases of wintering birds being recovered in the same 10-minute block 1-5 years later. One bird banded in Michigan was recovered 4 years later approximately 100 km south of the banding location (Young and Adkisson 2020).

In the Hamilton area and along the north shore of Lake Ontario, the Pine Grosbeak was usually seen feeding on mountain-ash berries. The crops and gizzards of those that were collected were full of black ash seeds (Thompson 1890). McIlwraith (1894) stated that it occurred wherever mountain-ash or red cedar berries were available. In Thunder Bay and many other locations in the province, mountain-ash berries are the most important food. Its abundance is directly correlated with abundance of this fruit in Thunder Bay. It initially feeds in the trees and later on the ground when melting snow reveals more fruit. The next favourite foods were lilac seeds and ornamental crabapples. Stragglers remaining later in spring fed on black ash seeds and occasionally on highbush cranberry, Manitoba maple, and white birch. It splits lilac seeds to obtain the insides (Austin 1968). In Parry Sound, it fed on mountain-ash, lilac, white pine, honeysuckle, maples, apples, and tamarack (Mills 1981). In Newmarket, it ate seeds of riverbank grape and American bittersweet (Dance 1986). At Deep River, it fed on crabapples; this is the predominant food eaten at the University of Guelph arboretum, where it also consumes mountain-ash berries (Earley 2008; Walker 1989)). In Algonquin Park, it has eaten buds of aspen, willow, balsam fir, white pine, sugar maple, and juneberry. It is attracted to salt and sand on roads and, in some winters, few are seen until these materials are applied to the highway (Tozer 2012).

Winter foods that the Pine Grosbeak has consumed elsewhere include seeds of ashes, lilacs, mountain-ash, roses, pines, birches, tamarack, balsam fir, grasses, hemp, burdock, ragweed, lamb's-quarters, tulip tree, wild grapes, northern wild raisin, greenbrier, privet, and cultivated honeysuckles; fruits of snowberry, crabapple, mountain cranberry, barberry, red cedar, black alder, hawthorn, buckthorn, sumac, bittersweet, apples, and nightshade; buds of apples, elderberries, pear, willow, poplar, birch, and alder; and pitch pine twigs (Austin 1968; Campbell et al. 2001; Crumb 1981; Taylor 1996; Young and Adkisson 2020). In Alaska, its diet was similar to that of Redpolls: seeds and buds of birch, alder, and willow, and sometimes tender spruce needles (Austin 1968). The Pine Grosbeak needs water in winter and commonly eats snow. In Alaska, a bird flew from a perch in a tree to hover briefly to take a drop of water from an icicle hanging from the roof of a cabin. This behaviour was repeated 5-10 times within 5 minutes (Crumb 1981; Wolfe 1996). It is readily attracted to salt, particularly in winter along roads. When it feeds on natural foods, it tends to feed on 1 item until it is completely depleted and then moves to another food source (Young and Adkisson 2020).

Gabrielson (1924) analyzed the contents of 365 stomachs collected in winter and determined that the diet consisted of 99.1% vegetable matter. Raspberry seeds constituted 14.37% of the diet; coniferous buds comprised 24.22% of the diet. Almost all buds were staminate flower buds of pine,

although a few leaf buds and spruce buds were eaten. One or both of these foods occurred in 217 stomachs and they were eaten in every month. Other items constituted high percentages of the diet, but some comprised the entire content of a few stomachs from 1 locality rather than general use over a broad area. Snowberry constituted 17.3% of the diet and had been eaten exclusively by 69 birds from British Columbia. Weed seeds represented 7.67% of the diet; 7 stomachs from Ontario contributed half this total. Red cedar berries and other coniferous seeds amounted to 4.15% of the diet, mostly from Connecticut birds. Birds from Ontario and Massachusetts ate most of the maple (2.78% of the diet) and ash (1.25%) seeds. Wild fruits constituted 14.34% of the diet. The most abundant fruits consumed were those of hawthorn, dogwood, mountain-ash, huckleberry, blueberry, crowberry, and viburnums. Most fruits were probably taken for the seeds because little pulp was found, although fruit pulp of mountain-ash, crowberry, and blueberry were frequently taken. Mast constituted 5.66% of the diet and was mostly beechnuts or acorns. Buds of willow and maple comprised 4.72% of the diet and the remaining 2.64% of vegetable matter included bits of pine needles, wood, grass, and fragments of unidentified seeds. The 0.9% animal food consisted of fragments of small beetles and weevil larvae, hymenopterans, and flies. All these occur in coniferous buds so it is likely that they were ingested incidentally.

In British Columbia and the Yukon, the Pine Grosbeak is a common visitor to bird feeders and is among the top 10 species at feeders (Campbell et al. 2001; Sinclair et al. 2003). Overall, it is an uncommon user of feeders and is most likely to visit feeders where it is a year-round resident. It rarely visits feeders during southward irruptions but is a common visitor to feeders in northern Ontario. Until the late 1980s, it was a rare feeder visitor in the Shield portion of the Great Lakes–St. Lawrence Forest Region but may have increased the frequency of its visits. At Deep River, there was no correlation between the number of birds present and the number that used a feeder. Over 9 years when Pine Grosbeaks were present, visits to the feeder occurred in 7 years. In 1 winter, 30 birds were present for 2-3 months but only 2 visited the feeder on 4 occasions. The maximum number of birds that visited the feeder was 15; only 0.25-11.5% of the birds that were present used the feeder. Usage of feeders may be a learned behaviour which may explain why only a small proportion of birds use them. It may prefer natural foods to those provided at feeders. It may use feeders week after week and is much more likely to occur at rural and suburban feeders than urban feeders. The proportion of feeders visited increases until late winter than drops off markedly in February and March, at which time flock sizes also decrease (Crumb 1981; Dunn 1989, 1990; Dunn and Tessaglia-Hymes 1989; Pittaway 1989; Tozer 1990; Walker 1989). Its favourite feeder foods are striped and black oil sunflowers and water. In Algonquin Park, it prefers to take sunflowers that have fallen to the ground from the feeder. Infrequently consumed feeder foods include fine cracked corn, millet, wheat, oats, milo, suet, and fruit (Crumb 1981; Dunn and Tessaglia-Hymes 1999; Tozer 2012).

The Pine Grosbeak is subordinate to the Evening Grosbeak and may not visit feeders where it is abundant. Alternatively, visitation by the Pine Grosbeak may be deferred until late afternoon after Evening Grosbeaks have departed. It may decrease in numbers in winters when Evening Grosbeak numbers are high, both at feeders and in the wild (Dunn and Tessaglia-Hymes 1999; Pittaway 1989).

The Pine Grosbeak commonly strikes windows during winter, particularly at houses where there are feeders. In the United States, it was 12.4 times more likely than average to strike a building and ranked 15th in overall vulnerability (Campbell et al. 2001; Loss et al. 2014; Young and Adkisson 2020).

Because it is attracted to roadsides by salt and grit, the Pine Grosbeak is frequently struck by vehicles. Considerable numbers may be killed in this manner, particularly during irruption years (Campbell et al. 2001; Tozer 2012; Young and Adkisson 2020).

The Pine Grosbeak may be vulnerable to conjunctivitis, a disease that affects the eyes and ultimately results in blindness and death. Outbreaks in both Pine and Evening grosbeaks occurred in February 1999 in the Saguenay area of Quebec and in the northcentral region of that province. Ten to 20% of birds at 14 feeding stations were sick, representing more than 100 birds of both species (Iron 1999).

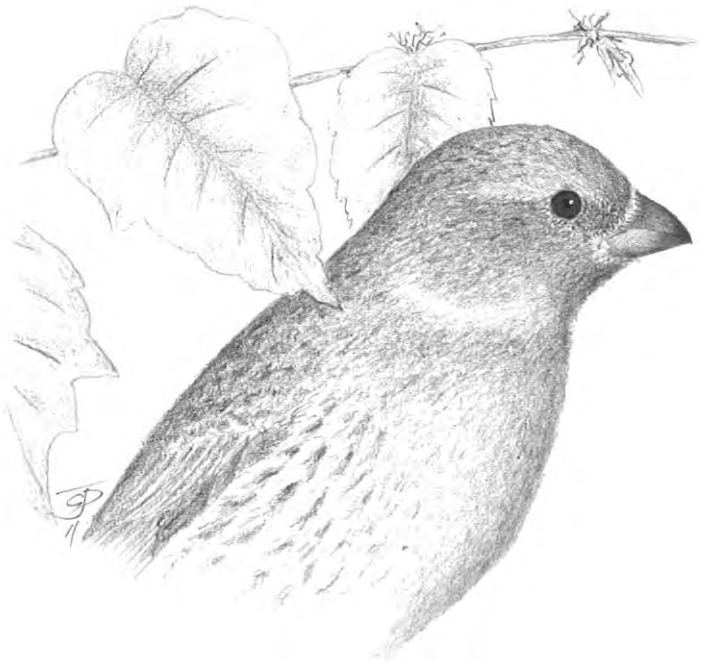
CBC data indicate that the Pine Grosbeak is consistently present north of latitude 50°N in North America. Highest concentrations occur in the Upper Peninsula of Michigan and along the north shore of Lake Superior in Minnesota and Ontario. High numbers also occur northeast of Georgian Bay (Root 1988; Young and Adkisson 2020).

There are no reliable trend data for the Pine Grosbeak in the core of its Ontario wintering range. South of the main wintering area, the frequency of irruptions appears to be declining and fewer birds occur during irruptions. This is the case throughout eastern North America as well as in Ontario. The reasons for this are unclear, but it has been suggested that wide-scale clear-cutting has lowered population levels (Breton in Gauthier and Aubry 1996; Young and Adkisson 2020). Although it appears to be declining, it is unknown if decreases of birds occurring south of the normal wintering area are representative of the trend of the entire population.

Freedman and Riley (1980) summarized CBC results for southern Ontario for 1929-77. There was a trend toward an increase in numbers beginning in 1960. The number of birds seen per observer was 0 to less than 1 until 1960, except that it was almost 3 in 1929. A regular cyclic pattern began in 1960 when numbers alternated between 0 and 2-3. In Elgin County, the high CBC counts were 149 in 1979 and 57 in 1977, but fewer than 10 are reported on most counts now (Lancaster et al. 2004). There are very few records after 1986 in Niagara Region (Black and Roy 2010). In the Hamilton area, it was detected in 8 winters during 1930-50 (38.1% of winters). From 1950 to the late 1980s, it occurred at least every other winter or often in every winter. Occurrences declined thereafter with only 2 winter irruptions during 1996-2005. Numbers reaching the area during irruptions also dropped (Curry 2006). In the Kingston area, typical flock sizes are 30 during moderate irruptions and as high as 400 during heavy irruptions (Weir 2008). In Muskoka and Parry Sound districts and Algonquin Park, the Pine Grosbeak is present almost every winter. In the park, it has been recorded on 34 of 38 CBCs (Mills 1981; Tozer 2012). CBC data indicate that the Pine Grosbeak increased in Ontario at an annual rate of 2.13% 1970-21 and decreased at an annual rate of 0.57% 2009-21 (National Audubon Society 2022).

House Finch

Haemorhous mexicanus



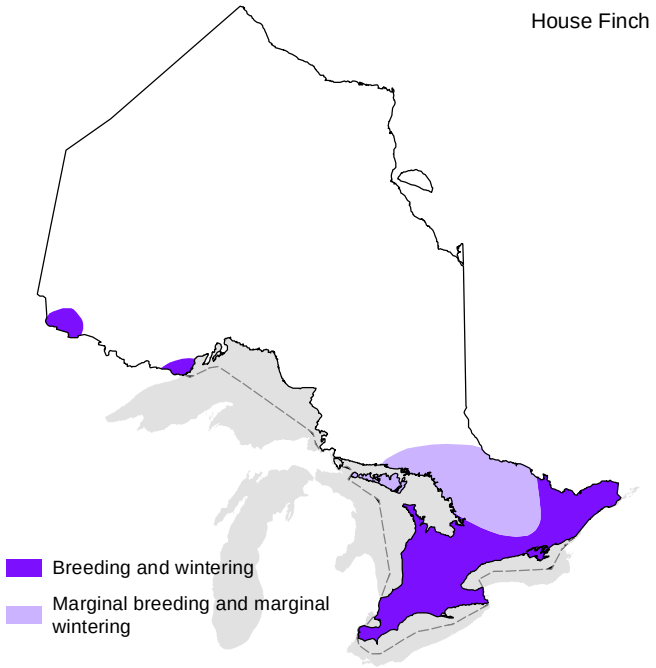
BREEDING SEASON

Habitat Requirements

In Ontario, most House Finch nests were near or on residences or buildings in both rural and agricultural areas. Three were in coniferous plantations, 3 were in woodlands in parks, 3 were in cemeteries, 2 were in abandoned pastures, and 1 was in a hawthorn meadow (Peck and James 1998b). It is strongly associated with humans and avoids areas of extensive forest. Consequently, its Ontario range is restricted predominantly to the urban and agricultural areas south of the Canadian Shield and in Rainy River District. It is absent from the Hudson Bay Lowland and the Canadian Shield except in larger urban centres (Leckie in Cadman et al. 2007).

The eastern population of the House Finch is nonnative, having been established by the release of California birds in New York in 1940. The 2 populations differ somewhat in their habitat preferences, although both are most abundant in urban and suburban areas with lesser numbers around rural dwellings and other buildings. The western population also nests in some natural habitats that probably represent its ancestral habitat prior to settlement by humans (Badyaev et al. 2020; Bergtold 1913).

Badyaev et al. (2020) concluded that the House Finch nested almost exclusively in settled areas in the east. It prefers areas with buildings, lawns, and small conifers but also occurs in urban centres



where it commonly nests on high-rise buildings. Smaller numbers occur in rural areas around houses and outbuildings on farms. It is rare in extensive coniferous and deciduous forests away from human settlement. It avoids mature pine stands and 20-30-year-old monoculture pine plantations. In Vermont, it nested in Christmas tree plantations planted in blocks of white spruce, balsam fir, and Fraser fir. Nests were more common in plantations surrounded by forest (0.67% of trees had nests) than those surrounded by agriculture (0.10% of trees had nests). Nests were 1.3 times more abundant in interior than edge trees. The House Finch exhibited the weakest preference of the species present for nesting in interior trees rather than those in rows at the perimeter of the plantations (Hughes and Hudson 1997).

In Colorado before human settlement, the House Finch nested primarily in treed floodplains of larger streams and along the base of the foothills, and, to a lesser extent, along streams up into the foothills. After settlement, it was the only species that was common around urban buildings until the introduction of the House Sparrow (Bergtold 1913). In the west, the House Finch is common in urban habitats where it prefers areas with ornamental shrubs, particularly conifers. It continues to breed in a variety of undisturbed habitats including deserts, desert grasslands, desert shrublands, oak savannahs, juniper–oak woodlands, riparian areas, open coniferous forests, and subalpine shrubs. It avoids dense coniferous stands but is common along their edges. It occupies open grasslands and short-grass prairies where abandoned farm equipment or buildings provide nest sites (Badyaev et al. 2020). Woods (in Austin 1968) concluded that it was always near a source of water in natural habitats. In California, it occupied oak savannahs at a higher rate than in montane hardwoods and oak woodlands, but not significantly. It was considered an oak–savannah affiliate. Its abundance was positively correlated with herbaceous cover and average tree diameter and negatively correlated with hardwood and shrub coverage (Wood et al. 2013). In British Columbia, it is closely associated with human-created habitats and most abundant around human habitation, particularly in suburban areas. It uses other anthropogenic habitats including city core areas, golf courses, semiopen parks, cemeteries, nurseries, airports, orchards, and vineyards. In Vancouver, it was most abundant in lightly wooded apartment and residential areas with 30% tree and shrub coverage, but avoided sparsely vegetated industrial and commercial areas. In open grassland landscapes, it is associated with shrub thickets in gullies and occurs around wetland margins. It avoids closed forest habitats and subalpine and alpine areas and is rarely observed in wilderness areas (Campbell et al. 2001).

Adults may roost singly in small groups in the canopy of trees or in cactus stands and occasionally in ivy under eaves of buildings, inside buildings, and under roof shingles. Occasionally the House Finch roosts with House Sparrows. When the female is incubating, the male roosts nearby, and the pair roosts together near the nest when it contains nestlings. Nest boxes are not used as roosts after nesting is complete. At 1 California site, males appeared to roost together as far as 2.4 km from their nest sites (Badyaev et al. 2020; Bergtold 1913; Evenden 1957).

All Ontario nests were elevated, mostly in coniferous trees, but also on or in buildings and in hanging flower pots. Tree nests were in spruce (44.9% of nests), juniper (35.5%), and white cedar (19.6%). They were usually near the tops of trees and most were against the trunk on horizontal branches. In larger trees, nests were occasionally distant from the trunk on a horizontal branch. One nest was on a rose trellis against a wall, 2 were under aluminum window awnings, 1 was on a verandah overhang, 1 was on an upright stud inside a garage, 1 was in a factory fan duct, and 1 was in a space between bricks on a building. Nests were 1-10 m from the ground with most 2.3-3.4 m up. Some were in old nests of Mourning Dove, Cliff Swallow, Barn Swallow, and House Sparrow. Some nests were used in 2 successive years or for more than 1 brood in a year (Peck and James 1987, 1998b). In St. Catharines, 1 nest was in a hanging flower basket and the remainder were in Chinese junipers and red cedars. Nests were 1.2-4.3 m above ground (average 2.6 m; Kozlovic 1988, 1998; James 1978b). Three nests in Rainy River were all in white cedars (Graham and Salvadori 1995).

Most nests reported elsewhere were on or in buildings or coniferous trees and shrubs adjacent to buildings. The House Finch commonly nests in ivy growing on the sides of buildings. In desert habitats, it commonly nests on cacti. The main requirements for nests in anthropogenic sites are a solid base and some overhanging structure that provides protection from the elements (Badyaev et al. 2020). In Vermont Christmas tree plantations where the trees were 1-3 m tall, it preferred to nest in trees that were 2.0-2.5 m tall. Mean height of nests was 1.1 m regardless of tree species. Nests were 95.2% shaded from above and 93.1% from the sides. It exhibited a strong preference for nesting in spruce with 9 times more nests per tree in spruce than fir. Shading was much higher in spruce suggesting that nest concealment may be important (Hughes and Hudson 1997). In British Columbia, 97% of nests were in human-influenced habitats; the other 3% were in forest, wetland, or grassland habitat. Human-influenced habitats included 46% suburban, 26% cultivated farmland, 10% urban, 7% rural, and 6% orchards. Sixty-two percent of nests were in trees and shrubs. Fifty-three percent were in conifers that were mostly ornamental species; only 8% were in deciduous trees or shrubs. Spruce was a preferred nest-tree species, including blue spruce. Eighty-three percent were in nonnative tree and shrub species and 9% were in vines or ivies that were usually growing on buildings. Eleven percent were in or on human-created structures including shed rafters, beams, shelves, under sundecks and carports, in window shades and wall vents, in covered street lamps, on porch light fixtures, on top of sliding garage doors, in an opening in a balcony railing, in bird feeders, in a coil of wire, in hanging flower baskets, and in nest boxes. Nests were 0-45 m from the ground with most 1.8-3.0 m up; the highest nest was on the 15th floor of a high-rise apartment building (Campbell et al. 2001). It occasionally nests on rock ledges and rarely in deciduous trees or shrubs or in cavities in trees. Unusual nest sites include in tin cans hanging on fence posts, on the ground, in old hats and stove pipes, in hollow limbs and woodpecker holes, and

in a haystack. Nests have been constructed in old nests of phoebes, Cliff Swallow, Barn Swallow, American Robin, towhees, blackbirds, and orioles (Badyaev et al. 2020; Bergtold 1913; Evenden 1957; Hamilton 1993a; Janssen 1989; Woods in Austin 1968). The House Finch nests in boxes built for it and in those designed for other species (Bergtold 1913). It also nests in Purple Martin houses and gourds intended for martins (Hill 1988b). Sometimes the first nest is used to raise a second or even third brood but just as often new nests are built for subsequent nests. In California, no nests were reused by a single pair within a breeding season but 7 of 24 pairs (29.2%) reused their nest from a previous year; 74% of all nests had been used previously. Old nests of other pairs may be refurbished and used and females frequently take material from old nests to build new ones. One nest in a haystack was used for more than 6 years, but probably not by the same individuals (Badyaev et al. 2020; Bergtold 1913; Campbell et al. 2001; Gill and Lanyon 1965; Hooge 1990; Woods in Austin 1968).

The House Finch is highly gregarious and tolerant of conspecifics. No resources are defended other than the immediate nest site. Close neighbours are tolerated and most aggression is directed to females that have nests more than 12 m distant. In urban areas, pairs commonly nest within 1 m of each other. In deserts, pairs often nest in loose aggregations 20-40 m apart. Two active nests on a barn beam were so close together that the nesting materials were interwoven on the adjacent sides. Both sexes guard their mates, presumably to reduce the incidence of extra-pair copulations (Badyaev et al. 2020; Kalinoski 1975; Woods in Austin 1968).

Natal philopatry tends to be lower in eastern populations, which may be partially migratory. In all populations, independent juveniles may wander considerably during the postfledging period, and this reduces natal philopatry even in resident populations. Juveniles that remain in an area for more than 2-3 weeks in late summer or autumn are likely to nest in that area in the following breeding season. In Michigan, 16 of 345 nestlings (4.6%) returned to breed. In Massachusetts, 12 of 45 juveniles (26.7%) did not leave the breeding area. In Arizona over 8 years, natal philopatry rates ranged from 7.9% to 13.2% (average 10%). In both Montana and Arizona, about 15% of birds did not leave their natal area and those that dispersed usually travelled less than 20 km. In California, a male nestling was recaptured the following year 12.2 m from its natal nest. In Montana, most newly arriving birds were hatched in other areas less than 20 km distant. In New York, 5 of 63 nestlings (7.9%) returned to the natal area. Others were recaptured as far as 24 km away in the spring of the following year. Of 16 nestlings in Colorado, 1 died shortly after banding, but 0 of the remaining birds returned (Badyaev et al. 2020; Bergtold 1913; Evenden 1957; Gill and Lanyon 1965).

In the west, the House Finch is predominantly a resident so birds tend to remain in the same area. Within breeding seasons, subsequent nest sites are usually within 10-20 m of the previous nest. In the east, 27.8% of males and 20.9% of females were recaptured at their previous breeding area; the mean distance between recaptures for 333 birds was 109 km. Within breeding seasons, eastern birds often move more than 1 km between nesting attempts (Badyaev et al. 2020).

Limiting Factors

Eggs have been found in Ontario nests from the third week of March until the first week of August. Most are present from the last week of May until the third week of June. At St. Catharines, 72% of breeding occurred from mid-May to late June. The timing of egg laying varied significantly, averaging 18 days earlier in a warmer spring than in more typical springs. Warm spring weather may

induce earlier egg laying, but the presence of nearby feeders may also be a factor (Kozlovic 1988, 1998; Peck and James 1998b).

Pair formation begins in winter flocks. Both sexes prospect and select potential nest sites. Nest prospecting may take as long as 2 weeks, usually 1-8 days. Pairs that return from the previous year only prospect for 1-2 days. First nests of the season take longer to build on average (10.4 days) than later nests (7.6 days). In Arizona, nest building took an average of 8.9 days (range 5-21 days). In Montana, nests took an average of 11 days to build (range 4-29 days): an average of 17.5 days for early nests and 4.5 days for later nests. In Colorado nest boxes, first nests took 3-6 days to build and later nests were completed within a day. In California, early season nests took 14-21 days to build; later nests were built as quickly as in 2 days. New York nests took 2-5 days to build, mostly 3 days. Early in the season, as many as 10 days may elapse between nest completion and the initiation of egg laying. In later nests, egg laying begins the day the nest is completed or the following day. Eggs are laid at the rate of 1 per day but occasionally 1 or 2 days are skipped. Incubation typically begins with the laying of the penultimate or final egg. When temperatures are lower than 4°C, incubation may begin with the laying of the first egg. The incubation period of 30 Ontario nests was 10-14 days, with 15 having incubation periods of 11-12 days. In St. Catharines, the modal incubation period was 13 days. Elsewhere, incubation periods of 11-18 days have been reported with most eggs hatching in 12-14 days. Shorter incubation periods are often associated with warmer ambient temperatures; colder temperatures may prolong the incubation period. The eggs may all hatch in 1 day but more frequently 2 hatch on the first day and the others follow at 1-day intervals. Eggs may also hatch at the rate of 1 a day with a noticeable size difference in the nestlings that carries over into the fledgling stage. The nestling period at 1 Ontario nest was 16 days. Elsewhere, nestling periods of 11-19 days have been reported. The median in British Columbia was 15 days and most studies report average nestling periods of 14-16 days. Young may leave the nest when they are only 11-12 days old if disturbed (Badyaev et al. 2020; Bergtold 1913; Campbell et al. 2001; Evenden 1957; Gill and Lanyon 1965; Kozlovic 1998; Peck and James 1987, 1998b; Woods in Austin 1968).

The House Finch regularly raises 2 broods in a season and some pairs raise 3 broods. Three broods have been confirmed in Ontario and many other locations. In California, birds that maintained their pair bond from the previous year raised significantly more clutches (2.5) than newly formed pairs (1.7 clutches). Seven of 9 returning pairs (77.8%) raised 3 broods. Renesting is common if a clutch is lost and nest building may begin within an hour of the loss of the previous nest. It has been known to attempt as many as 6 clutches within a season, but has never been documented raising more than 3 broods (Badyaev et al. 2020; Bergtold 1913; Campbell et al. 2001; Hooge 1990; Peck and James 1998b). Clutches of 2-6 eggs were reported in Ontario, with most containing 4 or 5 eggs (mean 4.39 eggs). Overall, clutches of 2-7 eggs have been reported with 70% or more of clutches containing 4 or 5 eggs. Mean clutch sizes tend to range from 4.2 to 4.5 throughout its range but may be as high as 4.75 eggs. In Indiana, most April nests contained 5 eggs; May and June nests contained 4 eggs. Clutch sizes of replacement nests tend to be smaller than those of first nests (Badyaev et al. 2020; Bergtold 1913; Campbell et al. 2001; Evenden 1957; Gilbert et al. 2005; Gill and Lanyon 1965; Hamilton 1993a; Peck and James 1998b; Woods in Austin 1968). The mean clutch size was significantly greater in the east (4.53 eggs) than in southern California (4.21 eggs) and the

northwest (4.35 eggs). Wootton (1986) concluded that larger clutch sizes in the east were probably because of higher predation rates and population densities in the west. Where predators are more abundant, birds may lay fewer eggs to conserve energy for renesting. Where densities are lower, the amount of available food is greater on a per individual basis. If higher clutch sizes in the east are due to predation rates, clutch sizes should remain high. If it is a result of lower densities, then clutch size should decrease as the population increases. It is possible that females reduce the clutch size when more than 5 eggs are present. In clutches of 5 or more eggs, 1 egg was often found outside the nest. Bergtold (1913) assumed that these eggs had been accidentally pushed out of the nest but it is conceivable that the female deliberately removed them to reduce the number of nestlings that had to be cared for. In Alabama, a female ate one of her own eggs from a clutch of 6 eggs. The proportion of single eggs disappearing from 6-egg clutches (2 of 12, 16.7%) differed significantly from the proportion disappearing from smaller clutches (1 of 205, 0.49%). This may have been a deliberate attempt to reduce clutch size but may have been a response to disturbance or a damaged egg (Gilbert et al. 2005).

Both sexes are capable of breeding in their first year. In all populations, the sex ratio is highly male biased so as many as 50% of males may not attract a mate. Brightly coloured males are more likely to attract a mate than dull-coloured males. The bright colours are a result of a rich diet and signal that the male may be superior in providing food to the female and nestlings. Brightly coloured males obtain mates sooner and nest earlier, possibly allowing time to raise an additional brood (Hill et al. 1994). In many populations, some yearling females do not breed (Badyaev et al. 2020; Gill and Lanyon 1965; Hill et al. 1994).

The mating system is monogamous. In Montana, loose behavioural interactions between 2 males and 1 female were observed in 5% of pairs, although only 1 male provisioned the incubating female and the nestlings. There is 1 case of a male with 2 females that laid a total of 10 eggs in a single nest. There are 2 records of a single female having 2 active nests only 5 m apart at the same time. Eggs were laid in the second nest during the incubation period of the first nest. It was presumed that the same male attended these nests but this was not positively confirmed (Badyaev et al. 2020; Evenden 1957; Woods in Austin 1968). In sedentary populations, the pair bond may be maintained throughout the nonbreeding season and into subsequent breeding seasons; 1 Montana pair remained together for 7 years. In California, the pair bond was maintained in 16 of 17 pairs (94.1%) when both members of a pair returned. The pair that did not reunite failed to produce young in the previous year and the male was the most promiscuous bird in the population, being responsible for most of the extra-pair copulations. Year-round maintenance of the pair bond allows pairs to nest earlier and raise more broods than newly established pairs. It also allows an individual to recognize the loss of a mate during the nonbreeding season and to find a replacement before the breeding season starts (Hooge 1990). Of 33 females observed for 2-4 consecutive years, 70% bred with the same male in at least 2 years. In another location where 18 pairs were followed for 2 years, 16 (88.9%) retained their mate. Of 56 breeding males observed for 2-5 consecutive years, 60% nested with the same female in any 2 consecutive years. In Michigan, approximately 10% of birds switched mates during the breeding season, almost always after nest abandonment by the female. Ninety-three percent of pairs remained together after the nest was depredated and 100% remained

together after nesting successfully. In Arizona, 16% of females switched mates during the breeding season, 43% after nesting successfully and 57% after nest predation or abandonment (Badyaev et al. 2020).

Intraspecific egg dumping is a rare reproductive strategy. Only 2 cases have been confirmed of more than 900 nests across the range of the House Finch (Badyaev et al. 2020). Both sexes engage in extra-pair displays. Females may display to a group of males followed by extra-pair copulations, often with more than 1 male. Most extra-pair copulations do not result in fertilization. In Michigan, 8.4% of nestlings in 14.3% of nests were fathered by a male other than the attending male. Nesting density was correlated with the incidence of cuckoldry. Factors such as plumage brightness, adult size, clutch initiation date, clutch size, and age of the male had no effect on the rate of cuckoldry (Hill et al. 1994). Overall, 6-10% of offspring are extra-pair. In pairs where both partners were local, nests contained 35% extra-pair young compared with 8% when at least 1 partner was nonlocal. In 3 Montana areas, the incidence of extra-pair young was 6.5%, 4.6%, and 9.0%. Occurrence of extra-pair young was associated with the total number of active nests in a local neighbourhood: 3 local nests resulted in 10% extra-pair young, 4 nests in 20%, 6 nests in 40%, and 7-10 nests in 50% extra-pair young (Badyaev et al. 2020).

The House Finch feeds on the ground or while it is perched on grasses, shrubs, cacti, or trees. In British Columbia, 60% of foraging occurred on the ground. Nearly half of foraging occurred in sparse grass or weed patches that represented less than 2% of available habitat. It feeds on herbaceous seeds either by picking them off the ground or by clinging to plants and picking seeds off flower heads. It frequently hovers at fruits and flowers and can feed and drink while hovering. In spring, it eats leaf and flower blossoms from shrubs and trees. It prefers to eat fruit that is still hanging on the tree. It sips maple sap from wounded branches and also visits hummingbird feeders. In the west, it is attracted to weeds and seed spillage along railroads; this is an important food source in winter. It is attracted to sodium and ingests salt where it is available. It also frequents calcium licks and soils and may make daily visits to calcium deposits throughout the breeding season (Badyaev et al. 2020; Bergtold 1913; Campbell et al. 2001; Woods in Austin 1968). In an aviary experiment, the House Finch was most efficient at handling seeds 25-65 mg. It needed to encounter a seed every 200-500 seconds to meet its midwinter energy demands (Benkman and Pulliam 1988). It strongly prefers fruits containing hexoses over those containing sucrose but is capable of assimilating both types of sugars. The preference for hexoses may be because these sugars are readily assimilated whereas sucrose must be hydrolyzed first (Avery et al. 1999). Avery (1996) treated oats, the preferred seed of adults, with a chemical so that they avoided oats. Adults that learned to avoid oats did not feed them to older nestlings and fledglings. Food preferences of adults can affect the diet of dependent young.

The male may courtship feed the female and feed her while she is incubating. In Arizona, 56% of males did not provision females during incubation. Females compensated by taking fewer off-nest bouts so that the incubation period was not prolonged (Badyaev et al. 2020). Young are fed regurgitated food for the first 1-3 days. In Colorado, nestlings were fed mostly dandelion seeds. When they were not fed dandelion seeds, nestlings were given the same types of seeds that the adults consumed. No animal food was found in crops or stomachs. In Michigan, nestlings were fed

buds from trees in April and early May (Avery 1996; Badyaev et al. 2020; Bergtold 1913; Evenden 1957; Gill and Lanyon 1965). Beal (1907) analyzed the contents of 46 nestling stomachs. The diet consisted of 2.4% animal food and 97.6% vegetable matter. The House Finch appears to be unique within its family, eating very little animal food and feeding nestlings mostly plant materials. Animal food consumed by nestlings consisted almost entirely of a minute beetle that lives on decayed fruit, a few aphids, and 1 grasshopper fragment. It is possible that most of the animal food was ingested incidentally with the plant material that the adults provided. Vegetation in the nestling's diet consisted almost entirely of seeds with the most important being sunflowers, poison oak, and 2 species that do not occur in the east.

In Colorado, House Finch adults ate almost any vegetable matter, but preferred seeds. In experiments, hemp seeds were preferred over others. It ate pieces of bread, apples, oranges, and almost any kind of table waste and will consume large quantities of fat, including suet. In arid areas, it drinks copious amounts of water (Bergtold 1913). Woods (in Austin 1968) reported that it ate watermelon pulp at a feeder. In British Columbia, it eats seeds from birches and bird feeders, and herbaceous seeds, and in spring it frequently eats fruit tree buds. It feeds on seeds of dandelions, yellow salsify, scotch broom, and goldenrods, and on the berries of crabapples, hawthorns, mountain-ash, apple, Saskatoon, blackberries, and wax myrtle. It occasionally damages blueberry and wine grape crop, but is considered a minor pest. Beal (1907) analyzed 1,160 adult stomachs of birds from the western population. The diet consisted of 2.4% animal food and 97.6% vegetable matter. The animal food was predominantly aphids, but it also consumed caterpillars and a few beetles that were mostly weevils. The vegetable matter consisted of 86.2% weed seeds, 10.5% fruit, and 0.9% miscellaneous. The most important seeds were those of knapweed, black mustard, prostrate knotweed, and stork's-bill. It rarely ate grain such as wheat, oats, and corn. Fruit attained a maximum of 27.4% of the diet in August. Favourite fruits were cherries, apricots, peaches, prunes, and pears and it also ate strawberries, elderberries, and blackberries. It pecks at larger fruits and may not eat them, or it may eat half of one and move on to the next. Only 63 stomachs (5.4%) did not contain plant seeds and 67% contained nothing else; 78.4% of stomachs contained no fruit. Badyaev et al. (2020) reported that chokecherry berries comprised as much as 70% of the diet some weeks in Montana. The House Finch may cause substantial damage to apple crops by consuming parts of the growing fruits. Large numbers may be attracted to ripe thistles in late summer and autumn. In the east, it eats ripe mulberries in the summer; seeds of amaranths may also be important in the diet. Elliott and Arbib (1953) reported that eastern birds ate mouse-ear chickweed seeds.

Parasitism by the Brown-headed Cowbird is rare in long-established House Finch populations but common in expanding populations. In Montana, the rate of parasitism peaked 5 years after a House Finch population was established; no parasitism occurred 15 years after establishment. In the core of the western population, parasitism is nonexistent or very rare. The probable reason for this is that the House Finch is a poor host for the cowbird. The finch feeds its nestlings an almost exclusive vegetable diet but cowbird nestlings need animal food to sustain themselves. Most cowbird nestlings die in the nest; a few fledge but these are considerably underweight. It is uncertain whether any cowbirds have been successfully reared to independence by House Finches. When finches expand into a new area, cowbirds parasitize them at a high rate because they are not

familiar with them and their nests are easy to find. Gradually cowbirds learn that few of their young are surviving in House Finch nests and the incidence of parasitism declines or even ceases (Badyaev et al. 2020; Evenden 1957; Woods in Austin 1968). In Guelph in the first Ontario study, Graham (1987) reported that 7 of 8 nests (87.5%) were parasitized; when nests found within the nestling stage were included, 10 of 13 nests (76.9%) were parasitized. Peck and James (1987) reported that 27 of 62 nests (42.2%) found in the province had been parasitized. In St. Catharines, Kozlovic (1998) reported that 33 of 82 nests (40.2%) were parasitized. van Twest (2001) did another study in Guelph and determined that 19 of 166 nests (11.4%) were parasitized. Peck and James (1998b) reported that 50 of 182 Ontario nests (27.5%) were parasitized. Since 1987, 23 of 95 nests (24.2%) were parasitized, a substantial decrease from the 42.2% they reported in 1987. Consistent with other colonizing populations, parasitism rates were initially very high in Ontario but have declined considerably. The cowbird has not yet learned to completely avoid House Finch nests as it has in many long-established western populations where the parasitism rate is 1% or less. In British Columbia where it first became established in 1935, 24 of 404 nests (5.9%) were parasitized (Campbell et al. 2001). In St. Catharines, the clutch size of parasitized nests (3.50 eggs) was significantly smaller than unparasitized nests (4.22 eggs). There were no differences in hatching rates, nestling growth, or fledgling rates in parasitized and unparasitized nests. The cost of parasitism was an average loss of 0.72 eggs per parasitized nest. Ninety percent of cowbird eggs hatched but all young cowbirds died in the nest. The House Finch began to nest about a week before the cowbird and many initiated nesting much earlier. Early nesting birds were able to avoid parasitism by completing their clutches before cowbirds started nesting (Kozlovic 1998). In Guelph, there was no significant difference in the clutch size of parasitized (4.4 eggs) and unparasitized (4.6 eggs) nests but unparasitized nests produced significantly more fledglings (3.7 compared with 1.8). Some nestling cowbirds survived for more than 3 days in the nest and this competition for food and space may have led to increased mortality of finch nestlings. Three cowbirds fledged but only one was encountered later; it is unknown if it survived to independence. Parasitized nests were abandoned at a higher rate than unparasitized nests, but not significantly (van Twest 2001). The House Finch often abandons nests that contain more than 2 cowbird eggs (Badyaev et al. 2020).

Diseases are the greatest limiting factor for the House Finch, with the most significant being mycoplasmal conjunctivitis. This disease causes swelling of 1 or both eyes. Diseased birds spend a larger proportion of their time feeding (86% compared with 28% for healthy birds), move at a lower rate (32% compared with 59%), feed singly more often, and associate with smaller flocks. Even when food is abundant, birds may lose weight and subsequently die. Due to reduced vision or blindness, diseased birds have reduced antipredator responses and are much more likely to be preyed upon than healthy birds. Heavily infected birds have difficulty seeing well enough to fly and spend most of their time on the ground. Prevalence of conjunctivitis is low in late spring and summer and increases in late summer and autumn, peaking in September or October each year. Juvenile females are most vulnerable to the disease but all sex and age classes contract conjunctivitis. During the breeding season, males in breeding condition are less likely to contract the disease than nonbreeders. The rapid increase in the prevalence of the disease in autumn may be caused by the recruitment of immunologically naive juveniles into the population. The disease may spread in autumn through contact at feeders and during migration in eastern populations. Eastern birds are

more vulnerable to conjunctivitis than western birds. The eastern population originated from a small number of birds and is inbred with lower genetic diversity, which may potentially make it more susceptible to disease. Conjunctivitis was first reported during the winter of 1993-94 around Washington, D.C. The disease spread rapidly in the east and was reported in Ontario as early as November 1994. Within 4 years of its initial detection, the disease spread throughout the eastern House Finch population, causing declines in abundance by as much as 60%. The peak of the disease occurred in 1995 and the rate of decline of the House Finch has been slowing since then. In Niagara Region, the presence of conjunctivitis was first confirmed in 1995 with its prevalence peaking in 1998 when 25-50% of birds were infected. An increasing proportion of the population is now resistant to conjunctivitis compared with several years ago. The disease is now at an endemic level in the House Finch. Conjunctivitis caused a significant decline in the Ontario population. Although the prevalence of the disease may have decreased, populations have not rebounded to their former numbers (Adelman et al. 2017; Altizer et al. 2004; Badyaev et al. 2020; Black and Roy 2010; Dhont et al. 1998; Fischer et al. 1997; Hartup et al. 2001; Hawley et al. 2007; Hochachka and Dhont 2000; Knight 2009; Yunick 1995b).

The House Finch is vulnerable to avian pox. This may cause damaged mandibles, blindness, and a reduced ability for males to have red plumage. Similar to conjunctivitis, this may lead to death either directly or indirectly due to impaired ability to see predators. The incidence of avian pox appeared to increase concurrently with the arrival of the West Nile virus (Campbell et al. 2001; Pellegrini et al. 2011).

West Nile virus was introduced into North America in New York City in 1999 and spread rapidly throughout the continent. The House Finch is a highly competent host for the virus and is fed upon frequently by the genus of mosquitoes (*Culex*) that is the vector. Similar to the House Finch, these mosquitoes are most abundant in urban areas and other areas associated with humans. In California, 19.6% of dead finches turned in by the public tested positive for the virus. In a laboratory experiment, 67% of experimentally infected birds died. Evidence indicated reduced survival in the wild and a decrease in population in California; laboratory tests indicated that mortality rates were higher than 60%. Those that survive have immunity to the virus so that the mortality rate within a population may decrease over time as acquired immunity increases (Kilpatrick et al. 2007; Pellegrini et al. 2011; Wheeler et al. 2009). The House Finch has been exposed to West Nile virus for approximately 2.5 decades so it is probable that most of the population is now immune to the virus.

Early nests have the potential to be destroyed by late snow storms. In St. Catharines, 4 of 5 nests were filled with snow during a storm on the last day of March; the other nest was under the eaves of a house (Kozlovic 1988).

In Alabama, all nests were infested by mites in the second half of the breeding season. This resulted in lower nestling mass and hemocrit values. Some nestling deaths were attributed to mites and there may have been increased mortality of fledglings. Stoehr et al. (2000) concluded that mites have the potential to reduce reproductive success.

The domestic cat is a significant nest predator. In a California study, almost the entire loss of nestlings was due to cats (Evenden 1957; Woods in Austin 1968).

In western North America, the House Finch is considered one of the most significant native pests because of depredation of fruit crops. In the late 1960s, more than 50,000 finches were destroyed by poison baits and trapping at a single orchard, and similar campaigns were widespread (Campbell et al. 2001; Woods in Austin 1968).

In many western populations, the House Sparrow is a significant nest competitor for the House Finch. The House Sparrow is dominant and excludes House Finches from potential nest sites; in addition, it destroys eggs and nestlings of finches. Finches are often so harried by sparrows that they abandon nests. In Colorado and California, most nest losses were due to a combination of House Sparrows and cats (Badyaev et al. 2020; Bergtold 1913; Evenden 1957). No evidence of competition with the House Sparrow has been observed in Ontario (Peck and James 1998b) or in Indiana (Hamilton 1993a) and there appear to be no such reports from the east.

Status

The House Finch is not native to Ontario or eastern North America, with native populations restricted to the west. In 1940, it was added to a list of migratory birds protected by agreement between the United States and Mexico. Until then, it was commonly sold as a cage bird in the east. Once the agreement was signed, selling caged birds became illegal. To avoid prosecution, it is thought that a single Long Island, New York dealer released his captive birds, which originated in California. The first nesting in New York occurred in 1943. By 1951 the entire eastern population was estimated at 280 birds. The first records off Long Island were in 1948 in New York, in New Jersey in 1949, in Connecticut in 1951, and in Ohio by 1964. Range expansion was by jump dispersal, with the sudden appearance of a few individuals, probably dispersing juveniles. In a few years, the leading edge of the core population would catch up with these pioneers and occupy the area. Colonization was rapid, with finches typically occurring in all major cities and most rural areas within 20 years of its first appearance in an area. Christmas Bird Count (CBC) data for the entire eastern population indicated that it increased at an exponential rate during 1962-71 (Aldrich and Weske 1978; Bock and Lepthien 1976c; Cecil and Dinsmore 1995; Elliott and Arbib 1953; Gill and Lanyon 1965).

The first Ontario sighting of the House Finch was in the Kingston area in 1970, but this record was not adequately documented. The first confirmed record was a female seen at Prince Edward Point on 27 August 1972. There were no further records until 1976 when it appeared at several scattered locations. The first nest in the province was found in St. Catharines on 20 June 1978. It spread widely in the 1980s from its original stronghold in the Niagara Peninsula. By 1983, it began a northward spread into the eastern lowlands between the St. Lawrence and Ottawa rivers. By then, it was fairly common along the shores of Lake Erie and Lake Ontario, but was still uncommon in the southern Georgian Bay area. It was most common in large urban centres along the southern Great Lakes and had begun to occupy the surrounding countryside. First nests reported from different areas include 1978 in Niagara Region, 1982 in Hamilton, 1985 in Guelph, and 1995 in Rainy River. Timing of the first atlas coincided with the initial colonization of the province by breeding birds, with its distribution confined to the area south of the Canadian Shield and greatest abundance from Long Point to Niagara and the Toronto area east along the north shore of Lake Ontario and the St. Lawrence River. It also occurred along Lake Erie and in scattered inland areas in larger population centres such as Ottawa, Kitchener-Waterloo, and Cambridge (Black and Roy 2010; Curry 2006;

Graham and Salvadori 1985; James 1978b; Kozlovic 1994; Kozlovic in Cadman et al. 1987; van Twest 2001). During the first atlas, it was observed in 1 square in 1981, 18 squares in 1982, 35 squares in 1983, 60 squares in 1984, and 108 squares in 1985. Results suggested that colonists were coming around both ends of Lake Ontario from New York. Thereafter, it appears to have spread east and west along the northern shores of Lake Erie and Lake Ontario and along the St. Lawrence and Ottawa rivers. Shorelines and rivers appeared to form major routes for dispersal (Dunn 1987). James (1991) considered the House Finch a common to locally abundant permanent resident near Lakes Erie and Ontario that rarely summered as far north as Georgian Bay and Renfrew County. It was a vagrant north to Marathon and Timiskaming District.

The second atlas revealed that the breeding range of the House Finch had expanded to include the entire area south of the Shield. There were scattered records on Manitoulin Island, in the Shield north to North Bay and Sudbury, on the north shore of Lake Superior including Thunder Bay, and in the Lake of the Woods area. Its probability of observation increased significantly province-wide and in all regions where it occurred. By the time that the second atlas was conducted, the House Finch population had already suffered a decline due to conjunctivitis. It was most abundant in areas of highest human population density: the Greater Toronto Area, the Niagara Peninsula, London, Ottawa, and Windsor. Moderate densities were present in the remainder of the Carolinian Forest Region, along the Lake Huron and southern Georgian Bay shores, and along Lake Ontario and the St. Lawrence River (Leckie in Cadman et al. 2007).

Cadman et al. (2016) reported that Breeding Bird Survey (BBS) data for Ontario indicated that the House Finch had increased at a rate of 13.8% per year from 1983 to 2016. This was the 6th largest increase for any Ontario species. This also includes the period when conjunctivitis was introduced, which caused a decline in numbers. BBS data for 1970-2021 indicate that the House Finch increased at annual rates of 1.94% in Canada and 21.4% in Ontario. During 2011-21, it decreased at annual rates of 0.273% in Canada and 6.05% in Ontario. All results were of low reliability except for the long-term Canadian trend, which was of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Unless they fledge prematurely, young are capable of sustained flight when they leave the nest. They may fly as far as 60 m on their first flight to a tree or house. In California, the average distance of first flights was 15.0 m and the longest was 38.1 m. Others drop to the ground on their first flight attempt and crawl into corners, under shrubs, or amongst leaves. Fledglings sleep near the nest, typically remaining motionless for the first 1-2 days, then moving around in the vicinity of the nest. Once young leave the nest, they never return. They start actively following the adults 4-5 days after fledging. The brood flies with the male for about 2 weeks after fledging. Juveniles try to feed themselves as early as 7 days but typically 12-16 days after fledging; they are still fed by the male 18 days after fledging. Juveniles can completely feed themselves 2.5-3 weeks after fledging (Badyaev et al. 2020; Bergtold 1913; Evenden 1957; Gill and Lanyon 1965).

Juveniles form flocks beginning in mid-July with peak numbers occurring in late October. The first flocks consist of both sexes but later flocks become sex segregated. Recently fledged males strongly dominate and displace recently fledged females, resulting in sex-segregated flocks. The sex-segregated flocks remain in the general nesting vicinity until they are 90-110 days old; these

gather in areas with abundant food supplies. Older juveniles form large mixed-sex flocks and start autumn dispersal and, in some cases, large-scale movements. After the onset of juvenile dispersal, many individuals travel 500-700 km. Some travel as far as 900-1,200 km within 4 weeks. Birds that stay within an area for more than 2-3 weeks during this period are likely to breed there the following year. Pairing by juveniles may occur during the postfledging dispersal period. Pairs of juveniles have been observed prospecting for nests and making attempts at nest building in October and November (Badyaev et al. 2020; Bergtold 1913; Campbell et al. 2001).

Because the House Finch nests predominantly near buildings, fledglings are highly vulnerable to being preyed upon by domestic cats. Many die if they are soaked by rain or struck by hail (Badyaev et al. 2020; Bergtold 1913).

MIGRATION

Western populations of the House Finch are nonmigratory. In recently established northern populations in the west, there are pronounced seasonal movements along river valleys and from natural to urban habitats. Movements are particularly pronounced in areas with significant snow cover; movements may exceed 200 km. Strong altitudinal movements may occur in response to snow cover. Movements appear to be strictly diurnal (Badyaev et al. 2020). In British Columbia, it was completely migratory for the first decade of its occurrence and it was 10 years before any birds spent the winter. It is now nonmigratory with stable populations year-round (Campbell et al. 2001).

In the east, the House Finch is partially migratory, with some birds remaining all winter and others moving south. It is unknown if individuals switch wintering strategies between years. In Ontario, small loose flocks of 12-15 have been observed flying over Lakes Erie and Ontario in October and large numbers fly west along the Lake Erie shoreline in Elgin County. Birds banded in Ontario have been recaptured in winter in Michigan and Indiana and birds banded in Ohio have been recaptured in Ontario. Regular movements have been documented in many locations in the Midwest and east, including Quebec. In Ontario, more than 40 birds travelled further than 100 km between the banding and recovery locations. Of 35 recovered Ontario birds, 31 were recovered in Ontario and only 4 were encountered further south: 2 in New York and 1 each in Ohio and Tennessee (Badyaev et al. 2020; Brewer et al. 2018; Brush 1987; Curry 2006; Hamilton 1996; Hansrote and Hansrote 1992; Lancaster et al. 2004; Paquin in Gauthier and Aubry 1996; Stewart 1989a, 1989b). In the Midwest, which included Ontario, the mean distance travelled by birds banded in summer and recaptured in winter was 344.9 km, with 1 bird travelling further than 1,000 km. Birds banded in winter and recaptured in summer travelled an average of 416.4 km (Hamilton 1991). Further east in the United States, birds banded in summer and recaptured in winter travelled a mean distance of 176.7 km compared with 192.1 km for birds banded in winter and recaptured in summer. Birds travelled significantly shorter distances from the breeding grounds in a moderate (259.8 km) than a cold winter (492.8 km). Results indicated that it will extend its southward migration during exceptionally cold winters (Hamilton and Novis 1994). Belthoff and Gauthreaux (1991) determined that males were most abundant at latitudes north of 38°N; females outnumbered males south of latitude 38°N. The larger bodied males were better able to withstand the cold than the smaller females. Winter mortality has been reported as far south as Virginia and South Carolina and this may force females to migrate further south.

At Prince Edward Point, spring migrants move through from mid-March to mid-April (Weir 2008). Autumn movement occurs in October and early November (Curry 2006; Lancaster et al. 2004), but at Prince Edward Point, migrants occur from late August to late September (Weir 2008).

Migration habitat is similar to breeding habitat. In autumn, the House Finch may move to more protected habitat in river valleys and these may be used as migration corridors. It is attracted to weedy areas such as roadsides, dykes, utility corridors, fallow fields, and grassy backshore areas along beaches (Campbell et al. 2001; Dunn 1992; Woods in Austin 1968).

James (1991) considered the House Finch an uncommon to locally common migrant in Ontario.

WINTER

Winter habitat is similar to breeding habitat, but the winter distribution is closely linked to the distribution of feeders (Badyaev et al. 2020). In Vancouver, the House Finch switched from lightly wooded apartment and residential areas with 30% tree and shrub coverage in summer to more open residential areas with 7% tree and shrub coverage in winter. There was a prevalence of feeders in these areas (Campbell et al. 2001). In California, its abundance was positively correlated with structures and human activities and negatively associated with streams, shrubs, and trees (Kalinowski and Johnson 2010).

Roosts are important in winter. Birds may roost singly but more often communally. Roosts may be in ivy on building walls, in a nook in a building, in dense hedges, and in ornamental evergreens. One female roosted in ivy close to her nest site of the previous year. Some communal roosts were used by birds from a wide area distant from the nesting areas. In Vancouver and Victoria, small flocks regularly roost in dense hedges, evergreens, and ivy on building walls. Larger roosts of 200-1,000 birds occur in ivy covering buildings in downtown areas. The probability of an individual roosting in the same tree in consecutive nights was 62% in autumn and 81% in winter (Badyaev et al. 2020; Bergtold 1913; Campbell et al. 2001; Evenden 1957).

Winter site fidelity of the House Finch is low even in resident populations. Winter flocks wander between food sources and individuals may switch flocks. In Arizona, males had a higher propensity to switch flocks than females. Males with less colouration had the highest frequency of flock switching. In British Columbia, the entire population shifts northward in warm winters. At an Indiana feeder, there was a high rate of turnover in winter with few birds remaining in the same area for more than 4 weeks. At a Georgia feeder, 55.7% of banded birds were not seen or captured again. Another 24.7% were recorded as many as 5 times. Forty-four percent of birds that were resighted were present less than 50 days. Only 14% were encountered over a span longer than a year. Young birds were encountered more frequently than adults and females were encountered more frequently than males; young females were encountered most often. There was a high turnover of birds, with only a small fraction of those observed in suburban Atlanta remaining at individual sites year-round. Fidelity was characterized by high site fidelity of adults during the breeding season and low fidelity of juveniles captured early in the summer but becoming higher later in summer. Most birds captured in autumn were encountered for as long as 3 months, and these represented wintering birds. Fidelity declined in late winter and by February most birds that were captured were rarely seen again. In the Midwest, only 31.6% of birds recaptured in a subsequent winter were within

25 km of the original banding site. Others were recaptured at an average distance of 274.0 km. In eastern populations, the mean distance between captures in different winters was 118.3 km. In New York, 673 of 6,842 birds (9.8%) returned in another winter and 146 of 1,517 (9.6%) and 511 of 4,314 (10.4%) returned to 2 Pennsylvania banding stations (Badyaev et al. 2020; Belthoff and Gauthreaux 1991; Campbell et al. 2001; Davis 2008; Elliott and Arbib 1953; Hamilton 1991, 1992; Hamilton and Novis 1999; Yunick 1995b).

The House Finch has a strictly vegetarian diet in winter. In Ontario, it has eaten black alder and giant ragweed seeds (Dance 2008; Dance et al. 2012). In addition to the seeds and berries reported in the summer diet, it has fed on sumac berries and sweetgum seeds in winter (Elliott and Arbib 1953; Sprenkle and Blem 1984).

In winter, the House Finch congregates at bird feeders and its distribution is closely associated with feeder locations. Where sunflowers are offered at feeders, this is the preferred food (Campbell et al. 2001; Dunn 1992; Elliott and Arbib 1953). In Virginia, Sprenkle and Blem (1984) tested wild birds' preferences for 3 types of mash (chick mash, chick mash plus oil, and chick mash and soy), milo, white millet, and sunflower seeds. When fed oil-supplemented mash, birds were able to maintain their body weights at temperatures lower than 20°C.Their body weight was significantly higher at all temperatures than birds fed the other mashes. In the seed preference tests, sunflower seeds were selected almost exclusively at all temperatures. No milo was eaten at any temperature. Its cold tolerance is enhanced by foods high in lipids; these foods are preferred, particularly sunflower seeds. In Pennsylvania, it selected 62.9% cracked corn, 17.2% niger, 11.9% millet, 6.8% canary seed, and 1.2% whole corn. Striped sunflowers were offered but not consumed. Feeding heights included 36.6% at 6 m, 32.4% at 4 m, 25.8% at 2 m, and 5.2% on the ground. It preferred elevated platforms to foraging on the ground (Nastase and Linville 1995). Throughout the United States and Canada, 212,140 visits to feeders were recorded. The House Finch fed predominantly at tube feeders but also on platforms. The proportion of birds using the various seed types included 71% for black oil sunflowers, 58% for 0.5-cm sunflower chips, 56% for 0.3-cm sunflower chips, 52% for niger, 47% for safflower, 41% for striped sunflowers, 34% for peanuts, 25% for red milo, 23% for white proso millet, and 23% for cracked corn. Seeds with greater levels of fat, fibre, or protein were more likely to be selected. Seed use was greater with seeds with hulls (93%) and greater fat (65%) and protein (22%) content. Black oil sunflowers had the highest levels of fat which may have contributed to its high preference (Horn et al. 2014; Johansen et al. 2014). Project FeederWatch results indicated that flock sizes varied considerably, but averaged 10-15 birds in early January with a steady decrease thereafter. The most preferred foods were black oil and hulled sunflowers, but striped sunflowers, mixed seeds, safflower, niger, and water were also preferred foods. Infrequent choices included millet, canary seed, cracked corn, milo, wheat, hulled peanuts and hearts, oats, canola, suet, peanut butter mixes, bird puddings, fresh fruit, baked goods, sugar water, and popped corn (Dunn and Tessaglia-Hymes 1999). The House Finch eats hemp and field mustard seeds at feeders, but typically only if sunflowers are not available (Elliott and Arbib 1953).

Visiting feeders may bring the House Finch in contact with the House Sparrow. In interspecific conflicts, the House Sparrow won well over 90% of contests with the House Finch. A loss of a contest simply means that the subordinate bird is displaced. Competition with the House Sparrow is unlikely

to be a significant limiting factor for the House Finch except perhaps at locations where the House Sparrow population greatly exceeds that of the House Finch (Hamilton 1993b; Kalinowski 1995).

The House Finch is not well adapted to the cold, and eastern populations appear to be less tolerant of cold than western birds. In British Columbia, birds either migrate during winter storms or perish. In Virginia and South Carolina, considerable mortality has been reported during extremely cold mid-winter weather. Winter survival rates of the House Finch may be low, particularly in eastern populations. Winter mortality has not been documented in Ontario, but it is probably a significant limiting factor because this is at the northern extent of its range. Birds that have access to high-fat foods at feeders, such as black oil sunflower, are more likely to survive than those that must rely on natural foods (Campbell et al. 2001; Dunn 1992; Sprenkle and Blem 1984; Stewart 1989a).

The House Finch is highly vulnerable to suffering mortality from striking buildings. At 1-3 storey residences, it was 80.1 times more likely than average to collide with a building and was the fifth-most vulnerable species. It was not within the top 20 species for striking low-rises or high-rises (Loss et al. 2014). It is probable that most of this mortality occurs in winter at houses that have feeders.

Several studies used CBC results to chronicle the initial increase in the Ontario House Finch population and its subsequent decline due to conjunctivitis. Kozlovic (1994) summarized data from 50 southern Ontario CBCs for 1978-88. In 1977, the total number of birds observed on counts in the province was 2, increasing to 7,496 in 1987. Greatest abundance occurred in the Niagara Peninsula where more than 40% of all House Finches were recorded. Numbers in Niagara Falls and St. Catharines peaked in 1985 and subsequently declined, but continued to increase in other areas. Notable increases were documented at London, St. Thomas, Hamilton, Port Colborne, and in Simcoe County. It did not occur regularly at Ontario feeders until 1982. Tozer (1997b) analyzed results for the same 50 CBCs for 1988-96. The previous exponential increase continued from 1958 to 1994, but a dramatic downward trend occurred in 1995 and 1996. Numbers in the Niagara Peninsula peaked at 4,478 in 1994 but dropped to 3,148 in 1995 and 1,684 in 1996. The House Finch was uncommon in the southern Georgian Bay region and the Ottawa valley in 1987, but it had expanded significantly in these areas by 1996 with no decline. It also spread north to several communities in the Canadian Shield with no subsequent decline. Population declines occurred predominantly in areas of its greatest abundance and were probably linked to conjunctivitis. On the St. Catharines CBC, 0 were seen in 1979, 5 in 1980, 81 in 1981, and 196 in 1982 (Foley 1983). There was an exponential increase on Niagara Region CBCs until 1994 after which the population declined to half its peak (Black and Roy 2010). On Elgin County CBCs, numbers tallied were 10 in 1982, 1,260 in 1989, and 2,344 in 1991. It declined in the mid-1990s, with numbers dropping to 500-700 per year (Lancaster et al. 2004). In Hamilton, it was first recorded on the CBC in 1978. In 1982, there were 95 and numbers increased exponentially to a maximum of 1,669 in 1989. Since the advent of conjunctivitis, counts are now about 500 per year (Curry 2006). In the Kingston area, numbers on CBC counts increased steadily from 1988 to 2000 followed by a decline from 2000 to 2006 (Weir 2008). Wilcox (2007) summarized the percentage of Ontario feeders that were visited by House Finches during Project FeederWatch counts: 55% in 1988, 69% in 1993, 73% in 1995, 63% in 1998, and 58% in 2003 and 2007. It was concluded that populations had stabilized. The proportion of feeders that are visited does not account for the numbers of birds visiting feeders so is not a direct indicator of population trends.

Similar population trends have been documented on CBC counts in other eastern locations. For 1985-89 prior to the advent of conjunctivitis, the population growth rate was exponential at a rate of 15% per annum, taking 5 years to double during 1971-89 (S. Davis 1991). Yunick (1995b) summarized numbers at his feeder in New York. It first appeared in 1964 and numbers peaked at about 1,300 in 1985, with a sharp decline to the 1970s level 1985-94, with 0 seen in the last year. Ontario CBC population trends were an annual increase of 21.55% 1970-2021 and an annual decrease of 2.94% 2009-21 (National Audubon Society 2022).

Purple Finch

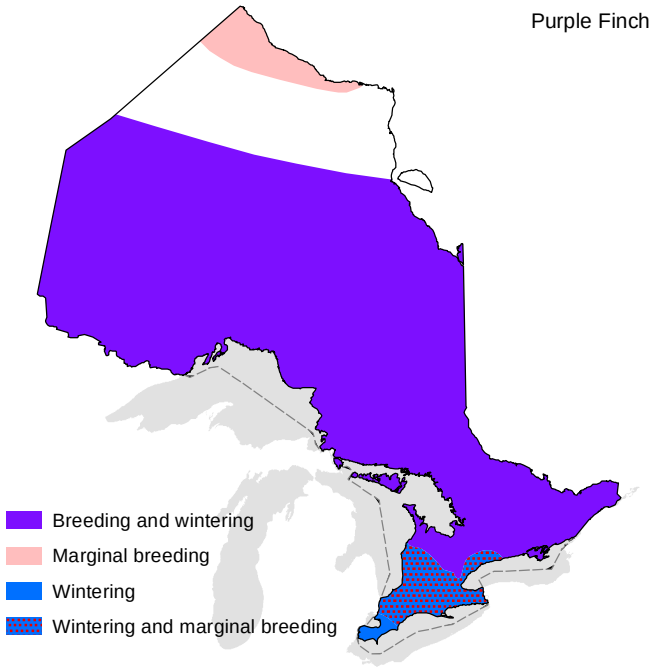
Haemorhous purpureus

BREEDING SEASON

Habitat Requirements

Ontario Purple Finch nests were in coniferous plantations that were predominantly Christmas tree farms (54.7% of nests), mixed forests (16.3%), coniferous forests (8.1%), unspecified woods (3.5%), sphagnum bogs and marshes (5.8%), residential and park areas (4.7%), shrubby pastures (4.7%), and islands and river shores (2.3%). Wooded habitat selected for nesting was usually open and occasionally wet (Peck and James 1987). Observer bias may have affected the results. Nests in Christmas tree plantations are easier to find than those in natural habitats. Most of these are south of the Canadian Shield but the Purple Finch is most abundant in the Canadian Shield where it occurs mostly in open coniferous and mixed woodlands.

In the Clay Belt in the Boreal Forest Region, the Purple Finch was most abundant in trembling aspen and balsam fir–white birch stands, followed by stands dominated by white spruce–white birch, tamarack–white cedar, white spruce, and black spruce; it was not observed in pure jack pine



stands. It occurred predominantly in moist to wet stands that were moderate to rich in nutrients (Welsh and Lougheed 1996). Near Pickle Lake, James (1980) observed it in low numbers in mixed forests. North of Lake Nipigon, it was twice as abundant in overmature trembling aspen than in immature spruce–balsam fir forest (Sanders 1970). Near White River, Venier and Pearce (2005) had only 4 observations of the Purple Finch in jack pine stands. Near Hearst, it nested in upland mixed clear-cuts 6-19 years old, in uncut mixed forests, and in lowland coniferous clear-cuts 11-24 years old (Welsh and Fillman 1980). It nested in coniferous and mixed forests and edge habitats in the Boreal Forest Region. It was characteristic of balsam fir but widespread in other types of coniferous forests where it was seldom regular or abundant. It is not found in pure spruce stands very often and tends to be absent or scarce in hemlock stands. It was characteristic of mature coniferous stands but scarce or lacking in young conifers. In Ontario, it occurred in stands dominated by balsam fir, spruce, hemlock, white and red pines, jack pine, tamarack, and poplar–white birch; it also occurred in bogs and fens with short conifers (Erskine 1977).

In white pine stands in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, the Purple Finch occurred in both old-growth and mature stands, but was more common in mature stands (Kirk et al. 2012). In Quetico Park, Apfelbaum and Haney (1999) reported relative abundances of 5 in 1-23-year-old stands, occasional visitor in 67-73-year-old stands, 0 in 112-176-year-old stands, and 14 in 367-370-year-old stands. In jack pine stands near Gogama, it was present in small numbers every year and in most ages and mixes of forests but never appeared to be a breeding species. James and Peck (1995a) concluded that it could potentially nest in any pine older than 10 years, but it appeared to be just foraging. In a mixed forest of sugar maple, yellow birch, balsam fir, and spruce near Sault Ste. Marie, it was associated with the number of hardwood saplings taller than 50 cm, but only slightly, and the percent coverage of hardwood saplings less than 50 cm tall (Holmes and Pitt 2007). In Parry Sound and Muskoka Districts, it bred in mixed forests, bogs, and along roadsides (Mills 1981). In open, young jack pine stands near Parry Sound, James (1979a) found it at moderate densities along 2 of 5 transects. In Algonquin Park, it was fairly common at edges of woods and in shrubby areas, particularly where raspberries occurred (MacLulich 1938). These areas may have been foraging rather than breeding areas. In white pine stands in Algonquin Park, Kingsley and Nol (1999) reported it in 20-28.6% of uncut stands, 40-54.5% of 10-16-year-old shelterwood cuts, and 16.7% of 2-9-year-old cuts. Also in Algonquin Park, Martin (1960) reported it in wet bogs; stands dominated by black spruce, black spruce–white cedar, white birch–poplar, balsam fir–spruce, white

birch–poplar–balsam fir–spruce, immature white pine, balsam fir–spruce-hardwood, and hemlock stands; and forest edge plots. He did not consider it characteristic of any habitat type.

In Durham Region, the Purple Finch occurred in a black spruce bog with a fringe of tamarack and white spruce, and a boggy stream bottom bordered by white cedar, balsam fir, and spruce. Speirs and Orenstein (1975) considered it a species of bog forests, although the latter habitat was a swamp. At Presqu'ile, it occasionally breeds in extensive coniferous plantations (LaForest 1993). In Halton Region, it nests in white cedar swamps mixed with white and black spruce, balsam fir, and tamarack (personal observation).

In the Carolinian Forest Region near Hamilton, the Purple Finch first began to nest in coniferous plantations in the mid-1950s and continues to do so (Curry 2006).

Throughout its range, the Purple Finch nests mostly in moist or cool coniferous or mixed forests, but also frequently at edges of bogs and in riparian corridors. Less frequently, it nests in deciduous forests with some conifers, orchards, plantations, pastures and lawns with scattered conifers and shrubs, hedgerows, suburban areas, city parks, forest edges, woodlands bordering waterways and roads, marshes, and edges of avalanche paths. It avoids forest interior and dense forest canopy and is associated with edges and small forest openings such as forest edges adjacent to clear-cuts and other clearings, lakes, rivers, creeks, ponds, and rock outcrops; and human-modified habitat along roads and power lines. In British Columbia, it breeds along riparian river corridors but is absent from dry river bottoms. In Quebec and Newfoundland, it was a forest generalist that was equally likely to occur in riparian areas, forest interior, and forest edges bordering on open habitat. It commonly nests in coniferous plantations in Quebec and the Maritime Provinces. In British Columbia, 63% of nests were in human-influenced habitats and 37% were in natural forests. Well-treed rural and suburban areas comprised 92% of the human-influenced habitat where nests were found. In the Yukon, the Purple Finch breeds in coniferous, mixed, and deciduous forests and is particularly common around well-treed residential yards (Austin 1968; Campbell et al. 2001; Crawford and Titterington 1979; Dawson 1979; Freedman and Johnson 1999; LaRue et al. 1995; Lent and Capen 1995; Morse 1979; Pauzé and Barrette in Gauthier and Aubry 1996; Sabo 1980; Sinclair et al. 2003; Taylor and Taylor 1979; Temple et al. 1979; Whitaker and Montevecchi 1997; Wootton 2020).

Several studies examined the Purple Finch´s preferences for forest age and the effects of natural succession. In New York, it decreased significantly in an agricultural field that succeeded to a second-growth forest over 35 years, increased significantly in a mixed forest that was undisturbed for 37 years, and increased significantly in a Christmas tree plantation over 25 years where the habitat was maintained but tree height increased (Brooks and Bonter 2010). In New York, it was never reported nesting in old-growth deciduous forest (Wootton 2020). In Pennsylvania, Haney (1999) reported it in 90.9% of old-growth mixed forests dominated by hemlock, white pine, and hardwoods. It was detected in 29.4% of forests statewide and in 48.5% of forests in the Appalachian Plateau. He considered it positively associated with old-growth forest. In northeastern northern hardwoods, Noon et al. (1979) detected it in 3% of plots in mature undisturbed habitat and 13% of plots in disturbed and early successional habitats. In northeastern poplar–white birch stands, including Ontario, it occurred in pole-sized and mature stands but not seedling- and sapling-sized stands (Back 1979). In northeastern stands dominated by white pine, red pine, or jack pine, it occurred in all age

classes and in stands of pine mixed with hardwoods (Capen 1979). In northeastern mixed forests, Temple et al. (1979) considered it a late seral species but not one of mature woods. In Newfoundland balsam fir stands, it was significantly more abundant in 40- and 60-year-old stands than in 80-year-old stands. It was associated with young stands on nutrient-rich soils. Younger stands had a high density of shrubs, pin cherry, and white birch and these were essentially absent in the older stands. Its decrease with increasing stand age was probably related to the accompanying decline in small deciduous trees, a probable food source, and decreasing deciduous litter (Thompson et al. 1999). In Wisconsin, it occurred in pole-sized and mature coniferous and mixed forests (Hoffman 1989a). The Purple Finch has nested in forest age classes from clear-cuts as young as 6 years to old-growth forests. Different studies have concluded that it is associated with young, mature, and old-growth forests. It is likely that forest structure is more important than age, with canopy gaps with deciduous trees and shrubs that bear fruit and large seeds being more important.

Some studies quantified microhabitat preferences of the Purple Finch. In a New York poplar–red maple stand, its abundance was positively correlated with the ratio of forest edge to area and the density of understorey vegetation (Wootton 2020). Also in New York, Keller et al. (2003) concluded that it was in a guild by itself. It was associated with conifers, foraging substrates more than 7 m from the ground, and edge. In subalpine areas of New Hampshire, Sabo (1980) described its habitat as midslope with wet depressions, 7.5 m canopy height, 64% canopy coverage, 64% conifer foliage volume, 30% conifer foliage volume 0-2 m from the ground, 45% deciduous foliage volume 0-5 m from the ground, and average of 10 cm diameter at breast height of live trees. In Wisconsin, it was most abundant in white birch–white cedar stands; equally abundant in red pine, poplar, and hemlock–yellow birch stands; and least abundant in sugar maple–yellow birch stands. It was not very common and not significantly associated with any vegetation parameters (Beal 1960).

Ontario nests were all in conifers: 51.2% in pines, 31.0% in spruces, 10.7% in balsam fir, 4.8% in white cedar, 1.2% in hemlock, and 1.2% in tamarack. Nests ranged from near the bottom to the top of trees but most were in the upper third, particularly in the preferred smaller trees. In small trees, most nests were at or near the trunk but nests have been found as far as 3 m from the trunk of larger trees. Nests were 0.8-18 m from the ground with most 1.5-7.5 m up (Peck and James 1987).

Although the Purple Finch nests predominantly in conifers, it occasionally nests in deciduous species. In the United States, 74 of 435 nests (17.0%) were in deciduous trees and 3 of 24 British Columbia nests (12.5%) were in deciduous trees (maples and a trembling aspen). Elsewhere, the preferred deciduous species for nesting include maples, oaks, and fruit trees, particularly apple. Other nesting substrates reported in the United States include 1.4% in coniferous shrubs, 0.7% in deciduous shrubs, 1.1% in vines, 0.5% in nesting platforms designed for Eastern Phoebes, 0.2% on a wreath of conifer branches, 0.2% on rock-crushing machinery, and 0.2% on an airplane. Southern populations nest significantly more frequently in deciduous species (25.0% south of Pennsylvania and 68.0% in southern California) than northern populations (5.8%). This is probably a direct effect of the relative abundance of conifers in the north and south. Most nests in larger trees are saddled on a horizontal branch with 78.6% of United States nests distant from the trunk. It also nests in the crown of trees, seldom in a main crotch of a branch, and rarely on the ground. Nests have been reported 0-18.3 m from the ground, with most 1.8-6.1 m up. In California, nests are preferentially

placed near water. There is no evidence to suggest that nests are used more than once (Austin 1968; Campbell et al. 2001; DeGarno and Strunk 1946; Grimm 1953; Wootton 2020).

It is uncertain whether the Purple Finch is territorial. Erskine (1977) considered all finches to be nonterritorial. North of Lake Nipigon, it ranged over a large area of undetermined size. Kendeigh (1947) surmised that the male´s song was related to mating behaviour rather than territorial defence. Many observations made by Martin (1960) in Algonquin Park were of birds flying and singing at great heights (45 m), also suggesting that this was a mating activity. James and Peck (1995a) observed it frequently during the breeding season in jack pine stands near Gogama but concluded that it was just wandering. Austin (1968) reported 6 active nests within a 0.2-ha hilly pasture with scattered red cedars. If the Purple Finch were territorial and the entire area was divided equally, the mean territory size would be only 0.03 ha, an exceptionally small area. In Maine, it wandered widely during the breeding season in spruce–balsam fir forests (Hensley and Cope 1951). Wootton (2020) stated that there was no evidence that males defend territories. There has been no documentation of territorial disputes or records of birds nesting close together or tolerating conspecifics near the nest. Some studies identified territory sizes for the Purple Finch. If it is not territorial, these would more appropriately be termed home ranges. In subalpine areas of New Hampshire, Sabo (1980) estimated the average home range size at 2.1 ha. In Quebec, most territories were 0.5-1.4 ha (average 0.9 ha); birds nesting in hemlock stands had an average territory size of 2.3 ha (Panzé and Barrette in Gauthier and Aubry 1996).

In New York, 184 of 1,855 juveniles (9.9%) returned in a subsequent year (Yunick 1983a). In the Adirondack Mountains in New York, 1,039 of 5,443 adults (19.1%) returned (Yunick 1983b); 13 of 823 (1.6%) and 418 of 1,770 (23.6%) returned at 2 New York sites (Yunick 1983a). In Michigan, 56.8% of adults returned to the same breeding area in a subsequent year (Wootton 2020). All 38 birds banded in Canada in summer were recovered in a later year at the same location or very nearby, suggesting breeding site fidelity (Brewer et al. 2018).

Limiting Factors

Eggs have been reported in Ontario nests from mid-May until the first week of August, but most are present in June (Peck and James 1998b). In Algonquin Park, nests are under construction from mid- to late May and dependent fledglings have been observed from mid-June to mid-August (Tozer 2012).

The nest takes 3-8 days to build and the female starts laying eggs 1-5 days after it is complete. Eggs are laid at the rate of 1 a day. It is unknown when incubation begins, but it is probably with the laying of the penultimate or last egg because eggs usually hatch within a 24-hour period. Incubation periods of 11-13 days have been reported in Ontario and 12-13 days elsewhere. The nestling period is 13-16 days (Austin 1968; Campbell et al. 2001; Peck and James 1987; Wootton 2020; Yunick 1983b).

Egg dates in Ontario and British Columbia suggest that 2 broods are raised but this has yet to be confirmed. Double broods have been confirmed elsewhere. It is probable that the Purple Finch raises 2 broods in much of its range. The interval between fledging the first brood and laying the first egg in the next nest is 1-2 days. Replacement clutches may be initiated if a nest is lost early in the season. New nests are constructed for second broods and replacement clutches. Clutches of 3-

6 eggs have been reported in Ontario, with most containing 3 or 4 eggs (mean 3.81 eggs). Elsewhere, clutches of 2-7 eggs have been reported. The mean clutch size of 258 nests from the United States was 3.94 eggs with 4 eggs most frequent. There is a tendency for clutch size to increase with latitude (Austin 1968; Campbell et al. 2001; Peck and James 1987, 1998b; Wootton 2020).

Both sexes can breed when they are 1 year old even if they have not attained adult plumage. Birds removed from a spruce–balsam fir forest in Maine were replaced suggesting that some birds were nonbreeders. During the replacement period, flocks of Purple Finches were observed so it is possible that the replacement birds were in their postfledging period. In New York, 15.7% of yearling males lacked a cloacal protruberance and therefore probably did not breed or breed successfully. Only 2 of 1,272 yearling females (0.16%) lacked brood patches and apparently did not breed (Hensley and Cope 1951; Wootton 2020; Yunick 1983b). The mating system appears to be strictly monogamous but limited study has been conducted. It is unknown how long the pair bond lasts. Mates are replaced if an original pair member disappears (Wootton 2020).

The Purple Finch usually feeds in the outer branches of trees at heights of 0.5-30 m, but occasionally feeds on the ground. It feeds predominantly on deciduous species rather than conifers. It feeds on flowers of domestic cherries in the west. None of the flower is eaten; it appears to feed on the small quantities of nectar in the flower. It may capture flying ants by sallying from a perch similar to a flycatcher. It occasionally drinks water, especially during hot weather in arid areas (Gullion 1950b; Wootton 2020). In subalpine areas of New Hampshire, foraging techniques included 0% aerial flycatching, 68.3% leaf gleaning, 11.5% leaf hawking, 7.2% leaf hovering, 1.0% twig pecking, 2.4% twig gleaning, 1.0% twig hawking and hovering, 2.4% branch pecking, 6.3% branch gleaning, and 0% litter pecking and gleaning, fallen log manoeuvres, and bole pecking and gleaning. Most (61.8%) foraging was distant from the trunk and 38.2% was near it. When feeding on foliage, 22.4% was on conifers, 77.6% was on deciduous species, and 0% was on herbaceous species. Foraging heights included 0% on the forest floor, 0% 0.1-2 m from the ground, 25.4% at 2-5 m, 54.8% at 5-8 m, and 19.7% above 5 m. It was a deciduous foliage specialist that preferred leaf gleaning in distal canopy locations (Sabo 1980).

The male feeds the female both on and off the nest while she is incubating. Both adults feed the nestlings by regurgitation with a diet consisting nearly entirely of seeds. Initially in spring, the Purple Finch eats buds and blossoms of predominantly deciduous species. In late spring and early summer, it feeds on insects and later switches to fruits in late summer and autumn, and finally to seeds and residual fruits in winter. Buds and blossoms of apple, cherry, peach, plum, poplar, fir, elm, tulip tree, maple, sweetgum, sycamore, ash, red cedar, common juniper, and mountain-ash are consumed. There is only 1 record of it feeding on spruce buds. In Algonquin Park, it feeds on trembling aspen catkins in spring. Insects that it eats include beetles, caterpillars, aphids, ants, grasshoppers, and spruce budworms. Fruit it consumes include those of strawberries, raspberries, blackberries, cherries, dogwoods, elderberries, viburnums, red cedar, winterberry holly, sumac, coralberry, hackberry, juneberry, cotoneaster, honeysuckle, grapes, and poison ivy. Ragweed seeds are a favourite but it also eats seeds of grasses, tulip tree, honeysuckle, white ash, elm, chickweed, hophornbeam, wild radish, dandelion, cocklebur, beech, birch, amaranths, and lamb's-quarters (Austin 1968; Tozer 2012; Wootton 2020).

The Purple Finch appears to be a spruce budworm specialist. In Maine in 1949, the diet of 4 birds consisted of 10% spruce budworms, 76% other invertebrates, and 14% plant material. The density of budworms was almost 2 times greater the following year. The diet of 49 birds consisted of 79% spruce budworms, 11% other invertebrates, and 10% plant material. It was one of the species that fed most heavily on spruce budworms (Mitchell 1952). In New Hampshire and Maine, stomachs contained an average of 11.9 budworms, the highest of all 25 species studied, including the Bay-breasted and Cape May warblers which are considered budworm specialists. It increased its consumption of budworms geometrically as densities of budworms increased, but the finch population did not increase with increasing budworm densities (Crawford and Jennings 1989). Near Manitouwadge, the number of Purple Finch territories increased in all ages of plots but especially in young and intermediate-aged stands as budworm populations increased (Venier et al. 2009). Morris et al. (1958) observed no finch population increase in New Brunswick as budworm populations increased.

The Purple Finch is an infrequent host of the Brown-headed Cowbird, except in Ontario where parasitism rates are higher. It accepts cowbird eggs if there are already finch eggs in the nest, but abandons the nest if no finch eggs are present when a cowbird egg appears. Mean clutch size is significantly lower in parasitized than unparasitized nests. The average number of fledglings produced was 1.88 in parasitized nests compared with 3.46 in unparasitized nests. One of 12 cowbird eggs (8.3%) produced a fledgling. The Purple Finch may be a poor host because it feeds its young predominantly vegetable matter and cowbird young require insects to grow adequately. In Ontario, 37 of 99 nests (37.4%) were parasitized. The high parasitism rate in the province is probably because most reported nests were south of the Shield where the Purple Finch is least abundant and the cowbird is most abundant. It is probable that the parasitism rate is much lower in the Shield where cowbirds are scarce and the finch reaches its maximum densities. In the United States, 22 of 372 nests (5.9%) were parasitized. Parasitism rates were significantly higher in the east (22 of 275 nests, 8.0%) than the west (0 of 97 nests, 0%). It is probable that western cowbirds have learned to avoid parasitizing Purple Finches because of the low likelihood of fledging young. In Quebec, 1 of 16 nests (6.2%) was parasitized. In British Columbia, 0 of 15 nests (0%) were parasitized but there are 3 reports of finches feeding cowbird fledglings (Campbell et al. 2001; Pauzé and Barrette in Gauthier and Aubry 1996; Peck and James 1998b; Wootton 2020).

In southern New England, the Purple Finch declined significantly after the House Sparrow was introduced. It was originally a common breeder there, often nesting in ornamental conifers planted in residential yards. It now occurs only as a migrant and a winter visitor (Austin 1968). It is uncertain whether the introduction of the House Sparrow resulted in a Purple Finch decline in Ontario. This finch did not appear to be common in residential and rural residential yards historically so it may not have been greatly affected by the House Sparrow.

Wootton (1987, 2020) concluded that there may be competitive interference between the House Finch and Purple Finch and that the introduction of the House Finch in the east resulted in a decline of the Purple Finch. He used Breeding Bird Survey (BBS) and Christmas Bird Count (CBC) data for 1966-79 and demonstrated that summer densities of the Purple Finch declined significantly with increasing House Finch populations. The conclusion that the increasing House Finch population

caused a decrease in the Purple Finch population appears to be incorrect. Much of the Purple Finch decline in the east occurred before the introduction of the House Finch and populations declined in vast areas where there are still no House Finches. With the exception of coniferous plantations, which are used sparingly by both species, there is very little overlap in their habitat use. The Purple Finch was eradicated by the House Sparrow from the nesting habitats that the House Finch prefers long before the House Finch was introduced. The most plausible reason for the more recent decline of the Purple Finch is the absence of major spruce budworm outbreaks that likely sustained larger populations in the past. Coincidentally, the major declines in areas affected by budworm outbreaks occurred during the period when House Finch populations were increasing. The House Finch appears to have little or no effect on Purple Finch populations. Spruce budworm abundance may be the most significant factor regulating its population (Bolgiano 2004; Dunn and Tessaglia-Hymes 1999; Leckie and Cadman in Cadman et al. 2007; Tozer 2012).

Selective thinning and other forest management prescriptions that retain some of the forest canopy are probably beneficial because the Purple Finch prefers open wooded habitat. Extensive clear-cutting has the potential to reduce populations by eliminating nesting habitats (Wootton 2020), but clear-cuts may provide important postfledging habitat and fruit. Vanderwel et al. (2009) predicted that it would increase in the Boreal Forest Region of Ontario if 30%, 50%, or 70% of the tree canopy was removed. In the Ontario Canadian Shield, it was equally abundant in early successional and mid-successional stands created by fire and clear-cutting. It was significantly less abundant in early and mid-successional stands than in mature stands (Zimmerling et al. 2017). In New York, Keller et al. (2003) could discern no clear trends in Purple Finch numbers over time since clear-cutting. Some canopy trees were retained in clear-cuts and these continued to provide habitat. In Wisconsin, it appeared to be unaffected by removal of trees in riparian buffers and the physical methods of harvesting had no effect (Hanowski et al. 2003, 2005). In Quebec, it was absent in clear-cuts, absent to very uncommon in strip-cuts, and present in low densities in final cuts (Falardeau et al. 1999).

Price (2004) predicted that the Purple Finch might disappear as a breeding species in southern Ontario if the average summer temperature increased by 2°C. In central Quebec and Labrador, it was associated with warmer temperatures and lower precipitation rates. In this area, climate change has the potential to be beneficial (DesGranges and LeBlanc 2012). In New York, Kirchman and Van Keuren (2017) studied the extent of occupation by the Purple Finch over an altitudinal gradient in the Adirondacks. Over a 40-year period, it shifted its range upwards by 475 m for the lower elevation and 150 m for the upper elevation. They concluded that the altitudinal shift was related to either climate change or natural succession.

Status

McIlwraith (1894) stated that the Purple Finch bred sparingly in southern Ontario. Fleming (1907) considered it uncommon in the Toronto area, although it was confirmed breeding in 1895. In Elgin County, it was a common summer resident in 1891, absent as a breeder in 1954, and a very rare breeder in 2000 (Lancaster et al. 2004). Baillie and Harrington (1937) considered it a fairly common breeder, particularly in the central and northern portions of the province, from the southern border to Lake of the Woods and James Bay. Baillie and Hope (1943) reported that it was common along

the northeast shore of Lake Superior where they saw as many as 20 a day. Smith (1957) considered it one of the most common species in the Clay Belt. In Algonquin Park, it was an abundant breeder in 1900, common in 1908-14 and 1922, fairly common in 1938, and occurred in all 70 squares during the first atlas (MacLulich 1938; Tozer 2012). Mills (1981) considered it a common breeder in Muskoka and Parry Sound districts. In the Hamilton area, it was absent as a breeding species in the 1930s and 1940s and first appeared as a breeder in the mid-1950s (Curry 2006). Breeding has not been confirmed in Niagara Region since 1972 (Black and Roy 2010). The first atlas indicated that its breeding range included most of the province except for Essex County. In the Hudson Bay Lowland, it was mostly absent except near Moosonee and near the Hudson Bay coast. It was scattered in distribution in the Carolinian Forest Region and areas south of a line from Goderich to north of Toronto. It was most abundant in the northern portion of its range with an area of high abundance in Nipissing and Parry Sound districts and Haliburton County (Middleton in Cadman et al. 1987).

The second atlas revealed that there had been no significant change in the range of the Purple Finch since the first atlas. It was documented in fewer locations in the northern Boreal Forest Region and in the Hudson Bay Lowland, but in more squares in the off-Shield portion of the Great Lakes–St. Lawrence Forest Region. Its probability of observation declined significantly province-wide, and in the Carolinian Forest Region, Shield portion of the Great Lakes–St. Lawrence Forest Region, Boreal Forest Region, and Hudson Bay Lowland. It increased significantly in the off-Shield portion of the Great Lakes–St. Lawrence Forest Region. The reason for the decline in the Shield and Hudson Bay Lowland is uncertain, but may be related to declines in spruce budworm populations. The increase in the off-Shield portion of the Great Lakes–St. Lawrence Forest Region may be due to natural succession and maturation of coniferous plantations. It was most abundant in the Shield portion of the Great Lakes–St. Lawrence Forest Region and in the Boreal Forest Region from Lake Nipigon and Wawa northeast to the Moosonee and Lake Abitibi regions. It was sparsely distributed in urban and intensive agricultural areas in the southwest, in the northwestern portion of the Boreal Forest Region, and in most of the Hudson Bay Lowland (Leckie and Cadman in Cadman et al. 2007).

BBS results for 1970-2021 indicate that the Purple Finch decreased at annual rates of 1.15% in Canada and 2.16% in Ontario. For 2011-21, it increased at an annual rate of 0124% in Canada and decreased at an annual rate of 4.73% in Ontario. The long-term trends were highly reliable; the short-term trends were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young can fly weakly after they leave the nest. They remain near the nest for a week (Wootton 2020); their movements thereafter have not been documented. They appear to be dependent on the adults until 3 weeks after leaving the nest (Middleton in Cadman et al. 1987).

Both adults and juveniles have been documented inhabiting clear-cuts 2-10 years old in deciduous and mixed forests. In Pennsylvania, 16 adults and 7 juveniles were captured in clear-cuts and 0 in adjacent mature deciduous forests. Vegetation in the clear-cut was 1.5-2.5 m tall and 10-15% of the original trees were retained (Stoleson 2013). In Quebec, Major and Desrochers (2012) captured 14 in clear-cuts dominated by balsam fir and white birch in addition to planted black spruce. Fruit-bearing species present included red elderberry, pin cherry, mountain ash, juneberry,

red raspberry, and squashberry. In deciduous clear-cuts in Minnesota, Streby et al. (2011b) caught 9 adults and 4 juveniles in 4 postfledging periods and 1 adult during the breeding season.

In Michigan, Akresh et al. (2009) captured 5 adults and 3 juveniles in mature riparian forests and 0 in mature upland trembling aspen–large-toothed aspen forests. Riparian forests had an understorey of alder and honeysuckle that was lacking in upland forests. Shrubs are important to the Purple Finch during the postfledging period, particularly those that bear fruit.

Austin (1968) reported a male feeding a fledgling juneberries.

MIGRATION

Western populations of the Purple Finch may be resident or exhibit altitudinal migration, moving from high elevations in summer to lower areas in winter. High CBC counts in British Columbia in some years suggest that irruptions occasionally occur (Bock and Lepthien 1976b; Campbell et al. 2001; Wootton 2020). In the east, some birds migrate south every year but there is a tendency for large southward movements to occur every other year. These irruptions usually coincide with poor seed crops in the north. Southward invasions of all boreal and seed-eating birds tend to be synchronized, but high Purple Finch numbers may not coincide with those of other species or be as regular (Bock and Lepthien 1976b; Kennard 1977; Wootton 2020). Most other boreal species depend heavily on the seeds of conifers whereas the Purple Finch feeds predominantly on deciduous species. Irruptions of this finch are probably correlated with poor seed and fruit crops of species such as ash, elm, birch, alder, and mountain-ash.

Banding records indicated that over half of Ontario birds remained for the winter, but some moved to the lower Mississippi River area. Others overlapped in the northeastern United States with Prairie Province birds. Some birds banded in Ontario during the breeding season were recovered in winter in Vermont and North Carolina (Brewer et al. 2018). A bird banded in summer in Muskoka District was recovered in West Virginia the following winter and 1 captured in Muskoka District was banded in autumn in New York (Mills 1981). In Pennsylvania, 62.4% of 4,469 banded Purple Finches were captured in March and April; 0 were banded in September and only 3 in October over a 10-year period. This suggested that it did not pass through Philadelphia in autumn, but was a common spring migrant (Groskin 1950). Blake (1962) determined that the Purple Finch was more common during spring than autumn migration in North Carolina. It is probable that it migrates during the day; Curry (2006) reported that it was observed actively migrating during the day in Hamilton.

In New York, males arrived approximately a week before females and adult males were recorded 15 days earlier than yearling males (Yunick 1983b). In many areas of Ontario, the Purple Finch is an irregular migrant and it may be difficult to distinguish migrants from breeding or resident birds. Migrants mostly arrive in early to mid-April and continue moving through until mid-May. Birds may be observed as early as late March; those lingering into June may be yearlings (Black and Roy 2010; Curry 2006; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). In Moosonee, Wilson and McRae (1993) saw as many as 30 3-5 June but no finches were seen later in the breeding season. It was uncertain if these were spring migrants or breeders. In New York, some adults departed in autumn 3-5 weeks before juveniles (Yunick 1983b). Wilson and McRae (1993) reported autumn migrants on 1 August at Ekwan, 10 September at Longridge, and 2 September at Moosonee. In the southern

Shield, most migration occurs in October (Mills 1981; Tozer 2012). In the south, autumn migration extends from mid-August to mid-November (Curry 2006; Lancaster et al. 2004; Weir 2008).

At Delta Marsh in Manitoba over 63 years from 1939 to 2001, the Purple Finch arrived significantly earlier with time at a rate of 2.21 days per 1°C increase in temperature. Climate change resulted in earlier spring arrival (Murphy-Klassen et al. 2005).

Migration habitat is similar to breeding habitat except that the Purple Finch is more likely to visit suburban and rural residential areas, particularly if feeders are present. In British Columbia, it prefers mixed open forests with a rich shrubby understorey and uses riparian and edge habitats more frequently during migration than in the breeding season. Migrants are often found around edges of beaver ponds, bogs and fens, lake shores, stream banks, woodlots, hedgerows bordering agricultural fields, and in trembling aspen stands. It also occurs in suburban and urban areas, edges of natural and human-made clearings, and in fields with scattered clumps of trees (Campbell et al. 2001). On 2 islands in the Gulf of Maine, it was significantly more abundant on the shrubby island than the treed island during both spring and autumn. Birds on the treed island gained more weight than those on the shrubby island. In autumn, at least 3 birds subsequently moved from the shrubby island to the treed island but none moved from the treed island to the shrubby island (Suomala et al. 2010, 2012). In Pennsylvania, an infestation of the viburnum leaf beetle resulted in a dramatic decline in southern arrowwood and an overall decline in shrub density and increase in snag density. The capture rate per 1,000 net-hours was 3.43 prior to the beetle infestation and 1.41 afterwards (Smith and Hatch 2017). Results suggested that shrub density was important to the Purple Finch. In Pennsylvania, the number of captures per 1,000 net-hours was 0.2 in forest habitat and 63 in shrub habitat; the difference was highly significant (Smith and Hatch 2008).

Site fidelity to migration stopover locations appears to be quite low. At a Tennessee site, there were no returns of birds banded in April and May; only 2 of 492 (0.41%) banded in March returned (Stedman 1989).

Feeders are used extensively during migration and the Purple Finch also takes sugar water from hummingbird feeders (Campbell et al. 2001).

James (1991) considered the Purple Finch an uncommon to common (rarely locally abundant) migrant.

WINTER

The Purple Finch is associated with snow in winter. It is less likely to be found where there are frequent changes between snow cover and bare ground (Keyser et al. 2023).

Winter habitat is the same as migration habitat. Choice of habitat is probably dictated by food availability rather than vegetation composition or structure (Wootton 2020). In Kansas, the Purple Finch occurred most frequently around margins of a pond, in weedy fields, and in a field of sunflowers (Fitch 1958). In South Carolina, it occurs in deciduous forests where it feeds on sweetgum and sycamore seeds. South of the extensively forested landscapes in the east, it is often seen in open country with flocks of Pine Siskins or American Goldfinches; it may also roost with these species. Roosts are usually in dense coniferous trees or thickets, but occasionally in open buildings or under

the shelter of a cupola roof (Austin 1968; Wootton 2020). In Tennessee, 200 roosted in cedars in a field densely overgrown with cedars interspersed with deciduous trees. Most roosted in this field but a few roosted in a cedar on an estate bordering a park. One afternoon, something disturbed about 20 birds in 1 tree and they flew across the road. A few days later, most birds moved to another cedar woods on the same road, so birds were then roosting at 3 locations (Laskey 1958b).

In Maine, the Purple Finch attempted to establish feeding territories at feeders. The first arrival at the feeder tried to keep all other birds off the feeder but invariably failed. Fighting intensified as the number of birds increased (Gobeil 1963). The Purple Finch is subordinate to the Pine Siskin in winter and dominant to the American Goldfinch (Wootton 2020). Shedd (1990) studied 1,585 displacement interactions between the Purple Finch and House Finch; 38.6% of interactions were between House Finches, 33.4% were between Purple Finches, and 28.0% were interspecific. Both species preferentially sought out members of their own species when making a displacement attempt. Female-plumaged Purple Finches won 95.6% of intraspecific displacements, significantly more than expected. In interspecific interactions, Purple Finches won only 9.0% of displacements, significantly less than expected. House Finches were competitively superior to Purple Finches at a feeder. Purple Finches could be effectively excluded from feeders where the House Finch is abundant.

The Purple Finch exhibits low winter site fidelity. Much of this is due to its irregular and irruptive movements. Individuals have been found wintering in widely disparate locations and birds often wander within winters. At Presqu'ile, it may be common in 1 year and absent in another with no real pattern (LaForest 1993). In Algonquin Park, it is absent most winters but present in years of bumper crops of both coniferous and deciduous seeds. Birds may appear there in February and March. These have likely wintered further north and moved south after exhausting seed supplies (Tozer 2012). In Indiana, its appearance is somewhat cyclic at 6-7-year intervals (Hamilton and Wise 1991). In Pennsylvania, invasions occurred in 1939, 1940, 1941, 1944, 1946, and 1947 (Groskin 1950). In New York, irruptions occurred in 1964, 1974, and 1976 (Yunick 1983a). In Tennessee, 19 of 1,166 birds (1.63%) returned in a subsequent year; 5 of 471 (1.06%) returned to a site 5 km distant. Another Tennessee study reported that 50 of 4,954 (1.01%) returned (Stedman 1989). In Philadelphia, 95 of 4,469 (2.1%) returned in a subsequent winter. Twenty-six birds were recaptured in a subsequent winter 16-1,208 km away (Groskin 1950). In New York, 0 of 1,999 birds returned. Birds banded there were recovered in winter in Tennessee, Georgia, Oklahoma, Louisiana, and Virginia (Yunick 1983a). Blake (1962, 1967) reported that 51 of 1,015 birds (5.0%) returned in a subsequent winter. Flocks wander widely within and between years and individuals do not remain in a particular flock (Wootton 2020).

In Tennessee, birds fed at residences where seeds had fallen on the ground and on the fruit of coralberries. In March, elm seeds were the favourite food, and the Purple Finch also ate hackberry seeds (Laskey 1958b). It is widely attracted to bird feeders. Some remain all winter at northern feeders but it is more abundant in the south. The number of feeders visited in the north increases as spring migration begins. During cold weather, birds may retreat to more sheltered areas and suddenly reappear in residential areas on warm sunny days giving the false impression that migration has occurred. It occurs at feeders in all habitat types but is less likely to be seen at urban

feeders, which also attract lower numbers. Black oil sunflowers are highly preferred over any other feeder offerings, but striped and hulled sunflowers are also preferred. Infrequently consumed foods include mixed seeds, millet, canary seed, safflower, cracked corn, niger, peanut butter mixes, peanut hearts, bird puddings, fresh fruit, water, meat scraps, and popped corn (Dunn and Tessaglia-Hymes 1999). Horn et al. (2014) reported that it was most common at hopper and tube feeders and preferred black oil sunflowers.

The Purple Finch is vulnerable to severe winter weather. Graber and Graber (1979) recorded its densities per km^2 in Illinois habitats before and after a prolonged severe storm: in bottomland forest, 1.0 and 0.5 (a 50% decrease); in upland forest, 21.2 and 0 (a 100% decrease); and in urban residential, 3.2 and 23.5 (a 630.8% increase). It exhibited a population shift to urban residential habitats, probably to visit bird feeders. They found 1 finch carcass, indicating that the storm caused some mortality.

The Purple Finch has been reported colliding with motor vehicles, windows, and other stationary objects (Wootton 2020). In the United States, it was not on the list of the top 20 vulnerable species for striking all types of buildings combined, or low-rises or high-rises. For 1-3-storey residences, it was the most vulnerable species, being 257.2 times more likely than average to strike a building (Loss et al. 2014).

James (1991) considered the Purple Finch a rare to common winter erratic in the south north to Manitoulin Island and occasional and rare to uncommon to Thunder Bay in the north. Freedman and Riley (1980) analyzed data from southern Ontario CBSs for 1929-77 and found that numbers were stable overall except for irruptions in 1950, 1953, and 1964. They concluded that populations had not changed overall in the last century.

Redpoll

Acanthis flammea

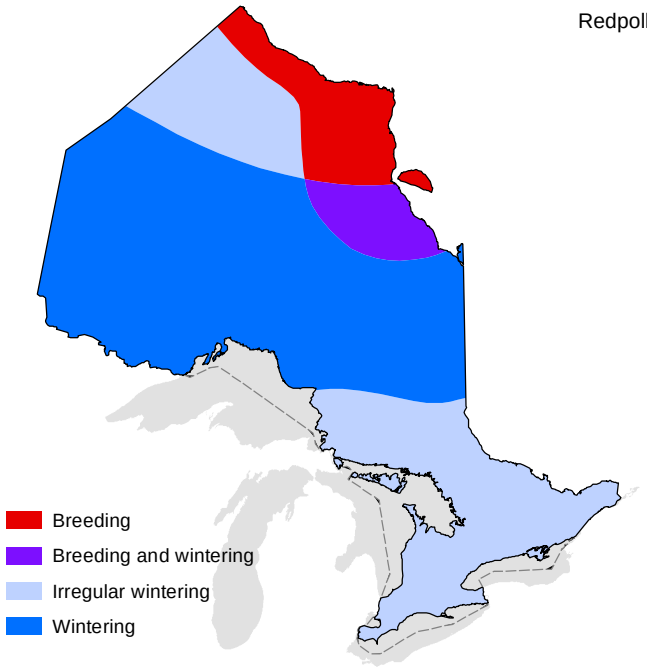
BREEDING SEASON

Habitat Requirements

Until 2024, the Redpoll was treated as 3 separate species and 2 of these (the Common Redpoll and Hoary Redpoll) nested in Ontario (Knox et al. 2024). Information on these 2 former species has been combined into this account, but an illustration is presented for both. This is because the Common Redpoll and Hoary Redpoll are easily distinguished in the field and there is still some debate about the taxonomy of the species.

In Ontario, the Redpoll nests on or near tundra or in riparian thickets. Nests have been found in spruce-willow swamps, willow thickets, and a semi-open alder-willow thicket. Almost all nests were near the shores of ponds and streams. Most nests were along the Hudson Bay and northern James Bay coasts (Peck and James 1987). One nest near the Little Shagamu River and Hudson Bay was in an open black spruce forest (Peck and James 1998b). Near Winisk, it was common in spruce-tamarack bogs (Schueler et al. 1974). Manning (1952) reported a nest on a ridge among dwarf birch along the James Bay or Hudson Bay coast. Breeding habitat in Ontario consists of wet tundra dominated by water, sedges, and bulrushes interspersed with low willow and swamp birch thickets;

numerous shallow lakes and ponds; and a parallel series of low gravel beach ridges extending inland. The beach ridges support a lichen-heath community dominated by cup lichen, mountain avens, crowberry, mountain cranberry, and Lapland rosebay. Approximately 7 km inland from the coast, widely scattered or small copses of white spruce become increasingly frequent on the ridges transitioning into lichen-spruce woodland about 10 km inland. The spruces are krummholz in character (stunted and twisted). Nests were on beach ridges with occasional or isolated krummholz white spruce; 2 were near willow or willow-birch thickets. Ridges supporting nests were bordered by wet sedge fens, small tundra lakes, and sedge flats overgrazed by Snow Geese (Burke et al. 2013).



Erskine (1977) considered the Redpoll characteristic of the ecotone between the Boreal Forest Region and tundra. In the west, it also occurs in subalpine areas in the transition zone between treed habitat and alpine meadows. In the arctic where trees are lacking, it nests on rocky slopes and gullies, south-facing slopes with shrubs, in sheltered shrubby gullies, and in and around settlements (Knox et al. 2024).

Hoary Redpoll

In Quebec, the Redpoll is one of the most abundant species in tundra and taiga habitats. On the northeast coast of James Bay, it nests in shrubs along the shoreline and around margins of islands, predominantly in alder and willow thickets. In the taiga area, it nests in patches of stunted spruce or scrub birch and in tamarack stands (Seutin et al. 1991; Seutin in Aubry and Gauthier 1996). In Manitoba, it is most common near the treeline but also nests in tundra. Near the treeline, it typically nests in scattered spruce but prefers dense willow scrub in other areas (Jehl 2004; Jehl and Hussell 1966; Jehl and Smith 1970). Near Churchill, it nested in white spruce–tamarack and black spruce–white spruce–

tamarack stands and in similar stands bordering on tundra; it also nested in riparian strips of willow (Gillespie and Kendeigh 1982). It was more common among thin lines or small clumps of dwarf black spruce near Churchill than among willows fringing ponds in open tundra (Grinnell 1943). In northeastern Manitoba, McLaren and McLaren (1981) reported low densities in the forest-tundra transition area and higher densities in tundra. Near Churchill, Sammler et al. (2008) considered the Redpoll to be in the willow-nesting guild. In the Mackenzie Delta, it is an abundant breeder in tundra and taiga habitats (Porsild 1943). In British Columbia, breeding habitat consists predominantly of subalpine willow thickets, mixed spruce and deciduous thickets at edges of openings, and edge habitat along streams and rivers. One nest was on a floodplain with scrubby thickets of alder, willow, and balsam poplar between channels. Nesting habitat is often associated with wetlands (Campbell et al. 2001). In the Yukon, most nesting occurs at higher elevations, often in willow or willow-birch thickets that are usually near water. It is most common along rivers, creeks, wet draws, and other wetland areas where shrubby habitats are most prevalent. Occasionally it nests at lower elevations, especially where birch trees are common (Sinclair et al. 2003). In Alaska, it nested in Fairbanks and in alder and willow habitats in tundra. In tundra, it nested in willows and alders along drainage channels, often over shallow water. It breeds in sheltered riparian shrubs; at the upper limit of subalpine low shrub habitats with scattered stunted conifers and dwarf birch, willow, and alder; and is frequent on floodplains (Baldwin in Austin 1968; Knox et al. 2024; Troy and Shields 1979; Walkinshaw 1948b). On Victoria Island in Nunavut, Parmelee et al. (1967) observed it only within or near the community of Cambridge Bay. Some nested in discarded spruce Christmas trees. Those outside the town nested in willow thickets. The Greenland subspecies breeds on the arctic archipelago of Canada and in Greenland. On Ellesmere Island, it was mostly confined to barren inland rocky areas where it nested in a deep gorge. It did not appear to require shrubs for nesting (Parmelee and MacDonald 1960). In Greenland, it is restricted to the interior where it frequents hillsides and mountain sides at higher altitudes. It requires willow or some other shrub of similar size for nesting. Along the coast, all plants trail along the ground and do not form erect shrubs so this habitat is unsuitable (Austin 1968).

At night, birds may roost communally in scrub birch. At Fairbanks, Alaska, the Redpoll roosted overnight in dense foliage of white spruce (Knox et al. 2024).

Most Ontario nests were in arctic willows. One was in a black spruce, 1 was on the ground in a clump of dead grasses at the base of a willow, and another was on the ground on a bank under willow branches. Three nests were in krummholz-form spruce trees 2-3 m tall, 0.6 m, 1.0 m, and 1.25 m from the ground. Nest distances from the tree trunk were 15 cm, 15 cm, and 43 cm. At 1 nest, the nest tree and several others nearby were isolated from any other trees by several kilometres (Burke et al. 2013). In willows, nests were placed centrally in crotches, usually below the midpoint of the shrub. Nest height was 0-4 m, but typically 0.3-1.2 m from the ground with most 0.4-0.6 m up (Peck and James 1987, 1998b).

Nests reported elsewhere in North America were 0-2.1 m from the ground, with most 0.5 m or less from the ground. North of the treeline, it may nest in human communities. In Alaska, 1 nest was in a picket-fence grave marker. Five Alaska nests averaged 71 cm above ground (range 30.5-99 cm). Of 25 nests in Alaska, 16 were in or under willows, 6 were in alders, 1 was in an unknown species of

shrub, and 2 were on artificial substrates; nest heights were 0-2.13 m. Another 8 nests in Alaska were in crotches of willows 45-91 cm from the ground. On Baffin Island, a nest was on the seat of a boat left beside a street in a town, and on Victoria Island one was built on a trailer. The trailer was moved several hundred metres before the nest was completed but the adults still completed the nest and raised a brood. In the Yukon, 1 nest was in a white birch in Whitehorse; 1 nest was on the end of a log protruding from a log cabin, near the roof. Four others were in open deciduous scrub or willows 0-20 cm from the ground. Most nests are in low shrubs or stunted trees, particularly willow, birch, and spruce but also alder, squashberry, and tamarack. Nests may either be saddled on a horizontal branch or in a crotch. Nests in spruce are well concealed under another branch. Nests in deciduous shrubs may be either conspicuous or hidden under clumps of dead leaves or among new foliage. Near Churchill, nests were in spruce, willow, tamarack, and birch at heights of 0.15-2.1 m. In Quebec, early nests are usually in conifers but July nests are built near the ground in small deciduous trees or shrubs such as alders, willows, or birch, or on the ground sheltered by a rock. On Ellesmere Island, 1 nest was in a niche in a vertical rock wall in a deep gorge. On Victoria Island, 1 nest was in an old Christmas tree with only the trunk and a few limbs and needles remaining. In Greenland, it nests in low willows or dwarf birches or in crevices in rocks covered by trailing twigs of willow. Where nest sites are limited, it has nested in cavities in driftwood and in an Inuit wooden grave. At Churchill, all nests built prior to 21 June were in conifers and later nests were in deciduous species. In open tundra lacking shrubs, tufts of grass or sedges, driftwood stranded by high tides, and human artifacts may be used for nest concealment. In the High Arctic, nests may be on the ground on rocky ledges. Further south, nests have been built on the ground on the banks of watercourses. A British Columbia nest was concealed under an overhanging lip of the bank of a river. In Manitoba, nests did not appear to be reused with nests for second or replacement clutches distant from the first nest. There is 1 case of a nest being reused on Baffin Island. A nest there had 4 distinct layers of lining suggesting that it had been used in 4 years. In Greenland, all nests appeared to have been used in previous years, enabling pairs to proceed rapidly to egg-laying in the shorter nesting season. Material from old nests is often used to construct new nests. The Redpoll has been reported adding lining to an old nest of an unspecified species (Austin 1968; Baldwin in Austin 1968; Campbell et al. 2001; Clement in Austin 1968; Grinnell 1943; Jehl 2004; Jehl and Hussell 1966; Jehl and Smith 1970; Knox et al. 2024; Lanoue and Seutin in Gauthier and Aubry 1996; Parmelee and MacDonald 1960; Parmelee et al. 1967; Seutin et al. 1991; Sinclair et al. 2003; Walkinshaw 1948b; Wynne-Edwards 1952).

The Redpoll appears to be nonterritorial. It nests either solitarily or in small groups but it is uncertain whether clustering of nests represents sociality or availability of preferred habitat. Birds move away from the nest on a daily basis and have been documented tens of kilometres distant in Asia. Birds are gregarious throughout the nesting season, occurring in loose flocks or all stopping together to feed in 1 location. Song appears to be solely for courtship and not for territoriality. Small foraging flocks occur throughout the breeding season and breeding birds, especially males, occur within these flocks (Baldwin in Austin 1968; Burke et al. 2013; Knox et al. 2024; Seutin et al. 1991).

No information is available on natal philopatry, but it is probably extremely low. In Alaska, 1 juvenile female returned to nest the year after it was banded; the number of juveniles that were banded was not stipulated (Troy and Shields 1979). The hatch-year female was banded in August. It

may not have been in its natal area when it was banded if it had already begun postfledging dispersal.

The return rate of adults in Alaska was among the lowest of all passerines at less than 1%. Large annual fluctuations in breeding densities have been documented in Manitoba, Quebec, Norway, and Finland. These fluctuations suggest that immigration and emigration of birds must occur at individual sites, providing additional evidence of low inter-annual site fidelity (Jehl 2004; Seutin in Gauthier and Aubry 1996; Troy 1983).

Limiting Factors

Eggs have been found in Ontario nests from mid-June until the end of July, with most present in the second week of June (Peck and James 1987). Burke et al. (2013) estimated that 17-19 June was the earliest that nests found in 2004 near West Pen Island could have been initiated, several weeks later than reported for Manitoba and Quebec. That year had the coldest April to June weather in the Hudson Bay Lowland for 1996-2007. Snow covered much of the area until mid-June. Nesting usually begins in late May in the Churchill area (Jehl and Smith 1970). At Churchill, nests took 4-7 days to build. Building may be interrupted for as long as 6 days during periods of poor weather. The first egg is laid 1-4 days after the nest is completed (mean 1.4 days at 33 nests). The interval may be longer during periods of inclement weather. At Churchill, eggs were laid at 1- or 2-day intervals, but mostly at 1-day intervals. Incubation usually begins with the laying of the penultimate egg. In Greenland, incubation may possibly begin with the laying of the first egg. The incubation period is 10-14 days. In Alaska 4-egg clutches, 3 eggs hatched on the first day and the fourth egg hatched the next day; in 5-egg clutches, 4 eggs hatched together and the fifth egg hatched the following day. In Alaska, the nestling period was 9-10 days; it was 11-12 days at Churchill. On Victoria Island, the nestling period was 11-12 days for some chicks but others in the same nest did not fledge until they were 15-16 days old (Grinnell 1943; Jehl 2004; Knox et al. 2024; Parmelee et al. 1967; Walkinshaw 1948b).

The Redpoll regularly raises 2 broods. Renesting is common if a clutch is lost. One Alaskan female renested twice before successfully fledging young. A maximum of 8 days elapsed between desertion of the second clutch and laying the fifth egg in the third nest. Ontario nests had clutches of 3-5 eggs, with most containing 4 eggs (mean 4.08 eggs). Elsewhere, clutches of 2-7 eggs have been reported, with most containing 4-6 eggs. On Victoria Island, all nests contained 5 eggs. In Greenland, clutches typically contained 5 or 6 eggs. Mean clutch size was 4.2 eggs in Alaska (Austin 1968; Clement in Austin 1968; Evans 1969; Jehl 2004; Jehl and Smith 1970; Knox et al. 2024; Peck and James 1987; Troy and Shields 1979).

The Redpoll is capable of breeding when it is 1 year old and breeds every year thereafter. The proportion of yearlings that do not breed is unknown. The mating system is assumed to be monogamous. Pairs have been documented remaining together for 2 or 3 nesting attempts within a season but there is no evidence of pair bonds persisting longer than a single season (Knox et al. 2024). In Manitoba, Seutin et al. (1991) documented a case of polyandry. A pair attended a nest containing nestlings 8-9 days old while another nest about 200 m distant was under construction. Two days later, the second nest contained a single egg and the same female and a yearling male attended this nest. Polyandry was advantageous and is probably more widespread than

documented. It has the capacity to raise 2 broods but the season is short so there is a great advantage to starting the second nest as early as possible. By selecting an experienced male for the first nest, success is more likely and older birds are likely to be on the breeding grounds earlier. Pairing with a young male for the second nest allows a male to breed that might not have had the opportunity otherwise. Polyandry is difficult to study in this species because subsequent nests may be considerable distances from each other. Extra-pair copulations are a part of the mating system. Little study has been devoted to this with the nestlings of only 6 nests having been tested genetically (Knox et al. 2024).

The Redpoll feeds in trees and shrubs, herbaceous plants, and on the ground. In trees and shrubs, it forages at or near the ends of small branches and may take several seeds from catkins at a time. Prior to leaf-out, it searches for insects on stems and in crotches and feeds in shrubs, herbaceous plants, and grasses and on the ground in the open. It also collects fallen seeds under trees. In low vegetation, it clings to thin stems to reach seeds. It uses its feet to hold food or stems and stores seeds in the diverticulum. It feeds predominantly in trees and shrubs in summer and more on the ground in early spring and winter except where birch and alder seeds are plentiful. In summer, it may forage for insects in conifers. In British Columbia it fed on spilled grain in open storage sheds. It feeds more on the ground in winter than in summer, usually on wind-swept and snow-free patches where seeds are exposed. It frequently drinks at puddles, ponds, or streams and eats snow in winter (Baldwin in Austin 1968; Campbell et al. 2001; Clement in Austin 1968; Grinnell 1943; Knox et al. 2024; Parmelee et al. 1967).

Most males feed the female (predominantly insects) during courtship and occasionally through to the nestling period. In Alaska, adults fed the young a white mash of seed kernels that consisted almost entirely of cottongrass seeds. Some mash contained insect parts and 1 female fed its young several insect larvae (Baldwin in Austin 1968; Knox et al. 2024). In Finland, the nestling diet by volume consisted of 61% insects and 39% seeds that were mostly birch. In Sweden, 1,203 animal food items collected from esophageal pouches of nestlings included 391 nematoceran flies, 241 fly pupae, 176 springtails, and other taxa; 4,770 seeds were consumed of which 4,585 were birch seeds. The diet consisted of 20.1% animal material, of which 51.7% were flies, and 79.9% seeds of which 96.1% were birch seeds (Grinnell 1943; Knox et al. 2024).

During summer, the Redpoll eats arthropods, particularly when feeding nestlings. It also eats plant material then and almost exclusively at other times of the year. Although it eats buds, leaves, flowering catkins, and algae, it subsists predominantly on very small seeds. Birch and alder seeds are the staples of its diet and it frequently eats willow seeds. In Alaska, adults ate mostly flies and caterpillars in June while they were feeding nestlings. From June to mid-August, the diet consisted of 20-25% insects and by mid-August, the diverticulae of many juveniles contained more than 50% willow catkins. In northern Alaska, the diet consisted entirely of seeds and buds of alder, birch, and willow. In early spring when snow is on the ground, grass seeds and lamb's-quarters seeds may be important in the diet. Six stomachs collected during summer at Fort Simpson, Northwest Territories, contained only the seeds of dwarf birch, white birch, and alders. On Baffin Island, it consumed spiders and seeds of willows, sedges, and grasses. In early June at Churchill before invertebrates became common, 10 stomachs contained 59% grit and 41% vegetation that was chiefly seeds of

buttercups, cottongrass, whitlow-grass, and mustards. Other seeds that may be important in the diet include those of shrubby cinquefoil, great willowherb, sedges, and tamarack. In Greenland, the summer diet is comprised mostly of arthropods, particularly spiders and leafhoppers, but it also eats wood-rushes and sedge seeds (Austin 1968; Baldwin in Austin 1968; Campbell et al. 2001; Evans 1969; Gabrielson 1924; Knox et al. 2024; Mills 1981; Porsild 1943; West et al. 1968b). Gabrielson (1924) analyzed the contents of 7 stomachs collected in Canada during the summer. The diet consisted of 25% animal material and 75% plant material. The animal food was predominantly spiders, ants, and flies. The vegetation consisted of seeds of the same plants that were consumed in winter.

The breeding ranges of the Redpoll and Brown-headed Cowbird barely overlap, so parasitism is rare. Only 2 cases of parasitism have been reported, both from Alberta (Knox et al. 2024).

Because of its northern breeding range, habitat loss is not an important limiting factor for the Redpoll. Localized habitat loss may occur due to activities associated with mining. In the Churchill area, Sammler et al. (2008) examined the effects of grazing by Snow and Ross's geese on the willow-nesting passerine guild, which included the Redpoll. In areas directly affected by grazing, density of passerines was significantly less by 2.4 times than in areas where grazing had not occurred. Goose grazing can have localized negative effects on Redpoll habitat.

Cold rainy weather has the potential to kill nestlings. All 5 nestlings died in a Churchill nest after 5 days of cold rainy weather in early July. Redpolls that began nesting in late May would have had time to fledge young before the storm (Jehl and Hussell 1966). Late springs may delay nesting (Burke et al. 2013). This may preclude second broods or replacement clutches and may result in smaller clutch sizes.

At Cambridge Bay on Victoria Island, breeding success in the settlement was low due to predation by children, cats, and natural predators such as weasels and lemmings (Parmelee et al. 1967).

The Redpoll may be highly vulnerable to climate change. It is intolerant of high temperatures and becomes less active, eats less, and drinks more in response to heat (Knox et al. 2024). In central Quebec and Labrador, it occurred mostly in stands with low summer temperatures and high rates of precipitation (DesGranges and LeBlanc 2012).

Status

Manning (1952) concluded that the Redpoll was a fairly well-distributed summer resident in certain locations along the Hudson Bay and western James Bay coasts. Baillie (1960) reported that it had been confirmed breeding at Fort Severn, east of Winisk, at Cape Henrietta Maria, and at Lake Attawaspiskat. Summer records suggested a much more extensive breeding range that included portions of Kenora, Thunder Bay, and Cochrane districts. Schueler et al. (1974) found that it was common in the Winisk area in spruce-tamarack bogs. The first atlas determined that it bred throughout the Hudson Bay Lowland. It was most abundant along the James Bay coast and at inland areas west of that coast (Middleton in Cadman et al. 1987).

The second atlas indicated that there had been no change in the range of the Redpoll or its probability of observation since the first atlas. Highest densities occurred along the Hudson Bay and

northern James Bay coasts and in the extensive tundra inland from Cape Henrietta Maria (Leckie and Pittaway in Cadman et al. 2007).

Breeding Bird Survey data indicate that the Redpoll decreased at annual rates of 2.99% in Canada and 1.15% in Ontario 1970-2021. Trends 2011-21 were annual decreases of 0.861% in Canada and 0.368% in Ontario. The long-term Canadian results were of medium reliability; the other trends were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

In Manitoba, 4 broods were cared for only by the male, 1 by the female, and 2 by both adults. It is likely that the male cares for the first brood if the female attempts a second brood (Seutin et al. 1991).

Young are able to fly weakly and follow their parents when they are 12-13 days old. By age 15 days, fledglings can fly strongly and were as far as 180 m from the nest on Victoria Island. After leaving the nest, fledglings and 1 or 2 of the adults form a family group that moves into riparian alder-willow thickets. By mid-July, dwarf birch scrub may be preferred. In Quebec, family groups aggregate into loose flocks in August and begin moving south in September. In British Columbia, flocks of adults and juveniles begin to form after late June. Redpolls appeared to congregate in flocks shortly after breeding and roam around the breeding range until they flew south in autumn (Campbell et al. 2001; Clement in Austin 1968; Knox et al. 2024; Parmelee et al. 1967). No information is available on how far juveniles wander from the natal area before autumn migration.

On Ellesmere and Axel Heiberg islands, juveniles and adults moved about singly and in small groups feeding on seeds. All birds collected had eaten poppy seeds. A juvenile had consumed adult insects and buds of alpine smartweed. Families wandered about in groups as large as 20 until they initiated migration (Parmelee and MacDonald 1960). In Alaska, birds nested in riparian willows. As cottongrass seed heads began to mature in late July, they spent more time on the open tundra away from the willows, although they were still attracted to willow catkins. Both adults and juveniles were observed feeding on cottongrass. Throughout its range, Redpoll adults and juveniles wander considerably during the postfledging period with no apparent attachment to any site (Austin 1968; Baldwin in Austin 1968; Jehl 2004).

MIGRATION

The Redpoll is both a regular and irruptive migrant. In all years, it withdraws from the extreme northern extent of its breeding range with few overwintering north to the treeline and none occurring north of it in winter. In non-irruption years, a few birds may travel south of the normal breeding range but most remain within the breeding range. The northern extent of its winter range is not well defined. Wintering birds remain in Greenland and southern Baffin Island and may occur regularly throughout the Boreal Forest Region (Knox et al. 2024). It does not occur in the Churchill area in winter (Clement in Austin 1968; Jehl 2004; Jehl and Smith 1970).

During irruption years, Redpolls may be abundant in southern Ontario and occur south into the mid-latitudes of the United States. In these years, some birds remain in the northern extent of the wintering range. Based on Project FeederWatch data, birds may be more prevalent in the north in irruption years than in non-irruption years (Dunn and Tessaglia-Hymes 1999; Hochachka et al. 1999a). Bock and Lepthien (1976b) used Christmas Bird Count (CBC) data for a 10-year period to

determine the frequency of irruptions into the United States. They concluded that irruptions occurred approximately every other year and that they were a result of poor tree seed crops in the north; many tree species set seeds only in alternate years. Their own data do not support the 2-year cycle theory. The interval between irruptions ranged from 1 to 3 years. Instead of 5 2-year cycles within a decade, there were only 3. No actual analysis of tree seed abundance in the northern portion of the breeding grounds has ever been undertaken (Erskine and McManus 2003). Approximately 2-year cycles in irruptions have been reported in Saskatchewan and Manitoba (Houston and Smith 2001) and the northeastern states (Kennard 1976), but there were anomalies in the pattern in all areas. In Ontario, there appears to be no regular pattern to irruptions. Freedman and Riley (1980) analyzed southern Ontario CBCs for 1929-77. Irruptions were irregular with intervals of 2-10 years, averaging 4 years. Tozer (2012) stated that major irruptions in Algonquin Park are very irregular. In the Kingston area, Weir (2008) reported that it was present in 50 of 60 winters and that moderate to heavy flights occurred in 30 of those. The actual periodicity of the flights was not presented, although they averaged every 2 years. Project FeederWatch data from a feeder at Branchton for the winters of 1988-89 to 2022-23 indicated that the Redpoll occurred in 13 of 35 years, an average of once every 2.7 years. In 4 of these 13 years, only 1-3 redpolls were observed on all counts, with 9 years with total counts of 81-406. The actual interval between irruptions ranged from 1 to 7 years. Twice irruptions occurred in consecutive years and in only 3 times was the period between irruptions 2 years (personal observation). Larson and Bock (1986) analyzed CBC data for northeast and northcentral states for 1901-80. Irruptions from 1920-50 were much less dramatic and regular than those occurring before and after this period. In the Atlantic Provinces, the Redpoll occurs in winter most years but is irregular in its abundance. Erskine and McManus (2003) concluded that this better explained the observed patterns rather than attempting to find periodicity in irruptions. Undoubtedly, food abundance is a factor affecting migration in North America, but there must be other factors involved. In the east, both yellow and white birch set seeds every other year. This does not appear to be the case in Alaska, yet irruptions occur in the west as well (Campbell et al. 2001). Another possibility is that summers with high food abundance result in high postbreeding densities that in turn cause irruptive migrations (Hochachka et al. 1999a). Larson and Bock (1986) suggested that there must be some other factor that overrides the masting effect of northern trees, such as climate change. Another possibility is that heavy snows may make food difficult to access even if it is relatively abundant.

The Redpoll is mostly a diurnal migrant but it has been heard migrating at night and nocturnal migration has been documented in Greenland. It typically migrates in loose flocks of 100 or fewer birds, but occasionally flocks as large as 10,000 occur. Banding of spring migrants in Alaska suggests that the composition of flocks is constantly changing. Flocks may be conspecific, but commonly include Pine Siskins and American Goldfinches and occasionally crossbills and Pine Grosbeaks. In both spring and autumn, fat deposition is limited and normally sufficient only for short movements. During spring migration in Alaska, the number of birds recaptured was significantly less than expected indicating that birds were constantly moving in and out of the site with few remaining long enough to be recaptured. The average length of stay of birds that were recaptured was 6.2 days. This result was considered biased because only those birds that remain can be recaptured. It was concluded that the average length of stay was less than 6.2 days. Spring migrants were banded

in Massachusetts. Of the first 24 birds that were banded, 19 were recaptured and stayed at the site 3-22 days. Only 4 of the last 24 birds that were banded were recaptured and the maximum period they stayed was 4 days (Campbell et al. 2001; Dunn and Tessaglia-Hymes 1999; Knox et al. 2024; Nunnely 1964; West et al. 1968b).

Hochachka et al. (1999a) summarized Project FeederWatch data for North America for the irruption year of 1993-94. The pattern was a sparse distribution in most of the wintering range from the beginning of the FeederWatch period in mid-November with increasing prevalence in the east through the winter, most noticeably in the northeastern states. There was no evidence of continuous and systematic movements of the entire population throughout the irruption. Prevalence increased in all regions as the winter progressed with numbers starting to decline in most areas at the same time. The Redpoll differed from more conventional migrants mainly in the varying distances that they travelled in different years. Rather than moving to a specific location, birds stop when they encounter a sufficient food supply.

Most birds leave southern and central Ontario in March or early April with some remaining until early or mid-May. Late records tend to be of stragglers following major irruptions (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). Wilson and McRae (1993) observed 3 at Shagamu on 31 May and these were considered migrants. Manning (1991) observed 7 on 21 May and 25 on 22 May on the Twin Islands in James Bay. Parmelee et al. (1967) reported that it was present on Victoria Island when they arrived on 31 May. On Ellesmere Island, the first spring birds were seen on 22 April. Autumn migrants were first seen on 8 September and all had left by 17 September (Parmelee and MacDonald 1960). The latest observation on Victoria Island was 12 September (Parmelee et al. 1967). At Ekwan, Wilson and McRae (1993) observed 22 on 1 August and these were likely either autumn migrants or a small group of postbreeding birds. At Longridge, they recorded 32 on 28 July and 75 on 12 September. Manning (1952) reported migrants at Moosonee on 25 September. The Redpoll usually arrives in Algonquin Park in late October or early November, but sightings occasionally occur from late September to mid-October. In some years, peak numbers do not occur until February or March in flight years, probably reflecting seed depletion further north (Tozer 2012). In the south, autumn arrival is in late October to mid-November, but peak numbers do not occur until February or March (Black and Roy 2010; Curry 2006; LaForest 1993; Weir 2008). Hochachka et al. (1999a) used Project FeederWatch data to chronicle the movements of Redpolls during the irruption year of 1993-94. During 15-28 November, low numbers of Ontario feeder watchers reported at least 1 Redpoll, including areas such as Moosonee, in the Lake of the Woods to Thunder Bay area, and scattered areas from Sault Ste. Marie southward. During 10-23 January, it was still present at Moosonee, at more feeders in the Lake of the Woods to Thunder Bay area, and occurred at almost all feeders south of Sault Ste. Marie. During 21 March to 3 April, it occurred from Lake of the Woods east through the Boreal Forest Region and in all of southern Ontario; it was not observed at Moosonee. In the Great Lakes Region (Ontario, Michigan, and Wisconsin), numbers grew from 15 November to a peak at the end of February with a drop-off thereafter into April. Its probability of observation at a feeder was 2% on 15 November, 55% at the end of February, and 50% at the end of March. Peak numbers at feeders occurred an average of

more than 7 weeks later than first sightings. This suggests that it takes some time before birds find feeders, or that they feed on natural seeds until they are locally depleted before visiting feeders.

Habitat used during migration consists of areas with an abundance of food. These may include open woodlands and scrub, particularly where birch, willow, or alder are common; weedy fields and roadsides; field edges; weed patches; and in towns and villages where the Redpoll may visit feeders (Knox et al. 2024; West et al. 1968b). During spring migration in Alaska, flocks concentrated in patches of lamb's-quarters exposed by melting snow. Birds dispersed once other areas became snow-free (West et al. 1968b). In the Saskatoon area, it occurs in weedy fields and ditches, grassy slough edges, shrubs, birch trees, mixed woods, and conifers. Flocks may be attracted to harvested fields of canola, flax, or sunflowers and remain in them for several weeks until the seed supply is depleted (Leighton et al. 2002). In British Columbia, it inhabits edges and deciduous vegetation along watercourses, alder and willow thickets, weedy grasslands and fields, roadsides, shrubby gullies, grain fields, birch and alder woodlands, orchards, abandoned landfills, hedgerows in agricultural areas, and suburban and urban gardens, particularly if bird feeders are present. Few occur in unbroken coniferous forests (Campbell et al. 2001). In the Yukon, it frequents shrubby areas in subalpine areas and at lower elevations. It is found along rivers, lakes, and wetlands and at forest edges, or in fairly open forests with an understorey of alders. Flocks often move along the tops of dense spruce forests, landing briefly to feed or rest (Sinclair et al. 2003).

During migration, the Redpoll feeds almost exclusively on vegetable matter, particularly seeds. It has been documented feeding on seeds of lamb's-quarters, grass seeds, grain in an open storage shed, and waste grain along railway tracks and near grain elevators. Birch seeds may be a staple during autumn migration (Campbell et al. 2001; Parmelee and MacDonald 1960; West et al. 1968b).

James (1991) considered the Redpoll a common to locally abundant migrant in the north and uncommon and erratic in the south. Largest flocks in the south often occur in February, but these may be spring migrants rather than birds that have spent the winter. Birds recorded on CBCs are more likely to be autumn migrants than winter residents.

WINTER

During winter irruptions, the Redpoll occurs mostly where the average minimum January temperature is below −12°C to −15°C (Root 1988). During extremely cold weather, it seeks areas that are sheltered from the wind, often in thickets of alder or willow in Alaska (Knox et al. 2024). It is a snow-associated species; important predictors of its presence are length of the snow season and absence of frozen ground without snow (Keyser et al. 2023). In the Yukon, it is most common at lower elevations in winter and most records are at bird feeders (Sinclair et al. 2003), suggesting that altitudinal migration may occur. Otherwise, winter habitat is similar to migration habitat. Where it remains north in winter, habitat used is similar to breeding habitat. The exceptions are that it withdraws from the High Arctic and areas above or close to the treeline and may be more prevalent in human settlements where there are feeding stations. In winter, it occurs within the Boreal Forest Region where it presumably seeks areas with plentiful birch and alder seeds. South of the normal wintering range during irruption years, it frequents similar areas as during migration. It may associate with other finches in winter such as the Pine Siskin and American Goldfinch (Austin 1968; Baldwin in Austin 1968; Knox et al. 2024).

Roosts are a very important habitat component in winter, particularly in more northern latitudes. In Germany, flocks of thousands have been observed roosting in spruce trees. The Redpoll also makes nocturnal roosting chambers in the snow. It excavates tunnels 27-40 cm long to a chamber 6-11 cm below the surface of the snow. When it leaves, it breaks through the roof of the chamber (Knox et al. 2024). In New York, Redpolls made temporary snow burrows during a cold (−15°C) and windy (32 km per hour) day. Birds excavated small burrows with their beaks and feet in a snow drift on a roof. Once the excavation was 5-7.5 cm deep, they turned around and roosted in them. Of the flock of 150-200, about half were engaged in this activity at any given time. As some left their burrows to go to feeders, others took up residence in the vacated burrows or displaced individuals already occupying burrows (Furness and Peterson 1987).

The Redpoll establishes a rigid social hierarchy in winter that remains constant until the development of sexual activities in late winter or early spring. Physical contact is rare and individuals simply avoid birds with higher status. This strategy results in no energy being consumed by aggressive encounters which is important to a species that experiences very cold winter weather. In winter, males are dominant to females. The hierarchy is linear from the most to least dominant male to the most dominant female down to the least dominant female (Dilger 1960).

Winter site fidelity of the Redpoll is very low, particularly south of the normal wintering area. Even where it consistently overwinters, site fidelity is low. Of 106 records of birds captured in 1 winter and recaptured in a subsequent winter, 5 were captured at the same location in the south and 56 in the northern wintering areas. At Fairbanks, Alaska, 16 of 5,200 birds (0.31%) returned; 0 of more than 1,800 returned in New Hampshire and 0 of 7,946 returned in New York. Many were recaptured further than 2,000 km from the original banding site and a Michigan bird was recovered in Russia. A few birds have been recovered in the south at the same location after having wintered somewhere else during the intervening year (Troy 1983; Yunick 1983a). In British Columbia, it is irregular and local in winter. Campbell et al. (2001) attributed this to its tendency to form large flocks so that most individuals from an area gather in relatively few locations. Its dependence on deciduous tree crops leads to concentrations in areas of high seed abundance. Once local seed crops are depleted, flocks move in search of another food source, thereby contributing to low site fidelity.

Conservation of energy is critical for a small bird wintering in harsh subarctic conditions. Many of the Redpoll's energy conservation measures are associated with its foraging behaviour and adaptations. It has a specialized diverticulum on the neck, a feature present in Redpolls and crossbills but absent in most other passerines. It fills the diverticulum with food just before nightfall and this provides the Redpoll with an additional source of energy over the night. When supplied with commercial food, the Redpoll's limits of temperature tolerance were −27°C to −38°C with both the lower and upper limits lower than for any other passerine studied. By substituting birch seeds, its natural food, its cold tolerance dropped to −51°C due to the high caloric value of the birch seeds. The amount of birch seeds that could be stored in the diverticulum and used at night would allow survival to −62°C compared with −30°C without it. The Redpoll is a common winter resident at Fairbanks, Alaska where temperatures occasionally drop to −60°C. Presence of the diverticulum is essential to its overnight survival. At a feeder, Redpolls hurriedly selected several seeds and stored them in the diverticulum. This reduced agonistic encounters at the feeder. Birds sought cover where

they shelled the seeds, thereby saving more energy while being concealed from predators. When feeding on birch seeds, it vigorously knocks seeds out of the catkins using its wings, legs, head, and tail. This burns more energy so this is completed as soon as possible. It then drops to the ground, quickly stores the seeds in the diverticulum and flies to shelter to shell and eat the seeds. Other adaptations it has for surviving cold weather include its abilities to increase digestive efficiency at very cold temperatures and to forage at very low light intensities (Brooks 1968, 1978). In Alaska, it fed on lamb's-quarters under the snow. Snow drifted over the plants but created tunnels and openings below the surface that allowed birds to access seeds. It digs small burrows in snow between foraging bouts during cold, windy periods (Furness and Peterson 1987). Feeding under snow allows it to access seeds and be sheltered from the elements (Cade 1953a). In the Mackenzie Delta, Redpolls disappeared during periods of stormy weather but reappeared on the first fine day even if the temperature was only -45°C (Porsild 1943).

In Algonquin Park, the Redpoll has fed on seeds of white birch, yellow birch, alder, white spruce, black spruce, and tamarack (Tozer 2012). Dance (2008) reported it feeding on black alder seeds in Oxford County. In Alaska, it feeds predominantly on seeds of alders and birches. In disturbed areas, it eats lamb's-quarters seeds and occasionally those of mustards and plants in the aster family (Cade 1953a). In Alaska, it consumed mostly birch seeds in winter but alder seeds comprised 25% of the diet (Knox et al. 2024). In winter in the Saskatoon area, redpolls eat seeds of a variety of weeds and grasses as well as those of shrubby cinquefoil, sunflowers, canola, flax, and birch (Leighton et al. 2002). Northern birds may feed on the seeds of willows (Clement in Austin 1968). Gabrielson (1924) analyzed 550 stomachs collected in winter in the United States. The diet consisted of 0.39% animal matter and 99.61% vegetable matter. The animal food included small cocoons that were probably those of clothes moths, fly larvae, bug eggs, and miscellaneous insect fragments. The vegetable matter was almost exclusively seeds, consisting of 34.62% alder seeds, 13.33% birch seeds, and 51.66% various weed seeds. Favourites included ragweed (24.7% of the diet), lamb's-quarters (11.81%), amaranths (4.79%), smartweeds, and catnip. Stomachs containing ragweed seeds were found throughout the northern United States indicating that it is actively selected. It also ate seeds of grasses and other species, fruits, and vegetable rubbish. Other seeds consumed included those of foxtails, timothy, panic grasses, sedges, willows, purslane, wintercress, blackberry, huckleberry, vervain, viburnums, knotweeds, love grass, amaranths, and beggar's-ticks.

The Redpoll is a common visitor at bird feeders. Different studies concluded that it prefers different seeds at feeders. In British Columbia, it is attracted predominantly to feeders with niger seed (Campbell et al. 2001). At a Massachusetts feeder, it selected millet over cracked corn, oats, barley, chick feed, buckwheat, hemp, and sunflowers. It stopped eating when the millet supply was exhausted and resumed when it was replenished (Knox et al. 2024). Results may have differed had niger seed been offered. In Canada and the United States, 7,945 observations of Redpolls feeding were made. The most abundant seeds eaten were 0.3-mm sunflower chips, 0.5-mm sunflower chips, and niger. It preferred hopper and tube feeders to platform feeders (Horn et al. 2014). In Saskatoon, it was attracted to feeders with niger, millet, black oil sunflowers, and flaxseed; it occasionally took suet (Leighton et al. 2002). Project FeederWatch data indicated that the favourite foods were hulled sunflowers and niger seed, but mixed seeds, black oil sunflowers, canola, water, and canary seed

were frequently eaten. Infrequently consumed foods included millet, cracked corn, suet, peanut butter mixes, bird puddings, baked goods, and milo. Once the Redpoll visits a feeder, it is likely to be faithful to it all winter, but the composition of flocks may change through the season. It tends to be most abundant and frequent at rural feeders (Dunn and Tessaglia-Hymes 1999). At a Yukon feeder, several gathered around a Pine Grosbeak that was eating sunflowers. Every time it opened a seed, the Redpolls quickly consumed the crumbs and occasionally snatched seed fragments from the grosbeak's bill (Sinclair et al. 2003). It also comes to sources of salt (Brooks 1978).

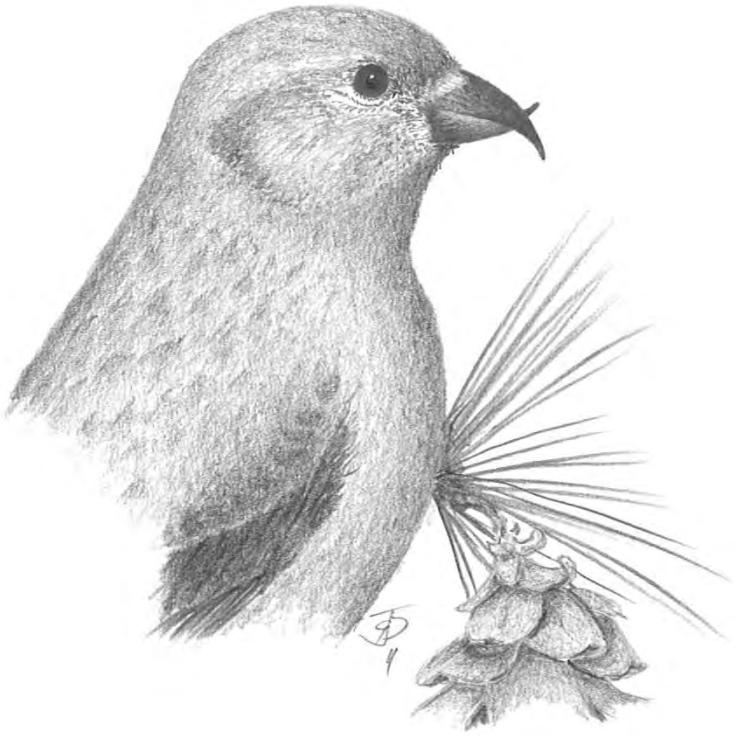
The Redpoll is attracted to roadsides by salt and sand in winter. Birds are frequently killed by vehicles as a result. It often strikes windows at houses in winter, particularly at residences with feeders (Campbell et al. 2001; Knox et al. 2024; Tozer 2012).

Salmonellosis killed large numbers of Redpolls in the eastern United States and Canada in early 1998 (Knox et al. 2024).

The Redpoll is a common winter resident in the north. In the south, it is erratic where it may range from absent to common or locally abundant. Numbers were highly irregular on southern Ontario CBCs 1929-77, with no apparent long-term trends to higher populations or more frequent occurrences (Freedman and Riley 1980). For 1970-21, CBC data indicated an annual increase of 0.50% in Ontario; from 2009-21, it decreased annually at a rate of 9.43% (National Audubon Society 2022).

Red Crossbill

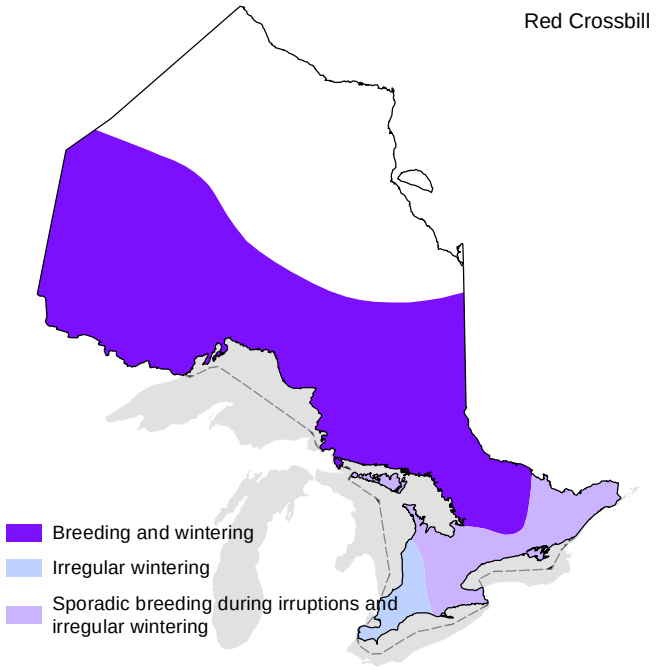
Loxia curvirostra



BREEDING SEASON

Habitat Requirements

Until 2011, the Red Crossbill consisted of a single species with 10 North American subspecies based on differing flight calls and bill morphology. The crossed mandibles are highly adapted to feeding on seeds that are extracted from conifer cones, with each bill type being highly efficient at extracting seeds from a particular species, or even subspecies, of conifer. Conifers and crossbills may co-evolve, with conifers developing cones that defend against seed extraction by crossbills and crossbills evolving their mandibles to become more efficient at removing seeds from cones. In Newfoundland, where the red squirrel was absent until the 1960s, crossbills and black spruce cones co-evolved over a period of 9,000 years. Black spruce cones in Newfoundland are longer, have more and heavier seeds, and thicker scales than those on the mainland where the red squirrel is the primary predator of seeds. The Newfoundland subspecies of the Red Crossbill has adapted a larger, deeper bill and is more efficient in feeding on black spruce cones in Newfoundland than on those from the mainland. The Red Crossbill is highly nomadic so 2 or more of the 10 different types may breed in a given location on occasion. When this occurs, birds selectively pair with birds of the same call type and very rarely with birds of another call type. Even where more than 1 call type regularly breeds in an area, bill types and flight calls remain constant with no evidence of birds with



intermediate characteristics. Many taxonomists are of the opinion that each call type represents an individual species (Benkman 1993a; Benkman and Young 2020; Edelaar and Benkman 2006; Groth 1988, 1993; Keenan and Benkman 2006; Parchman and Benkman 2002). Benkman et al. (2009) described what they considered a species distinct from the Red Crossbill in Idaho (the type 9 call of the Red Crossbill). It differed by feeding almost exclusively on the interior subspecies of the lodgepole pine. It has a deep bill that is highly adapted for foraging on these distinctive cones and is poorly adapted for foraging on cones of other conifers. All other types of Red Crossbills are highly nomadic whereas the Idaho species is very sedentary. Of more than 3,000 banded birds, none have been found outside of the 70 km^2 that supports this subspecies of lodgepole pine (Benkman 2011). In 2011, the American Ornithologists' Union concurred that these Idaho birds constituted a species distinct from the Red Crossbill and named it the Cassia Crossbill (Chesser et al. 2011). It is possible that the Red Crossbill will be further divided into additional species in future. Nonetheless, the habitat and behaviour of the 9 remaining types are similar except for their flight calls, bill structure, and the species of conifer seeds they are best adapted for foraging on.

Because of its specialized diet of conifer seeds, the Red Crossbill is restricted to breeding in areas that support conifers. In the Canadian Shield and Boreal Forest Region in Ontario, it is associated with coniferous and mixed forests. It typically nests in mature pine plantations south of the Shield. In the Boreal Forest Region, it is associated with spruces but it is more common in the Great Lakes–St. Lawrence Forest Region in the Shield where it frequents areas dominated by red and white pine. Ontario birds are predominantly larger-billed type 2 birds (the Ponderosa Pine Red Crossbill). Smaller-billed type 3 birds (the Western Hemlock Red Crossbill) may occur during irruptions; they are usually associated with hemlock or spruce. Type 1 (the Appalachian Red Crossbill) and type 7 (the Enigmatic Red Crossbill) also occur in Ontario during the breeding season, often following irruptions (Benkman and Young 2020; Lumsden and Smith in Cadman et al. 1987; Peck and James 1987; Simard in Cadman et al. 2007).

In the Clay Belt in the Boreal Forest Region, Welsh and Lougheed (1996) detected the Red Crossbill in only 2 of the forests they studied. Both were wet, nutrient-poor black spruce stands.

In the Shield portion of the Great Lakes–St. Lawrence Forest Region near Gogama, the Red Crossbill was numerous in jack pine stands, but only when jack pine budworms were abundant (James and Peck 1995a). At Pimisi Bay near North Bay, it nested in second-growth white pine and

red pine forests with lesser amounts of jack pine, balsam fir, white cedar, white spruce, and black spruce. Scattered deciduous trees among the conifers included white birch, yellow birch, trembling aspen, and large-toothed aspen; the understorey consisted of maples, willows, alders, and other shrubs (Lawrence 1949b). It was common in scattered locations within Algonquin Park, usually where there were tall pine trees (MacLulich 1938). Benkman (1987a) studied the Red Crossbill in 2 stands in the park. The conifer composition of the first stand was 58% white pine, 25% black spruce, 4% balsam fir, 6% white pine, 5% red pine, and 2% jack pine. The second stand was comprised of 1% white spruce, 84% white pine, 14% red pine, and 1% jack pine. In white pine stands in Algonquin Park, it occurred in 8.3% of 2-9-year-old shelterwood cuts, 9.1-10% of 10-16-year-old cuts, and 14.3-20.0% of stands with no recent history of cutting (Kingsley and Nol 1999). In Lanark County, it nested in an area of spruce and white pine where there was a heavy cone crop (Ross and Ross 1950). Nests have been found in large pine plantations in the Kingston area (Weir 2008).

In North America, the Red Crossbill breeds predominantly in mature coniferous and mixed forests, but only where there is an abundant supply of conifer seeds. The preferred species of conifer varies geographically and also with the type of crossbill. Spruce, pine, and hemlock species are the more important coniferous trees. Firs are important in the west but not in the east. Red and white pine stands are important in the east but it also nests in pitch pine stands. In the Yukon, it breeds mostly in lowland coniferous forests, white spruce forests, mixed conifers, and lodgepole pine stands; it occasionally breeds in black spruce forests. It prefers more open woodlands for nesting. During irruption years when it breeds south of its typical range, it may nest in anthropogenic habitats such as white or red pine plantations, linear strips of conifers on golf courses and similar habitats, and isolated trees in suburban areas and on university campuses. In British Columbia, 58% of nests were in mature coniferous forests and 38% were in treed suburban or rural areas (Austin 1968; Benkman and Young 2020; Bielefeldt and Rosenfield 1994: Campbell et al. 2001; Erskine 1977; Hagar 1960; Haggerty 1982; Johnson 1969; Leighton et al. 2002: Létourneau in Gauthier and Aubry 1996; Messineo 1985; Sinclair et al. 2003; Snyder 1951).

At night, the Red Crossbill roosts in dense foliage of conifers (Benkman and Young 2020). Birds of a captive nonbreeding flock preferred to roost in thick foliage of pine and cedar branches. In pine, they roosted in thick clumps of needles at the end of branches. No more than 1 or 2 birds roosted on the same twig (Tordoff 1954).

Lawrence (1949b) found 4 nests near Pimisi Bay: 2 in white spruce and 1 each in white pine and red pine. Nests were 7.0-10.7 m from the ground and 0.9-2.4 m from the tree trunks on a horizontal branch. Two nests were within 23 m of each other. One female was observed taking material from an old Red-eyed Vireo nest, but it was unknown if the material was used in nest construction. A nest near Pakenham was 6 m from the ground in a 9-m-tall white pine and 0.9 m from the trunk on a horizontal branch (Ross and Ross 1950). A nest in Algonquin Park was 18 m from the ground in a white pine and a Durham Region nest was 15 m from the ground in a red pine in a red pine plantation.

Almost all North American nests were in conifers. In British Columbia, 96% of nests were in conifers but it was not specified where the other nests were. A nest on a Minnesota university campus was in a white ash. In the east, the Red Crossbill commonly nests in pines (predominantly

red and white pines, but occasionally in pitch pine and possibly jack pine), white spruce, black spruce, and hemlock. There is a record of it nesting in a cedar tree in New York City and a Massachusetts nest was in a clump of ornamental Japanese black pines. Most nests are saddled on a horizontal branch but they are occasionally near the top of a conifer among thick tufts of needles and cones. Nests on branches are usually distant from the trunk and concealed from above by small boughs and clumps of needles. Often they are situated so that they receive sunlight the entire day. Nests have been reported 1.2-20 m from the ground; most British Columbia nests were 6-10.5 m from the ground. It occasionally nests in dead spruce trees, but only if there is abundant beard lichen for nest concealment. There is 1 report of a nest being reused in a subsequent year, but nests are typically used only once (Austin 1968; Benkman and Young 2020; Campbell et al. 2001; Haggerty 1982; Johnson 1969; Létourneau in Gauthier and Aubry 1996; Snyder 1951).

The Red Crossbill does not appear to be territorial. It occurs in flocks whether it is breeding or a vagrant and is social at all times. Breeding pairs may still remain part of a flock. Solitary nesting occurs, but typically a few to several pairs nest together with nests 20-100 m apart. At Pimisi Bay, strange crossbills often landed in nest trees. No battles ensued when this occurred. The territory consisted of nothing more than the nest tree and defence of it was low-key. There may be conflicts over cones, roosts, and perch sites, but these are more prevalent in the nonbreeding season. During courtship, disputes over mates may lead to chases and occasionally fighting, including aerial tumbling flights. It has a large home range, routinely travelling distances of more than 500 m to exploit food resources. At Pimisi Bay, birds travelled in excess of 800 m on each flight to obtain food and regularly flew at least 1.6 km to feed on road salt (Benkman and Young 2020; Jollie 1953; Lawrence 1949b).

There is no information on natal philopatry, but it is probably extremely low or nonexistent. Natal philopatry is highly unlikely to occur because conifers are usually unable to produce bumper crops of cones in successive years. Brewer et al. (2018) reported no recoveries of hatch-year birds in Canada.

Adults are nomadic and exhibit no breeding site fidelity. Birds typically breed in an area until the conifer seed crop is depleted then move to another area. Most conifers set seeds in alternate years with good crops at greater intervals. An exception is the interior subspecies of the lodgepole pine, which provides a consistent source of seeds. This has resulted in the evolution of the resident Cassia Crossbill that feeds exclusively on its seeds. No North American Red Crossbills have been recovered at the same location in a subsequent year. Some have been documented breeding more than 2,000 km from the breeding area where they were banded (Benkman 2011; Benkman and Young 2020; Brewer et al. 2018; Cornelius and Hahn 2012; Senar et al. 1993).

Limiting Factors

The timing of Red Crossbill breeding is linked to when conifer seeds are abundant and, to a lesser extent, photoperiod. In North America, it has nested from January through October and in December. Eggs may occur in Ontario nests from February to mid-August with most reported in April, but this is based upon a small sample size. Nesting is known to occur in the province in 2 periods: late summer to early autumn (late June to October) in response to maturing cones and in late winter (mid-January to May) where seed crops are maintained. In Algonquin Park and New York, timing of breeding was related to when there were sufficient conifer seed resources to raise

nestlings. When seed abundance was increasing, breeding was initiated before the crop was sufficient to support nestlings. In Algonquin Park, late summer breeding is associated with heavy crops of white spruce seeds. Once white spruce seeds decline in abundance, it switches to white pine seeds and finally to red pine seeds if the white pine seed crop becomes depleted. Cones of these pines begin opening in September and October. If there are insufficient pine seeds, it may emigrate as early as November. In Quebec, birds breed in jack pine stands in June and July, and this may be the case in Ontario. Photoperiod may play a minor role in the timing of breeding. In some areas, breeding may cease once there are 10.5 hours of daylight. In Ontario, the Red Crossbill could conceivably nest in spruce from August into October, in red and white pine in September and October and from mid-December to April, and in jack pine in June and July. Further study is required to determine the actual timing of Red Crossbill nesting in Ontario. When seeds are abundant, a population may breed in an area for approximately 9 months; it is unknown how long individual birds may continue nesting (Benkman 1987a, 1990; Benkman and Young 2020; Kemper 1959; Létourneau in Gauthier and Aubry 1996; McCabe and McCabe 1933; McNair 1985; Messineo 1985; Peck and James 1987; Tordoff and Dawson 1965; Tozer 2012). In Algonquin Park, nests have been found under construction from late December to early June; dependent fledglings have been observed from mid-August to late October (Tozer 2012).

In 1 case, a female dismantled an old nest and used it to construct a new one. The nest takes 3-5 days to build and 1-5 days may elapse between nest completion and laying of the first egg. One egg is typically laid per day but occasionally a day may be skipped. In cold weather, incubation starts with the laying of the first egg. It is not initiated until the last egg is laid in warmer weather. The male feeds the incubating female so that she does not have to leave the nest often or as long during cold weather. The incubation period at 1 Ontario nest was 13 days, 12 or 14 days at another depending upon when incubation was initiated, and 14 or 15 days at a third nest. Elsewhere, incubation periods of 12-16 days have been reported, with most eggs hatching in 14 days. Newly hatched young are covered with down which allows them to withstand temperatures below freezing for short periods. When it is very cold, young may become torpid and must be brooded to restore their metabolism before they can be fed. The nestling period at a Pimisi Bay nest was 17 days. Overall, young have been reported remaining in the nest for 15-25 days, occasionally as long as 35 days. The large variation in nestling periods is probably related to food abundance (Austin 1968; Benkman and Young 2020; Campbell et al. 2001; Haggerty 1982; Johnson 1969; Lawrence 1949b; Létourneau in Gauthier and Aubry 1996; McCabe and McCabe 1933; Peck and James 1987; Ross and Ross 1950; Snyder 1951).

The Red Crossbill is commonly double-brooded when conifer seeds are abundant. It is capable of raising 4 broods in succession in captivity, so it is possible that it does so in the wild. Although it has never been documented, it is possible that it may breed in 1 location then move hundreds of kilometres to breed in another location within the same year. Replacement clutches may be laid in a new nest if the first clutch is lost. Ontario clutches contained 2 or 3 eggs. Elsewhere, the clutch size is commonly 3 or 4 eggs, with clutches of 2 eggs uncommon and 5- and 6-egg clutches exceptional (Austin 1968; Benkman and Young 2020; Campbell et al. 2001; Johnson 1969; Lawrence 1949b; McNair 1988; Peck and James 1987; Ross and Ross 1950).

Both sexes are capable of breeding when they are less than 1 year old. Pairs in juvenile plumage have successfully fledged young in Ontario. Nonbreeding pairs are common during most of the year and some pairs apparently do not breed, probably due to inadequate seed supplies. Birds are apparently monogamous, with no records of polyandry, polygyny, or extra-pair fertilizations. Very little information is available on the mating strategies, however (Benkman and Young 2020; Lawrence 1949b; McCabe and McCabe 1933).

The crossed mandibles of the Red Crossbill are adapted specifically for removing seeds from conifer cones. Crossbills are the only species that can remove seeds from closed conifer cones. Each subspecies has a differently sized bill and palatine grooves and is best adapted for feeding on different species of conifers. The specialized bill results in it being inefficient at feeding on items other than conifer seeds. The entire ecology of the Red Crossbill depends on conifer seeds. It is adapted to extreme variations in conifer seed crops through nomadism, early onset of sexual maturity, rapid succession of broods, long potential breeding seasons that may include the shortest days of the year, tolerance of repeated cooling and extremely low temperatures, and slow development of young when food is scarce. The dependence upon conifer seeds can be costly. During major irruptions south into areas with predominantly deciduous cover, massive mortality may occur due to its low ability to exploit other food resources. These irruptions may result in the establishment of new populations. Extensive planting of red pine in the Great Lakes region resulted in colonization by a western subspecies. It has adapted by decreasing its bill size to extract seeds from the smaller cones of the red pine relative to the conifer species that it exploits in the west. There may be high mortality of young shortly after they reach independence because of their inexperience at extracting seeds (Benkman 1988a, 1993b; Benkman and Young 2020; Cornelius and Hahn 2012; Erskine 1977; Gabrielson 1924; Holoman et al. 1998).

The Red Crossbill often hangs upside down on attached cones or adjacent branches to probe for seeds. On hemlock, it tends to leave cones attached, turning and holding them upright with 1 foot. On pines, it sometimes detaches the cones by twisting or biting the stalk of the cone and holding it to extract the seeds. Cones that have fallen to the ground may be an important source of seeds in spring after snowmelt. The crossed mandibles are used to open the cone scales to expose the seeds. The palatine grooves in the bill are used to husk the seeds. It stores food temporarily in its crop when feeding nestlings or going to the night roost; the crop is capable of holding about 300 spruce seeds (Benkman 1987b; Benkman and Young 2020; Hess et al. 1998). At Pimisi Bay, it often hopped along the branches of pines much in the manner of a Red-breasted Nuthatch, searching for insects in bark crevices. A male captured a flying insect in flycatcher style (Lawrence 1949b). Hess et al. (1998) observed it gleaning on bark. It has fed on fallen almonds in an orchard, on woolly aphids in curled-up elm leaves by cutting open the cases with the bill, on woolly aphids within galls that it split with its bill, on caterpillars feeding in hemlock cones, on aphids on Manitoba maple, and on seed heads of common dandelion and other herbaceous species (Austin 1968).

The Red Crossbill selectively seeks tree species and individual trees and cones that provide the most profitable foraging. These include the conifer species that its bill is best adapted for removing seeds from the cones, trees with the heaviest crops of cones, and cones with the greatest number of seeds. As the seeds of its preferred conifer species become depleted, it may switch to another

species or move to another location. Trees with heavy cone crops are selected and may be exploited by a flock for several days until the number of seeds is diminished and the tree is no longer a profitable foraging site. Trees with sparser cone crops within a few metres of a tree laden with cones may be completely avoided. In Algonquin Park, birds forage initially on white spruce seeds but switch to white pine seeds when spruce seeds decline. If white pine seeds become depleted, it switches to red pine seeds. Birds foraging in Algonquin Park foraged on the most profitable conifer 53.8% of the time; 85% foraged on the most profitable conifer more than 60% of the time. Flocking enhances the profitability of foraging and provides maximum avoidance of predators. Flocks spend less time on unprofitable trees and find trees with good seed crops faster than individual birds. When husking seeds, birds raise their heads, allowing them to detect predators. The larger the flock size, the more likely a predator will be detected (Benkman 1987a, 1988b; Benkman and Young 2020; Smith et al. 1999).

Despite being highly social, the Red Crossbill may be aggressive while foraging. In a laboratory, the dominant bird often remained perched while others pried open the cone. The first bird to obtain seeds was invariably replaced by the dominant bird (Benkman 1988b; Hess et al. 1998). There is a pecking order in both males and females with a general dominance of all males over females. The pecking order is maintained predominantly by threat displays. Fighting may occur and this usually involves biting. Often threatening is not required and subordinate birds simply avoid dominant birds. Age and size are unimportant in determining dominance (Tordoff 1954).

Red and White-winged crossbills often forage together in the same flocks. White-winged Crossbills are dominant to Red Crossbills. After taking flight, mixed flocks often separate into Red Crossbill and White-winged Crossbill flocks. The 2 species of crossbills tend to forage on different species of seeds due to their differing bill sizes and efficiency rates of extracting seeds from different conifers. The Red Crossbill is more efficient at husking seeds of pines and hemlock than the White-winged Crossbill; the converse is true for the smaller seeds of spruce. Food overlap between the 2 species of crossbills is highest in summer when both forage on white spruce seeds. The rest of the year, the diet of the 2 species diverges. The large-billed type 2 Red Crossbill that is the most common subspecies in Ontario feeds predominantly on pine seeds; the White-winged Crossbill feeds mostly on white spruce, black spruce, and tamarack seeds. Red Crossbills are found mostly in stands dominated by pines and forage mostly on pines in mixed conifer stands. White-winged Crossbills inhabit mostly spruce stands and target spruce seeds in mixed conifer stands. Diet overlap between the 2 species may be 100% in late summer when both feed on white spruce seeds but this is a time when food abundance is high and increasing. Dietary overlap declines in late autumn and is nonexistent by late winter. There may be competition between the smaller subspecies of Red Crossbill and the White-winged Crossbill because hemlock seeds may be important to both their diets. In Alaska, where the small subspecies of Red Crossbill is present, the 2 species do not occur together (Benkman 1987a, 1988b; Benkman and Young 2020; Hess et al. 1988).

Other finches feed on conifer seeds and the Pine Siskin may join foraging flocks of Red Crossbills. Crossbills are the only finches that can remove seeds from closed cones. When seeds are readily available in open cones, the other finches have similar foraging rates as the crossbills, but crossbills require seed-encounter rates 2-3 times higher than the other finches. The other finches may

outcompete crossbills by lowering seed abundance below levels necessary for their survival (Benkman 1988a).

Both adults feed the nestlings by regurgitation. The male also feeds the female by regurgitation during incubation and the early nestling period. During courtship feeding, the male may offer the female salted grit and aspen buds. The material fed to young is a dark viscid paste that suggests that it may contain insect material, although this has not been substantiated. Nestling food that has been confirmed consisted of conifer and sunflower seeds that adults collected from feeders (Benkman and Young 2020; Haggerty 1982; Johnson 1969; Lawrence 1949b; McCabe and McCabe 1933).

In Algonquin Park, the most common subspecies of the Red Crossbill is type 2, which has a large bill, but type 3 is also present and it has a small bill. Type 2 birds feed on white spruce seeds in late summer and early autumn. These cones open in early September and intake rates of these seeds decline as they become depleted. Type 2 birds are fairly inefficient at feeding on white spruce and switch to white pine seeds as foraging profitability of spruce seeds declines and abundance of white pine seeds increases. When white pine seeds remain abundant, foraging on them may continue from mid-September to October, when cones contain an average of more than 10 seeds, to mid-June when only 0.19 seeds are present per cone. When the white pine crop becomes depleted, type 2 birds switch to red pine seeds. The smaller type 3 birds in Algonquin Park prefer white spruce and hemlock seeds. Throughout its range, this type appears to prefer to forage on hemlock, and foraged on it in Algonquin Park from December until the end of February (Benkman 1987a, 1988b; Tozer 2012). At Pimisi Bay, birds fed first on seeds of balsam fir and had emptied the cones by the end of December. Balsam fir seeds became an important food source again when the snow melted and uncovered seeds on the ground. It appeared to feed mostly on white pine seeds but also ate black spruce seeds. In addition to conifer seeds and dormant insects, it ate buds of aspens and birches and dried and frozen fruit of cranberries, wintergreen berries, and Canada mayflower berries (Lawrence 1949b). Conifer seeds are the most important food items in the diet. The preferred seeds vary geographically, by subspecies, and time of year. Outside Ontario, it has fed on white pine, Virginia pine, red pine, pitch pine, jack pine, white spruce, black spruce, Norway spruce, European larch, hemlock, mountain pine, and scotch pine. In addition, it eats staminate cones of conifers. It occasionally feeds on seeds, catkins, or buds of deciduous or herbaceous species such as yellow birch, tulip tree, sweet gum, cow parsnip, chokecherry, alders, willows, poplars, elms, and maples. It eats sunflower seeds which it may take directly from the plants or from bird feeders. It eats suet and hemp seeds at feeders. In Hamilton, it was observed digging seeds out of a squash that had been left out all winter (Austin 1968; Benkman 1987a; Benkman and Young 2020; Campbell et al. 2001; Haggerty 1982; Heck 1996; Hess et al. 1998; Létourneau in Gauthier and Aubry 1996; McIlwraith 1894; Messineo 1985; Sinclair et al. 2003; Snyder 1951; Tordoff 1954). In California from autumn to spring, the diet consisted of 1% insects by volume and the remainder was conifer seeds and other vegetative matter. It has eaten caterpillars, woolly and other aphids, and insects in galls of poplars and junipers (Benkman and Young 2020; Haggerty 1982). Budworms may be important in its diet. Near Gogama, it was abundant in jack pine forests when jack pine budworms were abundant, but absent once the budworms disappeared (James and Peck 1995a). On Anticosti Island, the crop of 1 bird was full of spruce budworms. Tremblay et al. (2018) concluded that budworm infestations may have influenced its foraging behaviour and that it may benefit from outbreaks by feeding on larvae.

Twenty percent of observations of Red Crossbills were in infested stands and 75% were within 1 km of an infested area. Gabrielson (1924) analyzed the contents of 243 stomachs: 202 were collected from November to April. The winter diet consisted of 96.47% conifer seeds and 96.0% of stomachs contained nothing else. Variation in its diet appeared to be geographical rather than seasonal. Pine seeds represented 78.29% of the winter diet (Virginia, ponderosa, white, and red pines), but it also consumed white spruce, black spruce, and hemlock seeds. In March, 1 stomach was filled with ragweed seeds and 2 contained 100% and 80% mast. Other vegetable matter included bits of wood, pine needles, and unidentified seeds. Animal food constituted only 1.07% of the winter diet and included spiders, caterpillars, and fly larvae, all of which may have been ingested incidentally. The summer food in 41 stomachs included 81.98% vegetable matter and 18.02% animal matter. Conifer seeds were found in 31 stomachs (75.6%) and constituted 68.34% of the diet. Other vegetable matter included seeds of a bulrush species and a plant in the aster family (1.69%), unidentified fruit pulp and skins (4.88%), and wood and debris (7.07%). The insect material consisted of 8.65% caterpillars plus 1 moth, 6.56% bugs (aphids and spittle bugs), 2.09% beetles (mostly weevils, but 1 click beetle larva), and less than 1% fragments of hymenopterans, an insect gall, and insect eggs. It has eaten ants, aphids, mourning cloak butterfly caterpillars, frozen apples, cottonwood buds, forest tent caterpillars, beechnuts, flowering crabapple fruits, and buds of apple, pear, and cherry trees. Results indicated that conifer seeds were the most important food items.

Minerals are important in the diet of the Red Crossbill. It routinely eats grit and other materials that contain calcium or sodium. It has been documented feeding where dishwater has been thrown on the ground, on snow discoloured by dog urine, on coal ashes and ashes of campfires, eating mortar from chimneys, and eating small bones. It is highly attracted to sources of salt. These may include roads that have been salted, beaches of saline water bodies, and shorelines of wetlands and water bodies where decomposing aquatic plants may provide a source of sodium and calcium. It also visits natural salt licks (Benkman and Young 2020; Campbell et al. 2001; Lawrence 1949b; Tozer 1994). Lawrence (1949b) concluded that salt consumption was not a daily necessity and that it might be restricted to the breeding season. No salt was eaten during snowstorms or rainy weather, but salty areas were visited by greater numbers of birds on days immediately following these events. In a laboratory experiment, it preferred 0.1 mole (M) sodium chloride and avoided 0.2 M sodium chloride. Dawson et al. (1965) concluded that it has no requirement for sodium chloride beyond what it eats in its diet. Its primary source of salt is roads and shoulders of roads. It is oblivious to traffic and large numbers are killed by vehicles every year (Benkman and Young 2020; Clark 1981; Lawrence 1949b; Messineo 1995; Tozer 2012).

Water is essential to the Red Crossbill; it drinks water or eats snow daily (Benkman and Young 2020; Lawrence 1949b).

Timber harvesting may be the most significant limiting factor for the Red Crossbill. Extensive deforestation occurred in the northeastern United States and Canada around the turn of the 20th century. Pines were particularly prized because they were excellent for ships' masts. The northeastern subspecies was almost extirpated as a result of this, but has somewhat recovered since, probably due to maturation of second-growth pine and hemlock (Dickerman 1987). Tozer (2012) estimated that white pine was 85% less abundant in Algonquin Park than in the 1880s. In

Newfoundland, this crossbill prefers old-growth black spruce forests. Both red and white pines may have previously provided important habitat, especially since this subspecies has a large bill better adapted to feeding on pine than spruce seeds. Both pine species were harvested extensively and continue to decline as a result of diseases. The minimum rotation age for harvesting on the island is 65 years and more frequently 80 years. Good cone-bearing usually begins at age 40 years for the conifers on the island and would therefore be available for 25-40 years prior to the next harvest. The potential effects of forest management on the Newfoundland Red Crossbill appeared to be understated in the recovery strategy (Sutton 2006). This subspecies is best adapted to foraging on pines which are now scarce and declining further. It currently forages mostly on black spruce cones. The red squirrel outcompetes the crossbill for seeds and squirrel densities are 2 times higher on Newfoundland than on the mainland (Benkman 1993b). In Washington and Oregon, only 10% of the original old-growth forest remains; only 2% remains in Alaska. The Red Crossbill is 30 times more abundant in old-growth (325 to more than 500 years old) forests on the western coast than in younger forests 65-140 years old. Older trees produce many more cones and are more consistent in producing cones than younger trees. In Alaska, birds foraged or perched only in mature stands. During extensive cone failures, only mature trees can support the Red Crossbill for extended periods. To protect it and prevent further declines, it has been recommended that large tracts of mature forests be protected and that rotation ages be increased (Benkman 1993b; Benkman and Young 2020; Holoman et al. 1998). It is highly vulnerable to changes in its habitat due to its reliance upon a single source of food. Loss of habitat generally results in a disproportionate decline in crossbills (Benkman 1993c).

Outbreaks of the larch cone maggot can severely decimate seed crops and cause the Red Crossbill to cease nesting and emigrate (Benkman 1990).

In Colorado, a massive die-off occurred as a result of salmonellosis. Several hundred dead birds were reported but the actual mortality toll could have been several thousand (Heck 1996).

Climate change is having an adverse effect on the Red Crossbill, at least in the west. Because of increasing temperatures, conifers are prematurely shedding seeds from their cones. According to the Breeding Bird Survey (BBS), numbers began to decline in 1980 when temperatures started to increase. Since then, it has increased 20-fold at feeders. Benkman (2011) predicted that it would continue to decline as a result of increasing temperatures, but that a higher proportion of birds would visit feeders in response to lower availability of conifer seeds.

Status

Type 2 birds, which are associated with pines, and type 3 birds, which are associated with spruce and hemlock, breed in the province. Type 4 (the Douglas Fir Red Crossbill) probably also breeds (Tozer 2012), mostly during irruptions and primarily in the area between Lake of the Woods and Thunder Bay, and type 7 breeds in central Ontario (Benkman and Young 2020). Baillie and Harrington (1937) noted that no nests had been reported, but breeding had been confirmed in Bruce, Nipissing, York, and Algoma. The Red Crossbill had been seen as far north as Hudson Bay leading them to conclude that its breeding range might include the entire province. The first atlas revealed that its breeding distribution was confined mostly to the Great Lakes–St. Lawrence Forest Region, predominantly in the Canadian Shield but also in more heavily forested areas south of the Shield.

There were scattered records in the southern Boreal Forest Region and in the northwest portion of this area. There were a few breeding records from the Carolinian Forest Region, mostly associated with mature conifer plantations in the Long Point area (Lumsden and Smith in Cadman et al. 1987). The breeding distribution of the Red Crossbill corresponds closely with the ranges of white pine and red pine (Kershaw 2001). During the initial 3 years of the first atlas, cone crops were poor and few breeding records were documented. Cone crops were excellent in 1984 and there were more breeding records in that year than in the 3 previous years combined. Additional breeding records were obtained in 1985 as a result of the carryover of the good pine and spruce seed crops (Lumsden and Smith 1987). James (1991) considered the Red Crossbill an uncommon permanent erratic resident across the province, north to Sandy Lake and Cochrane and south to Algonquin Park. It is occasional and rare in summer north to Fort Severn and Sutton Lake, and south to Norfolk and Haldimand counties. From autumn to spring, it is a rare to common erratic south to Lake Erie.

The second atlas revealed a similar distribution as in the first atlas, but there was no evidence of type 3 breeding due to a lack of a good crop of hemlock during the atlas. No breeding evidence was obtained for the Carolinian Forest Region. The probability of observation did not differ province-wide between the 2 atlases, but a significant decline occurred in the Great Lakes–St. Lawrence Forest Region south of the Shield and a significant increase occurred in the Boreal Forest Region (Simard in Cadman et al. 2007).

There are no reliable population estimates for the Red Crossbill anywhere within its range (Benkman and Young 2020). The BBS is conducted at a time when it is least likely to be breeding. Winter counts may include breeding birds as well as those that have irrupted from other areas. Its lack of site fidelity and extreme nomadism pose further constraints to estimating population numbers.

There are BBS results for the Red Crossbill, but they may not be very accurate. Data for 1970-2021 indicate that it decreased at an annual rate of 0.0415% in Canada and increased at an annual rate of 2.06% in Ontario. For 2011-21, it experienced annual decreases of 1.54% in Canada and 0.518% in Ontario. The Canadian results were of medium reliability; the Ontario results were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings from a Pimisi Bay nest remained in the nest tree their first day out of the nest. The next day, they flew to the edge of a lake but were not capable of flying horizontally, losing altitude as they went. Fledging occurred in late April and flying juveniles were observed throughout May. Family groups were joined by nonbreeding birds and failed breeders. Flocks consisted of 4-6 adults and 1-2 juveniles. These groups amalgamated by the end of May, with flocks containing as many as 2 dozen birds (Lawrence 1949b). In Idaho, birds began to congregate and move about as soon as the young left the nest (Jollie 1953). Young may return to the nest to roost for some days after leaving the nest. They waited in trees for several days after fledging to be fed but families were fairly mobile within a week (Benkman and Young 2020).

Lawrence (1949b) observed no pairs with more than 2 fledglings, suggesting that about half the young did not survive. If a female lays a second clutch, the male cares for the first brood. Adults may

feed the young as long as 33 days after they fledge. Juveniles are capable of extracting and shelling seeds when they are 45 days old (Benkman and Young 2020).

MIGRATION

The Red Crossbill appears to undertake regular migrations. Birds have a peak of fat deposits in May and June suggesting that spring movement is true migration. Migration is nomadic in nature, being variable in distance and direction. This differs from nomadic wandering with no preparation or seasonal scheduling (Cornelius and Hahn 2012). It makes 1-3 movements annually with spring movements more regular than those in autumn. Large flocks often occur in May and June and in September and October. In British Columbia, there is evidence that it withdraws from northern areas in winter. Most flights occur during the regular migration periods, but they may occur at any time of the year. Migration appears to occur only during the day (Benkman and Young 2020; Campbell et al. 2001).

The Red Crossbill occasionally undertakes nomadic irruptions. These involve long-distance movements within the Boreal and Great Lakes–St. Lawrence forest regions. Birds often move much further south into areas dominated by deciduous trees, where they are at risk of starvation. Irruptions into Ontario typically include type 3 and 4 birds, and additional type 2 birds may invade the province. Type 10 (the Sitka Spruce Red Crossbill) may irrupt to the Great Lakes area and the northeast where it feeds on red and white pines as well as jack and pitch pines. Irruptions may occur at any time of the year, but especially from late summer through winter. Irruptions are in response to poor conifer seed crops. Seed crop failure tends to be synchronous over large areas at scales of hundreds to thousands of kilometres. Birds tend to undertake long movements during irruptions. Birds from the Pacific Northwest and Alaska may irrupt to the Great Lakes area. Breeding may occur in areas outside its normal breeding range following irruptions provided that there is still a good seed crop. There is unlikely to be any consistent direction of flight during irruptions and birds stop when they encounter a plentiful seed source rather than flying to regular destinations (Austin 1968; Benkman 1987a; Benkman and Young 2020; Bock and Lepthien 1976b; Cornelius and Hahn 2012; McNair 1988).

In Ontario, most conifer seeds form in summer and are shed in autumn. Seeds are usually available to crossbills between July and October. Black spruce cones may carry seeds for a number of years. For any given species of conifer, heavy seed crops rarely occur in the same location in successive years. Tamarack may produce a good crop every 3-6 years, white spruce every 2-8 years, and white pine every 3-10 years. Asynchronous seed production among different conifer species may provide food availability in successive years, but emigration is required when this does not occur (Lumsden and Smith 1987). Brewer et al. (2018) reported that irruptions into the eastern United States occurred about once every 10 years. Freedman and Riley (1980) analyzed Christmas Bird Counts (CBC) for southern Ontario for 1929-77. There was no pattern in occurrences of the Red Crossbill or trends in its numbers. In the Hamilton area, modest numbers occurred about every other winter for 15 years beginning in the winter of 1950-51; birds were observed every winter from 1965 to 1974. After 1988, only 19 individuals were seen within 5 winters (Curry 2006). In the Kingston area, it was documented in 40 of 60 years; many were migrants that passed through the area (Weir 2008).

In Elgin County, most records are in March and April. It has occurred from 26 December to 7 June (Lancaster et al. 2004). In the Hamilton area, average spring departure is 31 March and the latest record is 12 June. Average autumn arrival is 6-28 November and the earliest record is 25 September (Curry 2006). At Presqu'ile, the Red Crossbill occurs irregularly from early November to mid-May, and there are 3 summer records. Extreme dates of occurrence outside summer are 6 November to 12 May (LaForest 1993). In the Kingston area, average spring departure is 28 March and average autumn arrival is 6 November (Weir 2008).

NONBREEDING SEASON

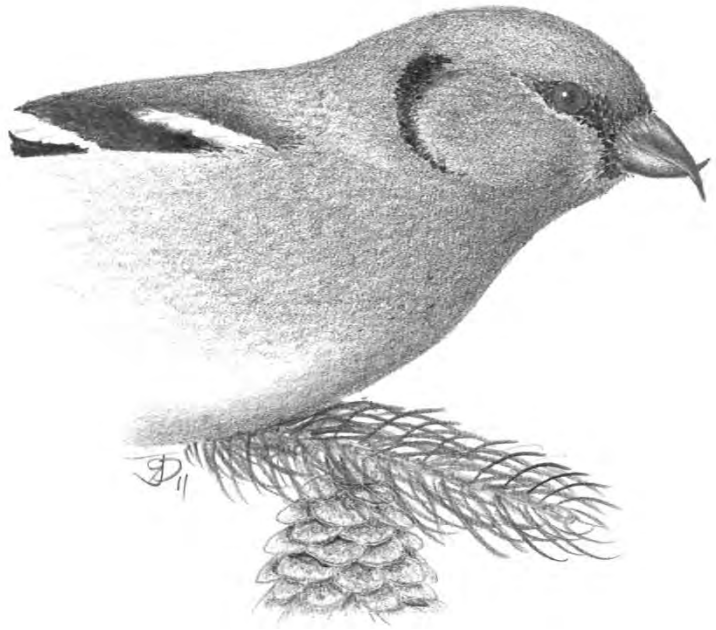
It is difficult to determine what constitutes the nonbreeding season for the Red Crossbill. It may potentially nest in most months of the year, but nonbreeding pairs may also be present all year. In Ontario, nonbreeding areas include the southern portion of the province where birds may overwinter during irruption years. Some of these birds may remain and subsequently breed.

During winter in the south, the Red Crossbill continues to be associated with conifers. It is found most frequently in mature coniferous plantations but may occur in solitary rows of conifers in windbreaks and on suburban and urban lots.

CBC data indicate that the Ontario Red Crossbill population increased at annual rates of 1.21% 1970-2021 and 13.12% 2009-21 (National Audubon Society 2022).

White-winged Crossbill

Loxia leucoptera



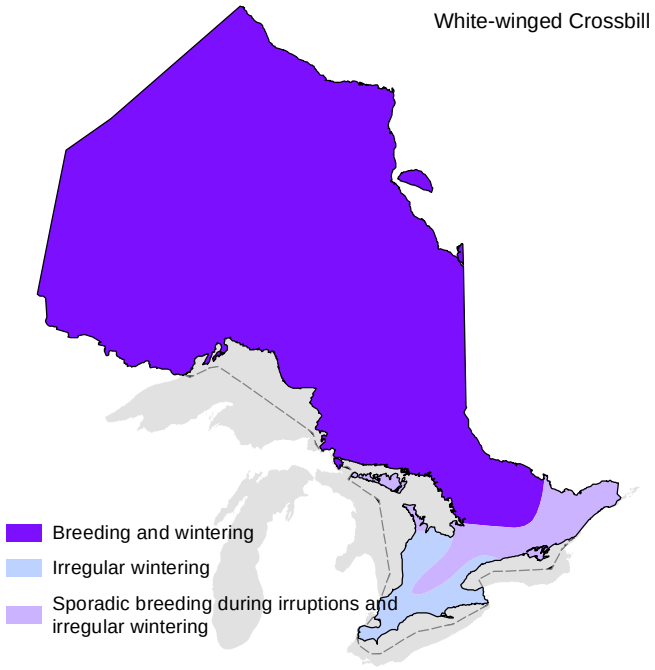
BREEDING SEASON

Habitat Requirements

White-winged Crossbill nests in Ontario were in coniferous forests (2 nests), coniferous plantations (1 nest), in mixed second-growth forests (3 nests), and in mixed Carolinian Forest Region woods (1 nest). These nests are not representative of its habitat in the province (Peck and James 1987, 1998b). It breeds in spruce and tamarack forests in the Boreal Forest Region and the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region. It may nest south of the Shield during or immediately after southward irruptions. In these areas, it nests mostly in older coniferous plantations, especially spruce plantations, but also in mature mixed woods. In Oxford County, it nested in a younger spruce plantation (Holdsworth and Graham 1990). The Carolinian mixed-wood forest where nesting was confirmed was at Old Cut at Long Point (Enright 1993a). A nest found in 2001 in Peel Region was in an area where there was a heavy crop of black spruce cones (Coady 2001).

In the Clay Belt in the Boreal Forest Region, the White-winged Crossbill was most common in black spruce stands, but also occurred in those dominated by trembling aspen, jack pine, tamarack, and white cedar (Welsh and Lougheed 1996). It is likely that the aspen stands contained some conifers because it relies almost exclusively on conifer seeds for food. It occurred in stands across the full spectrum of moisture regimes, but predominantly in wet stands. It is probable that the presence of conifer seeds is more important than habitat characteristics of the forest. In jack pine

stands near Gogama, it was common when jack pine budworms were abundant, but did not remain after the budworms were gone (James and Peck 1995a).



Throughout North America, the White-winged Crossbill is associated predominantly with the Boreal Forest Region because of its preference for spruce and tamarack seeds. It also occurs in mixed forests both within and south of this forest region, and occasionally nests in coniferous plantations and mixed forests south of its normal range. In mixed coniferous forests, it tends to select areas dominated by spruce and avoid those dominated by pines; the converse is true for the Red Crossbill (Benkman 2020). In Quebec, it breeds predominantly in the Boreal Forest Region but also further south in mixed forests and isolated coniferous forests. It occurs most frequently in stands dominated by spruce and tamarack and less frequently in stands of balsam fir. On Anticosti Island, it was associated mostly with white spruce and tamarack forests. Its frequency of occurrence was highest where forests were dominated by black spruce, white spruce, balsam fir, and tamarack. Its frequency of occurrence was much lower in the deciduous and mixed forests of the south (Létourneau in Gauthier and Aubry 1996). Near Quebec City, it was in a guild that was either restricted to or found in greater numbers in areas that had been logged. The higher abundance of these species in the sapling stage and young forests after logging indicated they were not restricted to mature stands (Imbeau et al. 1999). It is possible that it was not breeding at this time of the year. In Quebec in 6-year-old strip-cuts, it occurred in coniferous but not deciduous stands. In 10-year-old strip-cuts, it occurred in both types of stands but was more abundant in conifers. It was absent in strip-cuts 14-15 years old and in final cuts and occurred in coniferous but not deciduous clear-cuts (Falaradeau et al. 1999). In northeastern Manitoba, it was most abundant in coniferous forests without an understorey followed by mixed forests. It was present in trace numbers in coniferous forests with an understorey and in mixed scrub but was absent in deciduous forests, deciduous and coniferous scrub, heath, and tundra (McLaren and McLaren 1981). In northeastern lowland conifers, it was uncommon in young or low black spruce stands, most common in intermediate-aged to mature black spruce stands, and moderately common in white cedar stands (Dawson 1979). The White-winged Crossbill has nested in spruce plantations in Minnesota and Wisconsin (Bielefeldt and Rosenfield 1993, 1994; Little and Langeslag 1996). In the Prairie Provinces, it was in a guild associated with coniferous forests. It occurred only in forests 80 or more years old, predominantly in dry stands with a moderate nutrient status (Kirk et al. 1996). In British Columbia, it tends to be most abundant in mountainous areas or where spruce or tamarack occur. It is less abundant in drier areas where pine forests predominate. In the south, it

nests mostly in high-elevation subalpine forests. Further north, it breeds from valley bottoms up to the timberline (Campbell et al. 2001). In the Yukon, it inhabits lowland white spruce forests and also occurs in black spruce stands. It is common in mixed and riparian spruce forests. It has been reported occasionally in lodgepole pine forests. It is rarely encountered in deciduous forests (Sinclair et al. 2003). In Alaska, it is most abundant in spruce and mixed forests on floodplains followed by hills with black spruce forest on north-facing slopes, subalpine spruce forests, and lowland black spruce woodlands (Handel et al. 2009).

The White-winged Crossbill roosts nocturnally in dense foliage of conifers, with as many as 6 roosting together in the same tree. In Ontario, a male roosted in a white cedar in sight of the nest tree (Benkman 2020; Coady 2001).

Coady (2001) summarized the characteristics of 12 Ontario nests, including those described by Peck and James (1987, 1998b), Enright (1993a, 1993b), and Holdsworth and Graham (1990). All were in conifers 2.4-12.5 m from the ground, but most were 5-10 m up. Eight nests were in spruce (3 in white spruce, 3 in black spruce, 1 in Norway spruce, and 1 in an unidentified spruce). One nest each were in white cedar, jack pine, and balsam fir. Most were on horizontal branches either near the trunk or as far as 2 m from it. One was in a crotch between the trunk and 2 lateral branches. The nest was positioned so that it maximized the time that the nest was exposed to direct sunlight.

All nests reported in North America were in conifers, most frequently in spruce. Nests have been reported 0.8-21 m from the ground. Although most are on a horizontal branch at varying distances from the trunk, some are in the crown of trees, especially in shorter trees. In winter, nests tend to be on the southern and eastern sides of trees to gain better exposure to the sun. In Minnesota, 1 nest tree had no cones on it in an area with a heavy cone crop. This may have been an adaptation to discourage other crossbills from visiting the nest tree (Benkman 2020; Bielefeldt and Rosenfield 1993; Bond 1938; Little and Langeslag 1996; Taber in Austin 1968).

The White-winged Crossbill may nest singly but this occurs most frequently when it nests outside its normal range. Nests are usually clustered as a result of an abundance of food and favourable microclimates. Nest clustering may also enhance predator detection and defence. It may travel and forage in flocks year-round, even while it is nesting. Males often chase each other or females, especially prior to nesting. Males guard their females during the egg-laying stage, possibly in an attempt to prevent extra-pair copulations. Only a small area around the nest or nest tree is defended, and defence is very low key. It does not defend a feeding territory and routinely travels 1 km or more between nesting and foraging areas. Defence of food resources would probably decrease food intake rather than increase it. Nesting only occurs where seeds are abundant, so seed depletion as a result of other crossbills has little effect; energy would have to be expended to defend food resources. Defence of conifer cones would also inhibit flock formation. Birds in flocks have food intake rates 1.27 times greater than solitary birds (Benkman 1988c, 2020; Messineo 1985).

It is highly unlikely that the White-winged Crossbill exhibits any natal philopatry or adult site fidelity. It is extremely nomadic, searching for areas where conifer seeds are abundant and moving to another area as soon as the seed crop declines. Distances between successive breeding areas may be hundreds or even thousands of kilometres apart. Individual conifer species are incapable of

producing bumper crops of seeds 2 years in succession, so the likelihood of crossbills remaining in a given location for more than 1 breeding season is very low (Benkman 2020).

Limiting Factors

The White-winged Crossbill nests wherever conifer seed crops are sufficient to raise nestlings; this is the most demanding phase of breeding. When seed crops are increasing, it may initiate nesting as soon as the female can form eggs. Nests may be deserted if a warm dry spell causes cones to open and release most of their seeds (Benkman 1990). Breeding is opportunistic and may occur any time of the year provided that conifer seed crops are adequate. In the southern portion of its range, it infrequently nests in November and December. In Alaska, nesting occurs only between February and July (Benkman 2020). In Ontario, it has 3 nesting periods. The first coincides with the maturation of cones in early July when it feeds on developing cones of tamarack, white spruce, and to a lesser extent, red spruce. Nesting usually declines by November, but declines by early September when it feeds on tamarack seeds. Young may still be fledging in late December and early January during exceptional seed crops. The larger the cone crop, the longer it nests. During this nesting period in Algonquin Park, active nests have been observed in July, a nest was under construction in mid-August, and dependent fledglings have been observed from early August to mid-October. The second nesting period is in January and February when it requires large crops of white or red spruce cones that have held seeds through the winter. This is the least consistent nesting period and nests may be deserted if seeds fall out of the cones. During this period in Algonquin Park, nest construction has been observed from mid-December to late February, nestlings were present from early January to late February, and dependent fledglings have been observed in late March. The third nesting period begins in March or April when black spruce cones open, and nesting may continue into June. In Algonquin Park during this period, nest construction occurs in early to mid-March and dependent fledglings have been observed from early April to mid-June (Benkman 2020; Tozer 2012). As soon as nesting is complete, it searches for developing cone crops to begin nesting again. This may involve travelling great distances. Once an adequate food source is discovered, it begins nesting rapidly, nests several times in rapid succession, potentially nests much of the year, and begins nesting at a very early age (Benkman 2020).

No information is available on how long it takes to build a nest and if there is a delay between nest completion and the initiation of egg laying. Presumably 1 egg is laid per day. Incubation is almost continuous and may begin with the laying of the first egg, particularly in cold weather, but may be delayed until the last egg is laid when it is warmer. At the Long Point nest, incubation appeared to begin shortly after the nest was complete. The only information on the incubation period is from Ontario. The Long Point nest was abandoned after the female had incubated the eggs 14-15 days. The incubation period at the Peel Region nest was 14 or 16 days, depending upon whether incubation began with the laying of the first or third egg. No information is available on the nestling period. Nestlings may enter torpor during cold weather, and this may extend the nestling period (Benkman 2020; Coady 2001; Enright 1993a, 1993b; Little and Langeslag 1996).

In the southern part of the White-winged Crossbill's range, females may raise 2-4 broods in a year. Those in the north may raise 1 or 2 broods. During the July to September nesting period, birds that feed on tamarack seeds raise a single brood; those that feed on spruce seeds may raise multiple

broods. The actual number of broods raised has never been confirmed. It is possible, if not probable, that females may raise broods at widely disparate locations within a year. Adults appear to breed much more frequently than yearlings. There is circumstantial evidence that renesting may occur if a nest is depredated or abandoned. After the nest in Caledon Township was depredated, both adults returned to the nest several times. Each time, the female removed some material from the nest lining and flew off with it, suggesting that she was building a replacement nest. After a Minnesota nest was abandoned as a result of a snowstorm, a female was seen building a nest approximately 6 m from the original nest. It was assumed that the same female was involved, but there was no evidence to support this. Twenty days elapsed after the first nest was abandoned until construction started on the second nest. This was an unusually long interval between nest loss and initiation of a replacement nest. All Ontario nests contained either 3 eggs or 3 young. Clutches of 2-4 eggs are common; 5-egg clutches are rare (Benkman 2020; Bielefeldt and Rosenfield 1993; Bond 1938; Coady 2001; Little and Langeslag 1996; Peck and James 1998b; Taber in Austin 1968).

The White-winged Crossbill is capable of breeding when it is less than 5 months old. In Utah, all females and adult males were paired, but there was a population of unmated yearling males (Benkman 2020; Smith 1978). It appears to be monogamous, but it is unknown if females raising another brood retain their mate or mate with another male (serial polyandry). Polyandry is highly likely because the sex ratio is male biased. If females breed in different locations within a year, it is unlikely that the same mate would be retained. Some males and females associate with each other in the nonbreeding season as though they are paired. It is suspected that extra-pair copulations are part of the mating strategy. Males guard their females closely during the egg-laying stag. They also have relatively large testes, suggesting that extra-pair copulations may be common (Benkman 2020).

The mandibles of the White-winged Crossbill are designed specifically for feeding on conifer seeds, so it is inefficient at feeding on other plants. It has a smaller bill than all but 1 subspecies of the Red Crossbill. The White-winged Crossbill forages most efficiently and frequently on seeds of white spruce, black spruce, and tamarack, and also on red spruce to a lesser extent; the Red Crossbill forages most frequently on pines. The White-winged Crossbill husks the smaller spruce seeds more efficiently than the Red Crossbill. The converse is true for the larger seeds of pines and hemlock. Consequently, there is limited competition between the 2 crossbill species for food. Food overlap between them is greatest in summer when both feed on white spruce seeds. Seeds are most abundant and least limiting at this time. The White-winged Crossbill has evolved to harvest the more accessible but less abundant seeds in partially open black spruce cones (Benkman 1987a, 1987b). While foraging, certain trees may be used repeatedly but adjacent trees with seemingly equal numbers of cones may be ignored. Trees that are avoided typically have few seeds remaining in the cones, or seeds may be unavailable if the cones are closed (Benkman 2020; Little and Langeslag 1996). It usually forages on cones that are still attached to the tree, but it may feed on cones on the ground when they are exposed by spring snowmelt. Open cones are usually left attached to the tree, but closed cones are often removed by twisting them or biting the peduncle. Removal of cones distant from the foraging flock may also decrease agonistic interactions among flock members. It also forages on loose seeds among needles and on branches; they can be abundant after cones

open (Benkman 1997, 2020; Hess et al. 1998). At a feeder near Alliston, it fed on niger seeds in a tube feeder (Schmelefski 2002).

The White-winged Crossbill often eats ashes from fires, presumably for the minerals they contain. It may be attracted by smoke. In Algonquin Park, it ate dead wood from stumps and snags. The wood contained no evidence of mineral deposits, insects, fungi, or other organisms that may have provided a food source. The wood may be rich in ash and calcium and this may have been what the birds were seeking (Crins and McRae 1998; Crins and Strickland 1999; Lauzon and Nancekivell 1999; Taber in Austin 1968; Tozer 1999). Gallant (2008) reported it feeding on river otter feces and speculated that they were feeding on the fish bones in the scats, a potential source of calcium. The White-winged Crossbill is readily attracted to other sources of sodium and calcium, including natural mineral licks and roads that have had sodium chloride or calcium chloride applied to them. It is also attracted to dog urine in snow (Meade 1942; Taber in Austin 1968; Tozer 2012). In New York, flocks foraged regularly in a plowed field, but it was not determined what the birds were eating (Messineo 1985). It has been observed feeding on teasel twice in southern Ontario and has fed on wild parsnip seeds and on cow parsnip on treeless islands in British Columbia (Campbell et al. 2001; Curry 2006; Taber in Austin 1968). It occasionally gleans on bark at the base of trees and may peel off bark (Hess et al. 1998; Taber in Austin 1968). It has fed on snails or crustaceans among boulders on an Alaskan beach and on decayed garden fruits and seeds of lyme grass (Taber in Austin 1968). It drinks water or eats snow on a regular basis (Smith 1998; Taber in Austin 1968).

The White-winged Crossbill almost always forages in flocks. This increases foraging efficiency and its ability to detect predators. Solitary birds ingest significantly fewer seeds per unit time than birds in flocks. As flock size increases, the rate of aggression also increases. Adult males are consistently dominant to all females and to first-year males. Females fed at a progressively slower rate than males as the rate of agonistic interactions increased. In November and December, juvenile males avoid adult males and associate with adult females, which also avoid adult males. Aggression is highest in black spruce where all the cones are compactly located within 1 m of the narrow crown of the tree. Rates of agonistic interactions are lower on red spruce and even lower on white spruce where the branches are more continuous and cones are more uniformly dispersed. Agonistic rates are very low on tamarack and red pine where cones are widely dispersed throughout large crowns (Benkman 1997).

The Pine Siskin and Red Crossbill commonly join flocks of foraging White-winged Crossbills. When feeding flocks take flight, the siskins usually do not associate with the crossbills, and the crossbills typically divide into conspecific flocks. While foraging in conifers, both sexes of the White-winged Crossbill are dominant to the Red Crossbill (Benkman 2020; Hess et al. 1998). Crossbills are the only finches that can extract seeds from closed conifer cones. When cones open, other finches have similar feeding rates as the crossbills. Under these conditions, the other finches may outcompete the crossbills by lowering seed abundance below the threshold necessary for them to survive. Crossbills require seed encounter rates 2-3 times higher than other finches (Benkman 1988a). The Redpoll may irrupt southward in the same years as the White-winged Crossbill and this coincides with periods when seeds are most limiting. The Redpoll feeds on tamarack seeds at this time, so it may be a direct competitor of the White-winged Crossbill (Benkman 1987b).

Both adults feed the nestlings a regurgitated bolus that consists of seed kernels. The male feeds the female in a similar manner when she is incubating the eggs and brooding young nestlings (Coady 2001; Enright 1993a, 1993b; Taber in Austin 1968).

The White-winged Crossbill feeds almost exclusively on conifer seeds and may consume more than 3,000 seeds per day. Within its normal range, it feeds predominantly on seeds of tamarack and white, black, and red spruce. It feeds to a lesser extent on balsam fir seeds which may be less palatable because of their resin coating. Nonetheless, large balsam fir cone crops sustain populations in summer in southern Quebec, and it may also consume white cedar seeds. In the extreme southern portion of its range, hemlock seeds are often preferred. During irruptions south of its normal range, it may feed on seeds of nonnative conifers such as Norway spruce and European larch. Pine seeds are seldom consumed, but occasionally it eats red and white pine seeds (Benkman 2020; Hess et al. 1998; Lancaster et al. 2004; Létourneau in Gauthier and Aubry 1996; Little and Langeslag 1996; Messineo 1985; Sealy et al. 1980; Taber in Austin 1968; Tozer 2012). During an irruption into Manitoba when White-winged Crossbills were not breeding, it preferred tamarack seeds to spruce seeds. Of 117 feeding flocks, 83% fed on tamarack, 12% on black spruce, 3% on white spruce, and 1% on white cedar and forbs. Of 17 flocks flying over habitat dominated by black spruce, 16 (94.1%) settled in a tamarack and the other landed in a black spruce (Sealy et al. 1980).

Benkman (1987b) studied the foraging ecology of the White-winged Crossbill in Algonquin Park as well as in Quebec, Maine, and Vermont. It fed on seeds of white spruce, black spruce, and tamarack. The species selected was related to the abundance of seeds and how quickly seeds could be ingested. Intake rates on tamarack and white spruce increased from July through August and September as cones began opening, then declined as seeds were shed from the cones. The peak of foraging on tamarack occurred in August and September. The peak of feeding on white spruce and black spruce was in September and October. In 1 year in Algonquin Park, it foraged most effectively on white spruce from August to early January, with 80% of its time spent in white spruce and virtually ignoring black spruce. In late February, it foraged 61% of the time on black spruce even though white spruce was more profitable. In another year, it foraged nearly 100% of the time on white spruce, ignoring black spruce. There were 3 periods of change in its abundance that coincided with seed fall and conifer use. When seed profitability was high, it often remained in the area and influxes occurred into the park; it emigrated when profitability was low. The second period when it shifted habitats was in late February and March, coinciding with a decline in profitability of tamarack and white spruce and a switch to foraging on black spruce. It emigrated from the park in March 1983 when the average number of seeds per cone dropped from 9.4 on 1 February to 0.5 on 25 March. The third period of movement coincided with the switch from foraging on open black spruce cones to foraging on developing tamarack and white spruce cones in June and July. It often migrated at this time to areas of large crops of developing tamarack and white spruce cones and was first seen back at Algonquin Park on 17 July. The fewer species of conifers that are present in an area, the shorter the time period that it can support the White-winged Crossbill. When tamarack and white spruce seeds are abundant, it may switch to feeding on black spruce seeds later, but always does so by March. It often forages on hemlock seeds in winter because this tree holds its seeds during this period. The period between the falling of tamarack and white spruce seeds in late autumn and the opening of black spruce cones in late winter is when seed profitability relative to energy

requirements is lowest. It can meet its energy demands easier in late winter when black spruce seeds are available. In the northern Boreal Forest Region, black spruce is the most important species during seed crop failures because black spruce seed crops are the least variable and rarely fail (Benkman 2020; Messineo 1985; Taber in Austin 1968). It occasionally eats fruits and unusual food items. Some may be desperation foods when conifer seeds are scarce or absent. It has eaten juniper berries; sunflower seeds both from plants and feeders; seeds of crowberry, huckleberry, ragweeds, foxtails, lyme grass, teasel, and sweetgum; rotten garden fruits; berries from ornamental trees and shrubs; and suet at feeders (Benkman 2020; Campbell et al. 2001; Taber in Austin 1968).

Gabrielson (1924) examined the contents of 52 stomachs collected in the United States in February and September. The diet consisted of 93.12% vegetable matter and 6.88% animal matter. Conifer seeds comprised 76.21% of the diet, predominantly those of spruce and hemlock. No pine seeds were found in the stomachs, but 24% of the conifer seeds could not be identified to genus. Seventeen stomachs collected in February were 50% full of hemlock seeds and the remainder consisted of unidentified conifer seeds. One stomach taken in October was filled with balsam fir seeds and 1 collected in November contained juniper berries. Two birds had eaten nothing but buds and these constituted 3.84% of the entire sample. One stomach contained huckleberry and crowberry seeds. Weed seeds constituted 9.61% of the diet and included those of sunflowers, ragweeds, and foxtails. Various unidentified vegetable matter comprised 2.98% of the diet. Of the 6.88% animal food, 1.68% consisted of caterpillars and other larvae; the remainder was unidentified digested material. One large flock fed on larvae of pitch pine sawflies. It has been reported eating cankerworms and frozen apples. Sealy et al. (1980) examined stomachs of birds killed on roads during winter in southeastern Manitoba. Twenty-four diverticula and stomachs all contained tamarack seeds; 1 contained more white spruce than tamarack seeds; and 2 or 3 white spruce seeds were present in 2 other specimens. Arthropod remains and black spruce seeds were present in 3 and 2 stomachs respectively.

Timber harvesting reduces the quality and quantity of habitat for the White-winged Crossbill. In the Boreal Forest Region of Ontario, Vanderwel et al. (2009) determined that removal of 30% of the tree canopy had no effect on its abundance, but it declined when 50% or 70% of the canopy was removed. It appears to be less common in the Montreal area now due to removal of extensive stands of mature conifers as a result of logging and urbanization (Létourneau in Gauthier and Aubry 1996). Current forest management practices in the Boreal Forest Region are detrimental because construction of logging roads destroys habitat and shorter rotation periods result in forests being less productive for crossbills. Most conifers do not produce cones until they are more than 60 years old. Benkman (2020) recommended protecting more forested habitat, increasing rotation ages, and maintaining large tracts of mature forest throughout the Boreal Forest Region.

The White-winged Crossbill's habit of foraging on roads to obtain sodium or calcium chloride probably results in thousands being killed annually. Calcium chloride is poisonous to the birds, causing direct mortality or resulting in their being too sick to move out of the way of vehicles (Benkman 2020; Meade 1942; Messineo 1985; Tozer 2012).

Outbreaks of the larch cone maggot can decimate developing cone crops and cause the White-winged Crossbill to cease breeding or emigrate. It has been documented eating large quantities of

spruce budworms and pitch pine sawflies and disappeared from a forest in the Gogama area when the jack pine budworm was no longer present (Benkman 1990; James and Peck 1995a). It is possible that budworms and sawflies are an important supplement to the diet of birds breeding in the summer.

Birds that fledge in autumn may have reduced survivorship in their first winter because they are still inefficient at foraging and are subordinate to adults. Birds that fledged between August and October had significantly lower seed intake rates than adults in November and December. Juvenile females may suffer particularly high mortality because they are subordinate to all other sex-age classes and forage less rapidly when in flocks (Benkman 1990, 2020).

In Alberta, the White-winged Crossbill was significantly more abundant at seismic lines and pipelines than in adjacent forest interior (Bayne et al. 2016).

Benkman (2020) predicted that the Boreal Forest Region would shrink in response to global warming and that this would have a negative impact on the White-winged Crossbill.

Status

Baillie and Harrington (1937) reported that the White-winged Crossbill had been found more or less commonly from Middlesex County in the south to the northern limits of the province and west to the western end of Lake Superior. The first atlas demonstrated that its breeding range included the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, the Boreal Forest Region, and the Hudson Bay Lowland, although its distribution within these areas was spotty. There were scattered breeding records south of the Shield. Few records were obtained in the first 3 years of the atlas, with more breeding evidence obtained in 1984 and 1985 during a period of excellent cone crops for most conifer species (Lumsden and Smith 1987; Smith and Lumsden in Cadman et al. 1987). James (1991) considered the White-winged Crossbill an uncommon to common permanent erratic resident across the province, south to the Algonquin Highlands. It is occasional further south to Oxford County and Lake Ontario in summer and a rare to locally abundant erratic south to Lake Erie from autumn to spring.

The second atlas confirmed that the distribution of the White-winged Crossbill had not changed since the first atlas. Many gaps in its previous distribution were filled because of more widespread and frequent irruptions into the province. In addition, atlassers were probably more aware of its breeding phenology than during the first atlas. Its probability of observation increased significantly from the first atlas province-wide and in all regions where it occurred except the Hudson Bay Lowland. It increased in that region as well, but not significantly. It was most abundant in areas dominated by spruce, including the Hudson Bay Lowland, the Boreal Forest Region, and limited areas in Algonquin Park. Because of its nomadic habits and unusual timing of breeding, these data should be treated with caution (Coady in Cadman et al. 2007).

The White-winged Crossbill is not adequately surveyed at any season of the year to determine trends in its population. The Breeding Bird Survey (BBS) is conducted when many crossbills may not be breeding, and most of its breeding range is not covered by this survey. There are few Christmas Bird Counts (CBCs) in the core of its range. The facts that it is nomadic, exhibits no site fidelity, and can range from being absent to abundant in a given area make determination of its population

trends extremely difficult. In addition, populations fluctuate widely, declining precipitously during periods of widespread cone crop failures and rebounding quickly when a plentiful food source is found. Specialized studies would be required to determine its population status. Nonetheless, BBS and CBC data are available for it. BBS data for 1970-2021 indicate annual increases of 3.47% in Canada and 3.95% in Ontario. During 2011-21, there were annual increases of 8.08% in Canada and 6.6% in Ontario. All results were of low reliability except for the long-term Ontario results, which were of medium reliability (A.C. Smith et al. 2023). CBC data for 1970-2021 indicate an annual increase of 1.15% in Ontario; it declined at an annual rate of 1.81% 2009-21 (National Audubon Society 2022).

POSTFLEDGING PERIOD

During the first few days after fledging, the young remain hidden in trees where they wait to be fed by the adults. Fledglings can fly well a week after they leave the nest and start to follow the adults closely. Family groups then coalesce into larger flocks. When food is abundant, some young may remain in the vicinity of the nesting area, but others appear to travel widely. If food is scarce, all adults and juveniles disperse from the breeding area, often for great distances. Dependent fledglings may drink water on their own without adults being present. In New York, juveniles remained in nearby trees while adults fed on road salt and grit (Benkman 2020: Messineo 1995; Smith 1978).

MIGRATION

The White-winged Crossbill makes 1-3 or even more migratory movements each year, travelling by day. These movements are best termed nomadic migration because movements are fairly regular but are not in a fixed direction, to a specific destination, or of a set distance. Movements are mostly in easterly and westerly directions within the Boreal Forest Region. Movements may be very long distance and could conceivably be from Alaska and the Yukon to Newfoundland. Movements are related to the availability of conifer seeds. One movement coincides with cone development in mid- to late May when birds begin searching for large developing cone crops of white spruce or tamarack. Large movements often occur in late October and November coincident with declines in seed availability. Emigration occurs when seed crops are low or when warm dry weather results in cones shedding most of their seeds. The threshold seed intake rate is approximately 0.4 mg of seeds per second. When intake levels decline below this, emigration typically occurs. Movement out of areas is most pronounced where black spruce is absent. It is the most reliable seed source in winter and its absence, despite large crops of spruce and tamarack seeds, may be an impetus for movement. In spring of 1983, the White-winged Crossbill emigrated from Quebec and Algonquin Park and was largely absent from eastern North America, except along the Maine coast and in Newfoundland. It was also absent from most of the western portion of the continent, but was abundant in Alaska and the Yukon. Large influxes were noted more than 3,600 km to the east and southeast, arriving in Algonquin Park by mid-July. It appeared as though birds moved from Alaska and the Yukon to Ontario and Quebec in about a month, travelling through the Boreal Forest Region (Benkman 1987b, 2020).

In non-irruption years, the nonbreeding and breeding ranges are the same. In addition to its wanderings within the Boreal Forest Region, the White-winged Crossbill makes occasional irruptive flights south of its normal range. Bumper cone crops occur at intervals of 2-10 years but cone crops

fail over large areas every 2-4 years. Southward irruptions are a response to failed cone crops, but may also occur if the population increases and the larger number of birds depletes the cone crop. Southward irruptions usually occur in late October and November when spruce and tamarack seeds are depleted. Birds tend to leave southern areas in March or early April with some stragglers persisting into early May; some birds may remain south of the normal range to breed (Benkman 1987b, 2020; Hess et al. 1998; Messineo 1985; Sealy et al. 1980).

Bock and Lepthien (1976b) analyzed United States CBC results from 1962 to 1972 and concluded that the White-winged Crossbill irrupted southward at regular intervals of 2-3 years, and that its irruptions coincided with those of several other boreal seed-eating birds. Their own data do not support this conclusion very well. There appears to be no pattern to this crossbill's irruptions. It may occasionally occur outside its normal range in consecutive years, but occurrences may be separated by decades with no apparent pattern. Freedman and Riley (1980) analyzed southern Ontario CBC data for 1929-77. They found no clear trend in its abundance or patterns of irruptions. Major irruptions into southern Ontario occurred in 1950-51, 1955-56, 1960-61, 1963-64, 1971-72 (Speirs 1985), 1984-85 (Smith and Lumsden in Cadman et al. 1987), and 2008-09. Often a decade or more elapses between irruptions in some areas, including Pennsylvania (Hess et al. 1998), southeastern Manitoba (Sealy et al. 1980), and southern Quebec (Létourneau in Gauthier and Aubry 1996). When irruptions occur, they are usually coincident with other boreal species, particularly the Redpoll and Pine Siskin. Red Crossbills often appear in the same years, but not always.

In the south, departure of spring migrants is irregular and is usually in March or April, but may be as early as January or as late as May (Black and Roy 2010; Curry 2006; LaForest 1993; Weir 2008). Manning (1952) reported that spring migrants arrived at the Severn River on the Hudson Bay coast in the last half of May but did not remain to breed. Autumn migrants may arrive in the south from mid-October to mid-November, but occasionally not until January (Curry 2006; LaForest 1993; Weir 2008)

Numbers seen during migration are highly variable. In the Hamilton area during 1950-90, either large or small irruptions occurred at least every other winter, but they are now less frequent and smaller (Curry 2006). At Presqu'ile, small numbers are seen each year but about 100 flocks of 25-100 birds flew by within a period of 90 minutes on 27 February 1985 (LaForest 1993). The number of birds seen on the Algonquin Park CBC has ranged from 1 to 8,728, with an average of 1,405 (Tozer 2012).

During extensive cone failures and irruptions, the White-winged Crossbill may experience massive mortality. It is ill adapted to foraging on anything but conifer seeds, but the southern areas that it irrupts to are dominated by deciduous species. It is often forced to adapt to unfamiliar food sources that it is inefficient at accessing. In addition to mortality due to starvation, it is much more likely to be struck by vehicles during irruptions. Its extraordinary ability to produce multiple broods in a short period usually allows the population to rebound following irruptions (Benkman 2020).

NONBREEDING SEASON

The White-winged Crossbill may breed in every month of the year, but nonbreeders may be present at any time. In non-irruption years, it remains in the same habitat year round and consumes the same food items whether it is breeding or not. In irruption years, it seeks conifers in areas that are

predominantly deciduous, agricultural, or urban in nature. It searches for natural coniferous and mixed stands and older plantations, especially those dominated by spruce. It also forages in conifers planted around residential lots, in shelterbelts in agricultural fields, and along roads.

Pine Siskin

Spinus pinus

BREEDING SEASON

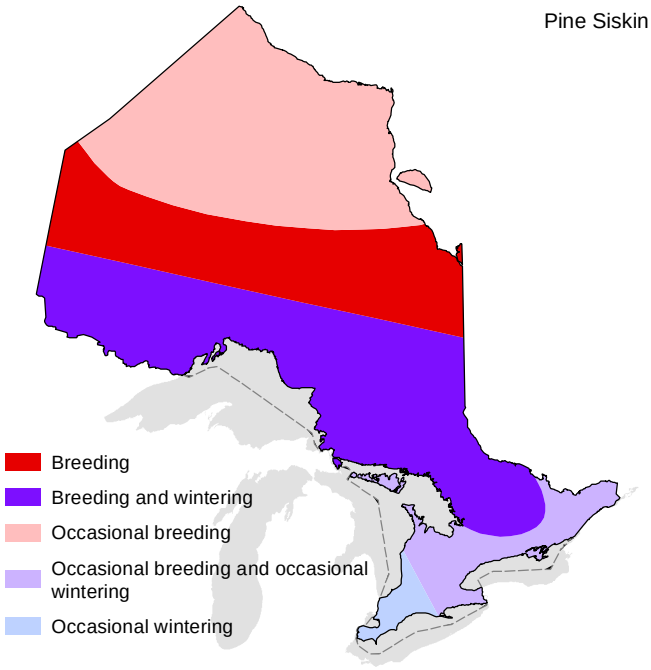
Habitat Requirements

In Ontario, the Pine Siskin has nested in coniferous and mixed forests and hedgerows. Four of 14 nests (28.6%) were on urban residential properties, 3 (21.4%) were in coniferous woods, 3 (21.4%) were on the University of Guelph campus, 2 (14.3%) were in mixed second-growth woods, and 1 each (7.1%) were in a tamarack bog and a hedgerow beside a road (Peck and James 1987). The nest records are not a representative sample, with many found south of its normal breeding range following irruptions.

In the Boreal Forest Region from Pickle Lake northwestward into northeastern Manitoba, the Pine Siskin was most abundant in coniferous forests without an understorey followed by mixed forests, coniferous forests with an understorey, and mixed scrub. It was not observed in deciduous forests, deciduous scrub, heath, or tundra (McLaren and McLaren 1981). Near White River, it was most abundant in jack pine stands 18-20 years after clear-cutting (Venier and Pearce 2005). It was most abundant in stands 60-223 years old at Manitouwadge (Venier et al. 2009). In the Clay Belt, it was most abundant in stands dominated by white spruce–balsam fir and black spruce, followed by trembling aspen stands mixed with balsam fir and black spruce. It occurred in stands that ranged

from nutrient-poor to nutrient-rich but was restricted to forests that were moist to wet (Welsh and Lougheed 1996).

In Algonquin Park, it was observed in 0% of 2-9-year-old white pine stands, 9.1-20% of 10-16-year-old stands, and 6.7-7.1% of stands with no recent history of harvesting (Kingsley and Nol 1999).



The normal breeding range of the Pine Siskin includes the Boreal Forest Region and the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region. Erskine (1977) considered it characteristic of the ecotone between boreal forest and alpine habitat. It is common and widespread in spruce forests but also nests in urban areas within the Boreal Forest Region. Breeding occurs mostly in open coniferous and mixed forests and occasionally in deciduous stands containing conifers (Dawson 2020). In Newfoundland, Whitaker and Montevecchi (1997, 1999) considered it a habitat generalist. In balsam fir forests, it was equally abundant along riparian edges, in forest interior, and at edges adjacent to roads and clear-cuts. There was no difference in its abundance in buffers adjacent to water bodies in intact forest and in areas where the adjacent forest had been clear-cut. In Newfoundland balsam fir stands, it was associated with nutrient-poor stands of young to moderate age (40-60 years). It was significantly less abundant in 80-year-old stands, which were somewhat more open, had larger numbers of dead standing trees, and lacked the deciduous small-tree layer that was present in younger stands (Thompson et al. 1999). In Quebec, the Pine Siskin's frequency of occurrence was highest in forest regions dominated by black spruce or balsam fir, but was still quite high in forests dominated by yellow birch. In the deciduous forest zone, it was associated with pockets of conifers scattered through agricultural, wooded, and urban landscapes. It often breeds nearby in the spring after frequenting a feeder in the winter (Rivard and Bombardier in Gauthier and Aubry 1996). Falardeau et al. (1999) reported it breeding in Quebec coniferous strip-cuts, including final cuts and those 6, 10, and 14-15 years old. It was rare in strip-cuts through deciduous forests. It occurred in both coniferous and deciduous clear-cuts. In Quebec black spruce stands, it was significantly more abundant in clear-cuts with 2-5-m tall saplings and 120-year-old forests than in 200-year-old forests and young clear-cuts with trees 5-11 m tall. Its abundance in burns with trees 5-11 m tall was not significantly different from that in any of the other stand types (Imbeau et al. 1999). In the Prairie Provinces, it was in a guild associated with conifers. It occurred mostly in old stands on dry soils that were moderate in nutrient richness (Kirk et al. 1996). In Saskatchewan, it was randomly distributed among landscapes but was slightly more common in large forest fragments with low forest cover within 5 km. It was significantly more common in white spruce stands than expected, moderate in abundance in mixed stands, and uncommon in

trembling aspen stands (Hobson and Bayne 2000). In Alberta, it was significantly more abundant in old trembling aspen–dominated stands than in mature and young stands. It was positively correlated with conifer density. Old trembling aspen stands are more likely to contain conifers than younger stands (Schieck et al. 1995). In British Columbia, conifers were an important component of Pine Siskin habitat in trembling aspen–dominated forests. In the taiga plains, it was most abundant in mature forests dominated by white birch, trembling aspen, and white spruce. Sixty-eight percent of nesting records were from low-elevation human-influenced or forest (28%) habitats. The human-influenced habitats included 30% suburban habitat, 21% cultivated farmland, and 16% rural areas. Results were not representative of the habitats that it used. It is a widespread breeder in subalpine forests (Campbell et al. 2001). In coniferous forests in southern British Columbia, it was negatively associated with deciduous riparian vegetation in spring, summer, and autumn, but significantly so only in summer (Wiebe and Martin 1998). In the Yukon, it inhabits open coniferous forests, especially those dominated by white spruce. It also nests in trembling aspen and mixed stands (Sinclair et al. 2003).

During or following irruptions south of its normal breeding range, the Pine Siskin may nest in a wider variety of habitats. These atypical nesting habitats tend to be over-reported in nest descriptions compared with their proportional use. In areas where high-elevation habitat is present, it may nest in more typical coniferous forest (McNair 1988) but also in hemlock stands (Messineo 1985). It may also breed in coniferous plantations (Bielefeldt and Rosenfield 1994; Messineo 1985) and wide-scale planting of conifers in the 20th century may have extended its breeding range southward (Dawson 2020). Other habitats that may be used for nesting south of the normal breeding range include planted conifers in urban and residential lots (McNair 1988; Messineo 1985; Pitelka 1942; Weaver and West 1943), road-side conifers (Knight 1994), university campuses and arboretums (Hull 1989; Perry 1965), ornamental conifers in parks and cemeteries (Dawson 2020), pine and oak barrens (Mossman et al. 1991), and small coniferous and mixed stands in urban and rural areas (Leighton et al. 2002).

All Ontario nests were in conifers: 57.9% in spruce, 21.2% in pine, and 5.3% in each of balsam fir, hemlock, tamarack, and white cedar. All were saddled on horizontal limbs. One was against the trunk and 8 were 1.1-2.5 m from the trunk and sometimes near the end of a branch. Nests were concealed and supported on the limbs by small branches, sometimes at forks. Nests were 1.8-10 m from the ground with most 3.5-6 m up (Peck and James 1987).

Within its normal range, the Pine Siskin nests predominantly in coniferous trees, but it occasionally nests in deciduous trees and shrubs south of its typical range. It commonly nests in spruces, pines, firs, hemlock, and white cedar. In more southern locations, red cedar, Norway spruce, and blue spruce are commonly used for nesting. It has nested in oaks, elms, Manitoba maple and other maples, cottonwood, lilac, juneberry, cypress, apple trees, and willows. Most nests are saddled on a horizontal branch, often distant from the trunk and occasionally near the tip of a branch. Less frequently nests are near the trunk or among small branches near the treetop. Nests on branches may be supported in part by twigs that also serve to conceal the nest. Others are not attached to the limb. These tend to be concealed by overhanging branches. Nest height is variable, and it may nest in shrub- or sapling-sized trees to large conifers. Nest heights of 0.6-30 m have been reported,

with most about 3-8 m up. It has been observed dismantling old nests of Pine Siskins, American Goldfinches, and orioles and using the material to build a new nest (Campbell et al. 2001; Dawson 2020; Hull 1989; Knight 1994; Leighton et al. 2002; Messineo 1985; Palmer in Austin 1968; Perry 1965; Rodgers 1937; Weaver and West 1943).

The Pine Siskin does not defend a feeding territory. A radius of 0.9-1.8 m is defended around the nest. The female will leave the nest to chase any birds that approach this close. The siskin is gregarious year round and breeding males may form small flocks as large as 6 birds. Males occasionally bring their flocks back to their nest tree, but both sexes chase them if they intrude into the defended territory. It may nest solitarily, but most often in loose colonies. Six nests were found in a single tree in Washington State. In British Columbia, 4 nests were found close together, but no 2 nests were in the same tree (Campbell et al. 2001; Palmer in Austin 1968; Weaver and West 1943).

No information is available on natal philopatry, but it is highly unlikely that any birds return to breed in the vicinity of their natal territory. The Pine Siskin is nomadic, breeding wherever there are abundant crops of conifer seeds. In Michigan, adults and young left the area as soon as the fledglings were proficient fliers (Hull 1989), but in other cases the family unit remained near the nest for several weeks.

There is no information on adult site fidelity. Banding returns indicate that birds may breed in widely disparate regions in different years. Some adults banded from May to June have been encountered in another state or province in the same months of a different year. There are 7 such encounters for Canada with an average distance of 1,375 km between the banding and recovery areas (Brewer et al. 2018). Cases of adult site fidelity are likely very rare to nonexistent.

Limiting Factors

Weaver and West (1943) stated that breeding could occur at any time of the year, but that is not the case. Nest building may occur from mid-February until August, mostly in April and May (Dawson 2020; Hull 1989; Messineo 1985; Palmer in Austin 1968). Eggs have been reported in Ontario nests from March until the third week of July, with most present from near the end of April until mid-May. The Pine Siskin is sporadic in its timing and distribution of nesting in the province (Peck and James 1998b). In Algonquin Park, nests are under construction in late March to mid-May, eggs are present mid-April to mid-June, and dependent fledglings are typically observed mid-May to mid-July with a few observations from late August to early October. Early breeding and highest densities are associated with large crops of conifer seeds, particularly those of spruce, white cedar, and hemlock (Tozer 2012). In Guelph, Salvadori et al. (2009) concluded that nest building occurred in late March or early April and that the final eggs were laid 8-15 April.

Nest construction takes 5-6 days and 2-3 days may elapse after nest completion until egg laying begins; eggs are laid on successive days. At 1 nest, incubation began with the laying of the first egg. At another nest, all eggs hatched on the same day suggesting that the onset of incubation was delayed until the penultimate or last egg was laid. It is possible that incubation may begin with the laying of the first egg when the weather is cold but be delayed in warmer weather. The incubation period is 13 days based upon a limited sample. The nestling period is normally 13-17 days but only 11-13 days in Nebraska. Young were weighed daily in the Nebraska nests, so they may have fledged

prematurely (Campbell et al. 2001; Dawson 2020; Hull 1989; Palmer in Austin 1968; Perry 1965; Weaver and West 1943).

It is likely that the Pine Siskin raises 2 broods, at least in some years, but this has yet to be confirmed. Peck and James (1987) concluded that second broods were a possibility in Ontario and Campbell et al. (2001) stated that egg dates suggested double broods in British Columbia. Palmer (in Austin 1968) stated that there was a strong probability of double broods in some years and that birds may change locations between nestings. It has been suggested that some birds may breed in the south early in the year and move north to raise a second brood. In a given population, there may be birds present in various stages of the nesting cycle, indicating that either some breed twice or different segments of the population breed at different times (Dawson 2020; Palmer in Austin 1968). If a nest is lost or abandoned, a replacement clutch may be laid (Dawson 2020). Clutches of 2-5 eggs have been reported in Ontario, with most containing 4 eggs (mean 3.40 eggs; Peck and James 1998b). Clutches of 2-6 eggs have been reported throughout its range, with most containing 3 or 4 eggs. Five- and 6-egg clutches are rare, and there appears to be no geographic variation in clutch size. It is unknown if there are seasonal differences in clutch sizes (Dawson 2020; Palmer in Bent 1968).

Both sexes are presumably capable of breeding when they are 1 year old, but this has yet to be confirmed. The mating system is apparently monogamous. It is possible that sequential polyandry occurs, but this requires documentation. The close association of the male to the female during nest building may represent mate guarding (Dawson 2020). If Pine Siskins raise 2 broods in different locations within a breeding season, it is possible that they switch mates.

Rodgers (1937) observed flocks landing in the top 1.8-2.4 m of alders and working down the trees on the cones. The regular procedure was to forage down to the lower limbs, never spreading over an area more than 3.7-4.6 m, then make a circular flight to the top of another tree and repeat the procedure. They also foraged in a nearly horizontal line through a group of trees without foraging throughout any of them completely. Direct flights among trees were either to distant trees or those within 3-4.6 m. Circular flights had a radius of about 23 m and probably functioned as reconnaissance flights to find potential suitable trees for foraging. In trees, siskins forage much in the manner of chickadees and crossbills, often hanging upside down under cones at the tips of branches. They are incapable of extracting conifer seeds from closed cones and are less dependent on conifer seeds in their diet than crossbills. Consequently, they forage on a wider variety of substrates and use more foraging techniques (Dawson 2020; Palmer in Austin 1968). In British Columbia, siskins foraged on winter moth caterpillars in an apple orchard. The number of birds and the amount of time an individual spent within a tree was correlated with larval density. Birds appeared to be responding to levels of leaf damage in their search of winter moth larvae (Roland et al. 1986). The Pine Siskin commonly forages on the ground. It may be attracted to lawns where it extracts seeds from dandelion heads. It visits weedy fields, clear-cuts, orchards, and sparsely forested areas where it feeds on seeds of various herbaceous species, soft stems and leaves of forbs, and tender buds and blossoms of deciduous trees. It may also drink from flowers that trap water. It commonly gleans arthropods from leaves and twig tips (Campbell et al. 2001; Dawson 2020; Rodgers 1937; Schaub 1951). It is ineffective in hulling seeds that have tough shells. At feeders, it

often eats fragments of thick-shelled sunflower seeds left by larger birds (Dawson 2020). Rodgers (1937) reported birds snatching insects out of the air. Batts (1953) reported a siskin feeding at a fresh Yellow-bellied Sapsucker boring in a sweetgum. It appeared to be taking sap because it hesitated between each feeding, presumably waiting for more sap to flow. Prescott (1985) observed siskins feeding nocturnally in Quebec on an area of bare grit where bird food had been placed. It was partially illuminated by a floodlight at a nearby cottage. The temperature was −30°C; nocturnal feeding may be a mechanism to survive cold nights. It regularly seeks minerals to supplement its diet. This may be accomplished by consuming road salt and grit, blue clay, fresh or decaying concrete, dish water, and plaster (Bennetts and Hutto 1985; Campbell et al. 2001; Dawson 2020; Lowther and Walker 1967; Messineo 1985; Palmer in Austin 1968).

The male feeds the female during the incubation and brooding periods. He regurgitates a semisolid yellowish or greenish paste, with the greenish paste being attributed to aphids. The male may also feed the female seeds and buds, one at a time (Knight 1994; Messineo 1985; Perry 1965; Rodgers 1937; Weaver and West 1943). The young are fed the same type of paste by regurgitation. Nestlings are fed predominantly aphids, but also alder, birch, and willow seeds (Dawson 2020; Palmer in Austin 1968; Perry 1965; Weaver and West 1943).

Adults eat predominantly seeds, particularly those of conifers, but also deciduous species such as alder, birch, and willow. The Pine Siskin also eats seeds of grasses and herbaceous species, especially those in the aster family (Dawson 2020). Gabrielson (1924) analyzed the contents of 266 stomachs collected in winter and 25 in summer, mostly from the mountainous western states. The winter diet consisted of 86.7% vegetable matter and 13.3% animal matter. Of the vegetable matter, 20.15% was finely divided unidentified material, 23.28% were seeds of conifers, 24.58% were weed seeds (mostly ragweed in the east and groundsel in the west) and 18.69% were birch or alder seeds. It frequently eats a single food item exclusively, with conifer seeds constituting 100% of the contents of nearly all 70 stomachs in which they occurred. The animal food consumed in winter consisted entirely of insects: 7.31% caterpillars, 1.38% aphids, 2.17% scale insects, and 2.44% fragments of beetles, grasshoppers, and other insects. The summer diet consisted of 71.92% vegetable matter and 28.08% animal matter. The vegetable matter consisted of 20% conifer seeds, 19.2% weed seeds, and 32.72% unidentified material. Seeds consumed included those of sweetgum, willow, juniper, and plantain, with lesser amounts of foxtails, elms, smartweeds, amaranths, chickweeds, catchflies, blackberries, clovers, catnip, lilac, and stork's-bill. It occasionally consumed buds of fruit trees. Animal food consumed during the summer included 8.48% aphids, 4.68% caterpillars, and 14.92% spiders, bugs, fly larvae, weevils, and other insects. In winter in California, it consumed book lice, scale insects, and small caterpillars (Rodgers 1937). In Kansas, it fed on sunflowers seeds from patches of this plant near a pond and in a fallow field (Fitch 1958). It ate black alder seeds in Ontario (Dance 2008). Other items it has eaten include seeds of dandelions, thistles, tamarack, hemlock, pines, elms, sweetgum, and maples; buds of elms and maples; berries of honeysuckles and red cedar; soft stems and leaves of a variety of forb species; blossoms of ornamental flowers; seedlings of garden vegetables such as beets, lettuce, radishes, and onions; and a variety of insects including chalcid wasp larvae, sawfly larvae living within leaf galls, spruce budworms (eggs, larvae, and pupae), and wood-boring insects that may be captured by breaking dead twigs off trees (Dawson 2020; Palmer in Austin 1968). During a spruce budworm outbreak in Maine, budworm larvae and pupae constituted 68% by volume of

the food that 1 bird had consumed (Mitchell 1952). Near Manitouwadge, abundance of the siskin was not related to spruce budworm abundance (Venier et al 2009).

The Pine Siskin is occasionally parasitized by the Brown-headed Cowbird, but the reported rates of parasitism are often inflated. Much of the siskin's breeding range does not overlap with that of the cowbird and this parasite avoids the coniferous forests that the siskin prefers. Nests initiated in March and early April are unlikely to be parasitized. Most nest records are from south of the siskin's normal breeding range following irruptions, and this brings the 2 species into contact. Nests that are parasitized have a poor success rate in fledging young of either species. In Kansas, only 3 siskins and 1 cowbird fledged from 16 parasitized nests; 7 unparasitized nests fledged 14 siskins. The siskin is a poor host for the cowbird because it often abandons the nestling cowbirds when they are 6-7 days old and the diet fed to young siskins is inadequate to raise cowbirds. In Ontario, 3 of 20 nests (15.0%) were parasitized. In British Columbia, 6 of 62 nests (9.7%) were parasitized but the results were considered biased due to the disproportionate number of nests from low-elevation areas in the sample. In 2 areas of Kentucky, 26 of 67 nests (38.8%) and 28 of 51 nests (54.9%) were parasitized (Campbell et al. 2001; Dawson 2020; Hull 1989; Peck and James 1998b; Perry 1965).

There appear to be no significant habitat losses or degradation for the Pine Siskin in Ontario. Maturing conifers in plantations and around dwellings and farmsteads may provide habitat during irruption years. No adverse effects of timber harvesting have been identified, but occasionally sample sizes are too small and its irregular breeding habits make it difficult to assess potential impacts. It is less dependent on conifer seeds than crossbills and some of the other finches, so it appears less vulnerable to removal of old-growth forests and shorter rotation ages. In the Ontario Canadian Shield, it was equally abundant in early successional and mid-successional clear-cuts and burns in the same seral stages. There was no difference in its abundance in early successional, mid-successional, and mature stands (Zimmerling et al. 2017). In response to partial harvesting in Alberta, the Pine Siskin colonized mixed forest when 50% of the canopy was removed and decreased when the entire canopy was removed. In coniferous forest, it became extirpated when any canopy was removed. None of the changes in population size were significant (Harrison et al. 2005). In British Columbia, there was no difference in its abundance in clear-cuts, remnant forest patches within clear-cuts, or old-growth forest. In Wyoming, it was significantly more abundant in old-growth subalpine forests that were altered by old strip-cut logging than it was in unfragmented forests (Campbell et al. 2001). In Idaho, Medin and Booth (1989) found no difference in its abundance before and after single-tree selection harvesting.

The Pine Siskin is well adapted to nesting in the cold when the ground is still snow-covered. The nest is thick-walled and insulated; the male feeds the female during incubation and brooding so that she can stay on the nest most of the time; it is not dependent upon long days for reproductive development, with testis size related more to food availability; it can store 1.1-1.5 g of seeds which produce enough energy to rest at night for 5.5 hours at −20°C; and it may forage opportunistically at night (Dawson 2020; Prescott 1985). Despite these adaptations, heavy snowstorms or sleet may result in nest losses and, in severe cases, starvation if the primary food sources become covered with snow. There are numerous reports of nests being blown out of trees by the wind, or tilting so much that the nestlings fell out (Campbell et al. 2001; Dawson 2020; Palmer in Austin 1968; Rodgers 1937).

In Alberta, there was no difference in the Pine Siskin's abundance at seismic lines and pipelines compared with forest interior adjacent to these facilities. It was significantly less abundant at well pads than in adjacent forest interior (Bayne et al. 2016).

Price (2004) predicted that the Pine Siskin might no longer breed in southern Ontario if the average summer temperature increased by 2°C. Although the extent of natural coniferous and mixed forests may decline as a result of climate change, it is likely that plantations and nonnative conifers will persist. In central Quebec and Labrador, it was closely associated with stands having a high summer temperature and high rates of summer precipitation. It could be adversely affected if climate change resulted in less precipitation during the growing season (DesGranges and LeBlanc 2012).

Status

Baillie and Harrington (1937) considered the Pine Siskin a nomad in Ontario, occurring irregularly but fairly commonly throughout the province, north at least to the transcontinental railway. They concluded that it probably bred throughout its range, but irregularly at any given location. In the summer of 1937, it was common in the Lake of the Woods area. During the first atlas, breeding evidence was obtained through much of the province, except in the extreme northeastern portion of the Hudson Bay Lowland and southwestern Ontario. In the southwest, it was widespread on the Bruce Peninsula but largely absent west of the Greater Toronto Area except for widely scattered records. Many records may have been obtained after breeding was complete. Breeding occurred predominantly in the Canadian Shield (Middleton in Cadman et al. 1987). James (1991) considered the Pine Siskin a common summer resident in the province north to Sandy Lake and Moosonee and south to Lake Simcoe and Ottawa, and rare north to Fort Severn and Attawapiskat and south to Lake Erie.

The second atlas indicated a similar breeding distribution as during the first atlas, with the exception that there were very few breeding records for the Hudson Bay Lowland. In the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, there was a high turnover in the squares that were occupied during the 2 atlases. This may be related to its nomadic movements in response to conifer seed abundance. Its probability of observation declined province-wide, but not significantly. There was no change in its probability of observation in the Carolinian region, where it remained rare, and in the Boreal Forest Region. It declined significantly in the Great Lakes–St. Lawrence Forest Region and in the Hudson Bay Lowland. It was most abundant in the Boreal Forest Region, particularly in the northwest. This is in contrast to the first atlas when it was most abundant in the Shield portion of the Great Lakes–St. Lawrence Forest Region. This is probably a manifestation of its tendency to be most abundant wherever conifer seed crops are most plentiful. Abundance is likely to shift again in future atlases depending upon food availability (Pittaway in Cadman et al. 2007), but will probably be concentrated in the Canadian Shield and Hudson Bay Lowland where confers are most abundant.

It is difficult to measure population changes for the Pine Siskin. Its nomadic nature means that it may be abundant in 1 year and absent the next, and this may apply to broad regions in addition to specific locations. Birds that nest in Ontario in 1 year may nest hundreds or even thousands of kilometres distant the following year. The Breeding Bird Survey (BBS) is conducted in June and siskins

may have completed nesting by then. In addition, the BBS does not cover its entire breeding range. BBS data suggest that the Canadian Pine Siskin population peaked in the 1980s and has been declining significantly ever since. It is uncertain how reliable these data are. BBS data for 1970-2021 indicate that it decreased at annual rates of 1.2% in Canada and 1.85% in Ontario. For 2011-21, it decreased at annual rates of 0.909% in Canada and 1.66% in Ontario. All results were of medium reliability, except for the short-term Ontario results, which were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Adults may feed fledglings for as long as 3 weeks after they leave the nest (Middleton in Cadman et al. 1987). Fledglings are fed undigested food items such aphids (Rodgers 1937).

In Michigan, all family groups left the natal territory 1-3 days after the young left the nest. In New Hampshire, fledglings remained near the nest tree for several weeks and visited nearby feeders and bird baths. Appearance of juveniles at feeders during winter irruptions suggested that some young may remain in the vicinity of the natal area for extended periods. In areas where breeding is erratic, fledglings may accompany adults and other family groups on lengthy flights, continuing to receive food from adults en route (Dawson 2020; Hull 1989; Salvadori et al. 2009; Weaver and West 1943).

MIGRATION

It was thought that the Pine Siskin migrated exclusively during the day, when large flocks may occur (Dawson 2020), until Watson et al. (2011) recorded numerous nocturnal flight calls in Maine. This was during an irruption so it is possible that nocturnal migration might occur only during extreme food shortages that induce long-distance movements.

Near the Pacific Coast, the Pine Siskin makes altitudinal movements, descending to lower elevations during winter. In the east, it moves short distances in a north-south direction and makes almost continent-wide movements in a south-southwest–north-northeast orientation. In the east, it may also make periodic irruptive movements far south of its normal wintering range. It is uncertain if the east-west movements occur on a regular basis and if they coincide with irruptions (Palmer in Austin 1968).

Brewer et al. (2018) reported that Ontario birds winter directly south and southeast of their breeding range, mainly in the Great Lakes states, but as far south as Texas and Louisiana in irruption years. Several birds banded or recaptured in Ontario exhibited strong east-west movements, providing no clue as to whether they were eastern or western breeders. This may result from some western birds travelling south in some winters and east to southeast in others. Birds captured in Ontario were banded in Edmonton (2,700 km distant) and Texas (2,055 km); a bird banded in Ontario was recovered in California (2,537 km). The maximum distance travelled by a bird banded or recovered in Canada was 3,983 km. Even in non-irruption years, siskins appear in southern Ontario. It occurs every year in Hamilton (Curry 2006) and a few birds migrate through Prince Edward Point in non-irruption years (Weir 2008). In New York, 9 of 4,045 Pine Siskins (0.22%) were recovered elsewhere at distances of 13-3,470 km. Seventy-seven percent of movements were in a north-south or northwest-southeast orientation that was limited to the eastern states and provinces. Distances travelled by these birds averaged 481 km (range 150-1,437 km). The other 23% of birds moved in an east-southeast–west-northwest orientation and travelled longer distances, averaging 2,099 km

(range 1,356-3,470 km; Yunick 1997). Longley (1992) reported a bird banded in Minnesota that flew approximately 2,100 km westward to Alberta. Two birds banded in Virginia flew northward to be recaptured near Montreal (990 km) and Quebec City, a distance of 1,239 km (Hansrote and Hansrote 1992). Banded birds that were recovered in British Columbia originated in states south of there, in Ontario, and in states along the Atlantic Coast south to South Carolina. The average distance between the banding and recovery locations was 2,800 km (range 360-4,300 km). A bird banded in December in Tennessee was recovered in British Columbia the following December, having travelled approximately 3,800 km (Campbell et al. 2001).

The cause of irruption appears to be widespread collapse of conifer seed crops in an area, resulting in birds moving to other areas where food supplies are more abundant (Dawson 2020). Strong et al. (2015) examined how climate affects conifer seed crops and consequently irruptions of boreal seed-eating birds. Seed production is favoured by a warm dry spring and summer in the year of cone initiation and a warm summer in the subsequent year. They analyzed climatic and Project FeederWatch data for the Pine Siskin across North America. Two irruption modes were detected, with the west-east irruption mode dominating the Boreal Forest Region and the north-south mode dominating the region south of the boreal forest. The north-south mode was positively correlated with spring precipitation in the previous year in the boreal forest and negatively in the Appalachian Region. This suggests a dipole pattern where unusually wet conditions throughout the Boreal Forest Region coincide with unusually dry conditions in the Appalachians. Wet years in the Boreal Forest Region coincide with a small cone crop whereas dry years in the Appalachians coincide with large crops. West-east irruptions tended to follow, at a 2-year lag, anomalously warm and dry summer conditions over western North America paired with anomalously cool and wet summers in the east. Large seed crops occur the year following 2 years of warm, dry conditions. This results in high recruitment and a large population in the west in the year of the irruption. The seed crop in this year will be low because trees must replenish their reserves after a strong cone crop. Conditions in the east are nearly the opposite of the west: wet conditions in the summer 2 years prior to irruption and cool conditions in spring and summer with a weak cone crop in the year before the irruption. This results in low recruitment and a low siskin population. This dynamic supports a migration pattern whereby Pine Siskins move back and forth in the coniferous forests from Alaska to Newfoundland searching for cone crops. Climate change may alter the strength, periodicity, synchrony, or orientation of irruptive patterns because of predicted changes in spring and summer temperatures.

Some studies investigated the periodicity of Pine Siskin irruptions and how synchronized they are with those of other boreal seed-eating birds. In New York, Yunick (1981) reported an almost biennial rhythm to its irruptions, but the pattern was broken in 4 of 18 years. Dawson (2020) reported that irruptions often occur in every second year, but they may also take place in consecutive years or at intervals of more than 2 years. Bock and Lepthien (1976b) reported irruptions into the southeastern states over a decade with intervals of 2 years twice and intervals of 1 and 3 years once. In the Kingston area, Weir (2008) reported major flights in 21 of 60 years or an average of approximately every 3 years. In Algonquin Park, high numbers occur every 5 or 6 years (Tozer 2012). Freedman and Riley (1980) analyzed results of Christmas Bird Counts (CBC) for 1929-77 for southern Ontario. Peak years for the Pine Siskin did not exhibit synchrony with other species, with the possible exceptions of 1955, 1969, and 1971. Bock and Lepthien (1976b) found that irruptions into the

southeastern states were highly synchronized with those of other northern seed-eating birds during 1962-72. Larson and Bock (1986) used CBC data to investigate the synchrony of irruptions of the Pine Siskin, Red-breasted Nuthatch, and Redpoll for 1901-80. The number of years of complete synchrony of the species was much higher than expected by chance from 1901 to 1920 and 1951-80; there was no evidence of synchrony from 1921 to 1950. Results indicated that the pattern and synchrony of irruptions of boreal seed-eating birds can decay and re-form over long periods.

Southward movements of the Pine Siskin occur from mid-August to November. Northward movement occurs from late February to May, but mostly in April and May. Its movements are erratic and can occur at other times as well (Dawson 2020). In irruption years, it arrives as early as September with major flights in October and November; in very heavy irruptions, it may arrive in mid-August. The northward migration is typically in March and April in New York, but may extend well into May in major flight years (Yunick 1981, 1996a, 1997).

In southern Ontario, spring migrants leave in mid- to late May (Black and Roy 2010; Curry 2006; Lancaster et al. 2004; Weir 2008). Wilson and McRae (1993) observed 1 bird at Brant on 21 August and 2 on 23 August, well north of the expected range. It was uncertain if these were autumn migrants or birds dispersing after breeding. Migrants arrive in the south predominantly in mid-October, but may occur in mid-September or even mid-August (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

In British Columbia during the nonbreeding season, the Pine Siskin occurs predominantly in coniferous and mixed forests, but also in deciduous woodlands where alder or white birch provide an abundant source of seeds. It inhabits weedy areas where seeds are abundant such as utility rights-of-way, roadsides, fields, recent clear-cuts, and other disturbed areas. It is attracted to orchards and backyards, especially those with bird feeders (Campbell et al. 2001).

The Pine Siskin is not known to exhibit any site fidelity to migratory stopover sites. In New York, Yunick (1983a) banded 2,007 migrants and 0 returned. In Virginia, Hansrote and Hansrote (1992) banded more than 1,500 siskins and had no returns.

Widespread failures of food supplies and subsequent irruptions probably decrease the survival rate of the siskin (Dawson 2020).

The abundance of the Pine Siskin within the Boreal Forest Region during migration is uncertain. Because of its nomadism, it probably varies from absent to abundant in different years at a given location. This is also the case in the portions of southern Ontario that are south of its normal wintering range.

WINTER

In non-irruption winters, the Pine Siskin mostly remains in coniferous and mixed forests in the Boreal Forest Region and the Shield portion of the Great Lakes–St. Lawrence Forest Region in Ontario. In irruption years, its winter habitat is similar to migration habitat. In winter, it commonly occurs in flocks with the American Goldfinch, Redpoll, and crossbills (Campbell et al. 2001; Dawson 2020; Palmer in Austin 1968).

The Pine Siskin defends food resources in winter, both from conspecifics and similarly sized finches. At a 0.9-m by 0.9-m platform feeder, the first arrival attempted to defend the entire feeder from other siskins. It may also defend a small area immediately around the head of a feeding Evening Grosbeak, where it feeds on crumbs of seeds that the grosbeak has broken up. The siskin is dominant to the American Goldfinch and Purple Finch, but subordinate to the larger Evening Grosbeak (Dawson 2020; Palmer in Austin 1968; Schaub 1951).

The Pine Siskin may exhibit site fidelity to an individual feeder or a general region within a winter, but rarely appears at the same location in a subsequent year. In Massachusetts, some birds remained at a feeder for approximately 2.5 months, 2 were seen at a feeder 2.4 km distant, and 1 was seen at a feeder 27 km away (Schaub 1951). In New York, 8 birds turned up at other local feeders in the same winter within 40 km of the banding site (Yunick 1981). At a Quebec site, 926 of 3,966 birds (23.3%) were recaptured in the same season and 715 of the 926 (77.2%) were recaptured where they were banded (Rivard and Bombardier in Gauthier and Aubry 1996). In Virginia, 0 of more than 1,500 birds returned in a subsequent year (Hansrote and Hansrote 1992) and 0 of 1,803 birds returned in New York (Yunick 1983a). In Oklahoma, 4 of 1,322 birds (0.3%) returned in a subsequent winter, after an interval of 4 years in 1 case (Dawson 2020).

The Pine Siskin is readily attracted to feeders in winter, especially those offering niger and sunflower seeds (Dawson 2020). Project FeederWatch data indicate that it prefers hulled sunflowers, niger seed, black oil sunflowers, and water. Infrequent choices include mixed seeds, millet, canary seed, striped sunflowers, safflower, cracked corn, milo, wheat, peanut hearts, suet, peanut butter mixes, bird puddings, and canola (Dunn and Tessaglia-Hymes 1999). In Canada and the United States, 30,574 siskin feeding bouts were documented. The most abundantly consumed seeds were 0.3-mm and 0.5-mm sunflower chips and niger seeds. It preferred tube and platform feeders over hopper feeders (Horn et al. 2014).

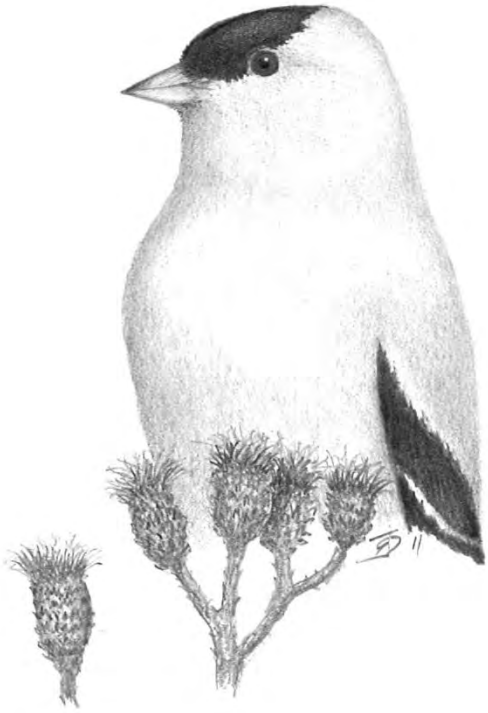
The Pine Siskin's feeding behaviour has the potential to result in extensive mortality, particularly during irruption years. It is highly susceptible to salmonellosis and may become infected at feeders. In Tennessee, several died of this disease during warm rainy days in mid-March (Rodgers 1991). During the winter of 1992-93, thousands died of salmonellosis in British Columbia, Washington, and Oregon (Campbell et al. 2001). Siskins are killed in large numbers on roads where they are attracted by salt. In British Columbia, a single passing car may kill hundreds (Campbell et al. 2001; Tozer 2012; Yunick 1997).

Severe winter weather may cause mortality. Wind, snow, and ice may curtail feeding opportunities and result in starvation (Dawson 2020).

James (1991) considered the Pine Siskin a common to locally abundant winter erratic in the south, becoming occasional north to Sioux Lookout and Cochrane. Numbers vary considerably due to its erratic nature. Freedman and Riley (1980) analyzed CBC data for southern Ontario from 1929 to 1977 and discerned no long-term trends in its overall numbers.

American Goldfinch

Spinus tristis



BREEDING SEASON

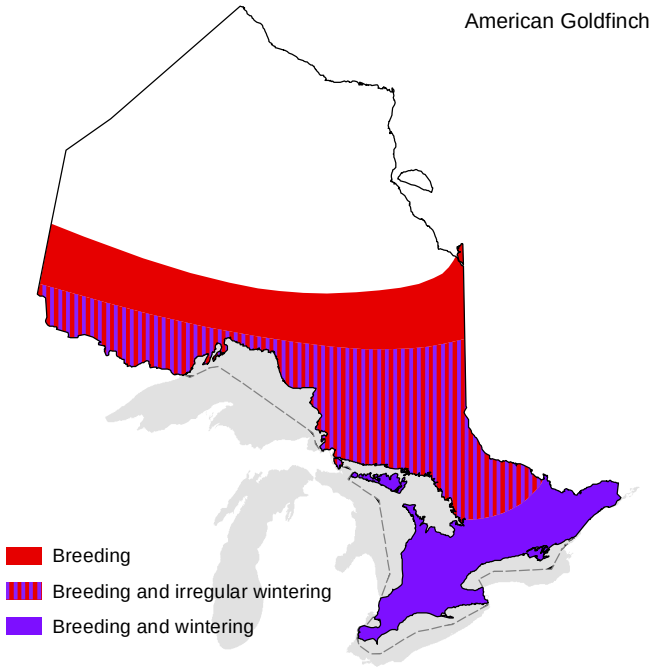
Habitat Requirements

Ontario American Goldfinch nests were in a variety of open and semiopen habitats. Most (54.1%) were in agricultural landscapes, including overgrown fields, pastures, hawthorn meadows, orchards, fencerows, and conifer plantations; 20.9% were at roadsides and shorelines of rivers, ponds, and marshes; 12.2% were in woodlands and swamps; 10.7% were along residential streets and in gardens, farmyards, and cemeteries; 1.5% were in willow swales and heath muskegs; and 0.5% were in sand-dune areas. Hawthorn meadows were the preferred habitat, with nests there very close and approximating coloniality. In woodlands, nests were either at edges or the canopy was open (Peck and James 1987).

In the Clay Belt, Welsh and Lougheed (1996) reported the American Goldfinch in a black spruce stand and a stand dominated by trembling aspen, balsam fir, and white spruce. Both stands were fairly wet and ranged from slightly below moderate to rich on the nutrient scale.

In Muskoka and Parry Sound districts, the American Goldfinch nested in bogs and open forests or clearings as well as along river edges, hydro transmission line corridors, and field edges (Mills 1981). In shelterwood cuts in white pine stands in Algonquin Park, it occurred in 14.3-20% of stands

with no recent history of harvesting, 10-18.2% of stands 10-16 years after cutting, and in 16.7% of stands 1-2 years after cutting (Kingsley and Nol 1999).



In the Great Lakes–St. Lawrence Forest Region south of the Shield, Speirs and Orenstein (1975) reported it in all 11 plots they surveyed in Durham Region. These included mature and very young pine plantations, with the latter still dominated by willow shrubs; an old orchard overgrown with hawthorns and apple trees; a bog; a coniferous swamp; and a variety of open deciduous woodlands. Highest densities occurred in shrub-dominated habitats: the very young plantation and the overgrown orchard. They considered it a species of early forest succession. In Guelph, Middleton (1979) studied it in 3 habitats. The natural habitat was 68 ha comprised of 25% old-field habitat, 50% willow scrub, and 25% maple-elm woodlot. It also nested in a 10-ha area that the university had developed as a nursery and in a 20-ha residential suburb that had been settled for approximately 20 years. The nursery appeared to be suboptimal habitat.

In Elgin County in the Carolinian Forest Region, the goldfinch nests in both rural and urban settings (Lancaster et al. 2004). In the Hamilton area, McIlwraith (1894) reported it in cultivated fields, orchards, and gardens. South of the Shield, its abundance was significantly negatively correlated with the amount of forest cover more than 100 m from edge and the amount of forest cover within 2 km. It was also negatively correlated with woodlot size and the amount of regional forest cover, but not significantly (Austen et al. 2001).

The American Goldfinch strongly favours weedy and grassy fields and floodplains with early successional growth for breeding. It may also use cultivated fields, roadsides, vineyards, orchards, and gardens. Its main food plants are in the aster family, with a preference for thistles, and it rarely nests far from them. The most common nest cover includes low shrubs, deciduous saplings, isolated mature trees, or forest edges. It avoids mature or extensive forests and prefers shrubs in early successional growth with a clear space on at least 1 side of the nest site (McGraw and Middleton 2020). Nests may be either in upland meadows or shrub thicket swamps and marshes with scattered trees and shrubs (Tyler in Austin 1968). In Quebec, it is found predominantly in southern urban and agricultural landscapes, although it also frequents regions of extensively forested habitat. It is less common in densely wooded landscapes where it is mostly restricted to clearings, burns, and clear-cuts, and along logging roads, hydro transmission line corridors, and shorelines of lakes and rivers. Near Montreal, it nests in abandoned fields and on edges of forests. It frequents mostly open areas with abundant food plants and preferably a few trees or shrubs for perching (Lepage and Limoges

in Gauthier and Aubry 1996). Falardeau et al. (1999) reported that it was absent in young, medium-aged, and old strip-cuts in Quebec, but occurred in low densities in final strip-cuts and clear-cuts. In the Prairie Provinces, it was in a guild concentrated in young aspen stands, but species in this guild also occurred in wet marshy areas and riverine mixed woods. The goldfinch occurred mostly in stands 20 years or younger on moist sites with moderate nutrient richness (Kirk et al. 1996). Flack (1976) concluded that aspen stands were not particularly suitable for it. In aspens, it preferred riparian woodlands, small groves, and edges. In northeastern poplar–white birch stands, it occurred in moderate densities in sapling- to pole-sized stands and was absent in seedling- to sapling-sized and mature stands (Back 1979). In Saskatchewan, Hartley (1994) reported the goldfinch in 6.3% of plots in planted grasslands 3-5 years old; it was absent in native grasslands and wheat fields. In British Columbia, it breeds in open riparian shrublands adjacent to weedy areas and agricultural areas that have shrubs for nesting and patches of thistles and dandelions for foraging. It prefers to breed there in weedy fields and early successional growth as well as cultivated fields, roadsides, orchards, and gardens. Thirty-one percent of nests were in natural areas and 69% were in human-influenced areas. Natural habitats included remnant stands of deciduous or coniferous trees (20% of nests), riparian habitats (6%), shrublands (3%), and grasslands (2%). Nests in human-influenced habitats were in orchards (30%), agricultural sites (25%), gardens (9% rural, 8% urban, 6% suburban), woodland edges (9%), riparian habitats (9%), and meadows (4%; Campbell et al. 2001). In the Boreal Forest Region, Erskine (1977) considered the goldfinch a species of open shrubby habitat. It also occurs in the earliest stages of succession in burns and clear-cuts. Overall, it is associated with artificial grasslands and shrublands, and often occurs at the boreal forest–prairie ecotone. In New York, it nested in purple loosestrife above water on intermittently saturated soils. Nests were in flooded freshwater marshes, patches of unmowed wet meadow, a wet meadow within a dry old field, extensive wet old fields, and a roadside wetland (Kiviat 1996). In Pennsylvania, it nested on hydro corridors through forests, but was absent in the adjacent forested habitat (Yahner et al. 2002). In Pennsylvania, it occurred in 9.1% of old-growth mixed forests compared with 94.4% of forests statewide and 92.4% in the Appalachian Plateau (Haney 1999). In Ohio, it inhabited 20 ha of wet prairie and deciduous scrub that had not been tilled for 10-20 years. The fields were grown up with thistles and other forbs and were separated by shrubby hedgerows (Holcomb 1969). In oak savannahs in Indiana, highest densities occurred where tree height was 8 m, the shortest category. Its abundance was 80% lower where tree heights were 12 m (Grundel and Pavlovic 2007a). Several studies examined goldfinch habitat use in Michigan. Stokes (1950) studied it in a mix of park and marshland 9.7 ha in area. The park consisted of lawn, shrubs, and shade trees; the remaining 6.5 ha was a peat marsh. Except for the occasional Manitoba maple and willow, the marsh was devoid of trees. Common elderberry was the most common shrub. Next in abundance were red-osier dogwood, buttonbush, and tartarian honeysuckle. Grasses and sedges covered most of the marsh, with common forbs including Joe-pye-weed, giant sunflower, goldenrods, asters, thistles, nettles, spotted jewelweed, wild cucumber, smartweeds, swamp milkweed, and dodder. Drum (1939) reported it in an open woodlot of maple and poplar with scattered pines, oaks, and white birch. The woodlot was fragmented by paths, firebreaks, and roads. Pin cherry, juneberry, and sumac were common and the ground flora was dominated by catchflies and blueberries. Nickell (1951) reported that highest concentrations of goldfinches occurred in open swamp habitats, but many nests were present in shrubs in uplands distant from wetlands. It also nested in fencerows, tree and shrub fringes along roads, abandoned

farm and pasture land, old orchards, house lots, and landscaped subdivisions. He had 3 study areas. The first was an unmowed area along a lake shore that supported thistles and other species in the aster family. The second consisted of second-growth oak-hickory forest, dense spruce-tamarack bogs, a leatherleaf bog with scattered black spruce, old pastures, old apple orchards, and open swamps of tamarack, steeplebush, buttonbush, and swamp birch. This site was marginal habitat due to the limited number of suitable nest sites and a scarcity of its preferred food plants. There were 3 habitat types at the final study area. The first included forest edges and adjacent open fields. The second consisted of shrubby fields, both close to and distant from lakes and swamps. They had scattered growths of hawthorns, gray dogwood, elms, staghorn sumac, wild plum, cherries, ninebark, tartarian honeysuckle, and blackberries. Herbaceous species present that were of most use for feeding and nesting included lesser burdock, bull thistle, Canada thistle, common dandelion, wild lettuces, common milkweed, and chicory. The third and most important habitat was a marshy area that could be either wet or dry during the breeding season. The dominant shrubs were gray dogwood, red-osier dogwood, silky dogwood, willow, elderberry, steeplebush, buttonbush, and poison sumac. Scattered trees occurred among the shrubs. Forbs present that were important for feeding and nesting included broad-leaved and narrow-leaved cattails, swamp thistle, swamp milkweed, and nodding beggarticks. Berger's (1957) Michigan study area consisted of a hawthorn meadow. Nests were also along roadsides, in shade trees in towns, and along edges of woods. On rehabilitated strip mines in Illinois, it was most abundant in early shrub habitat where the oldest trees were 10 years old, followed by late shrub habitat where the oldest trees were 37 years old. It was absent in bottomland and upland forests and in areas of bare soils (Karr 1968). Graber and Graber (1963) reported highest densities in Illinois in edge shrubs followed in order of declining abundance by orchards, ungrazed grasslands, shrub-grown areas, forests, pastures, oat fields, and marshes. It was 39 times more abundant in edge shrubs than in marshes. In Wisconsin, it was common in alder thickets (Hoffman 1989b); rare in northern mesic forests (Hoffman 1989a); present in upland forests where it preferred edges and small tracts and occasionally occurred in the canopy of stream gorges (Mossman and Hoffman 1989); was documented in 64% of floodplain forests, mostly in wet forests and shrubby edges (Mossman 1988); occurred in 18% of conifer plantations (Bielefeldt and Rosenfield 1994); and was abundant in pine and oak barrens (Mossman et al. 1991). In Arkansas, Shugart and James (1973) reported highest densities in a woody field, followed in order of declining abundance by clonal persimmon tree plots and a burned field. It was absent in a mowed hayfield, a broomsedge field, and 5 types of forest plots. It was the most abundant species in the 2 plots in the early tree stage of succession. In Missouri, it occurred in very low densities in prairie dominated by little bluestem, big bluestem, and Indian grass (Winter and Faaborg 1999). In Iowa, Benson et al. (2013) reported it in monotypic stands of reed canary grass. It was associated with densely vegetated fields that were grass-dominated with a well developed litter layer. In the same state, it nested in Conservation Reserve Program fields (Patterson and Best 1996). In Kansas, all goldfinch activities were concentrated in weedy fields (Fitch 1958). In South Dakota green ash woodlands that were narrow bands less than 30 m wide, it was significantly more abundant in late than early seral stages. Older woods had more chokecherry in the understorey than younger woods, resulting in a greater foliage density less than 2 m from the ground and less patchiness in this layer (Rumble and Gobeille 1998). In North Dakota, it occurred in moderate density in idle prairie plots that had not been grazed, burned, or mowed for 5-19 years and supported considerable shrub

cover. It was significantly more abundant in this habitat than in grazed grassland with no shrubs and homogeneous fields of alfalfa and wheat grass (Renken and Dinsmore 1987). In North Dakota, it occurred at moderate density in plots with 30-80% shrub coverage and was absent in plots with 5% shrub coverage (Arnold and Higgins 1986). In North Dakota, it was common, occurring in all forest types. Highest densities occurred in early seral stages of deciduous habitats, including juneberry thickets and willow shrub communities (Faanes and Andrew 1983). In Montana, Walcheck (1970) reported it in a 7.1-ha cottonwood forest, but it was absent in sagebrush shrublands, sagebrush grasslands, and a pine-juniper woodlot. In northeastern northern hardwoods, Noon et al. (1979) reported it in 8% of plots in mature undisturbed forests and in 13% of plots in disturbed and early successional habitat. In northeastern mixed forests, Temple et al. (1979) considered it associated with scattered stands of tall trees and shrubs. Taylor and Taylor (1979) considered it a bird of large and small openings and forest edges, but not of forests.

In North Dakota, the American Goldfinch was more abundant in landscapes with less than 30% tree cover at the 400-m scale. It responded positively to an increase in tree cover within 100 m in open landscapes, but negatively in forested landscapes (Cunningham and Johnson 2016, 2019).

In the mid-Atlantic states, the goldfinch's abundance was positively correlated with mean canopy height but negatively with the number of trees within a 0.04-ha circle, the amount of forest within 2 km, and the number of trees larger than 38 cm diameter at breast height (Robbins et al. 1989).

The American Goldfinch is not an area-sensitive species, but most study on this has been done in forests which are not preferred habitat. Johns (1993) surveyed trembling aspen groves in Saskatchewan that ranged in size from 0.04 to 36.7 ha. Its presence was unaffected by woodlot size or the degree of its isolation. Freemark and Collins (1992) and Robbins et al. (1989) concluded that it was not area sensitive in forested habitat. The goldfinch is also not area sensitive in its preferred shrubby habitats, where it may inhabit very small patches.

During the breeding season, individuals or pairs roost overnight close to the nest (McGraw and Middleton 2020). No information appears to be available on the roosting substrate.

Ontario nests were elevated, usually in living deciduous or coniferous trees and shrubs. Three nests were in herbaceous species: one each in burdock, goldenrod, and an unspecified species. Deciduous trees and shrubs (94.1% of nests, 25 species) were greatly preferred to conifers (5.9% of nests, 4 species). Nests were in hawthorns (40.8% of nests), maples (18.9%), willows (18.3%), apple (8.3%), birches (7.1%), and dogwoods (6.5%). Of 63 nests, 87.3% were in upright crotches or forks and 12.7% were on lateral branches. Nests were more often distant from the trunk than near it, at distances of 0.9-4.6 m from the trunk; most were 1.2-4 m from the trunk. More nests were reported from the tops of trees and shrubs than at the midpoint or lower. Several nests were in the same tree or shrub as in the previous year, and one was 30.5 cm above a previous year's nest. In all cases, it was unknown if the same birds were involved in the different years. Nests were 0.3-16.8 m from the ground, with most 1.2-2.4 m up (Peck and James 1987). In Guelph, Middleton (1979) described nests in 3 habitats. In the natural habitat, 37.5% of 200 nests were in shrub willows, 20.2% were in hawthorns, 13.4% were in maples, 13.0% were in juneberries, 4.3% were in trembling aspen, 2.4% were in white cedar and elderberry, 1.4% were in beech and alder, 1.0% were in yellow birch, red-

osier dogwood, and white elm, and 0.5% were in basswood and an unidentified shrub. Mean nest height was 1.8 m (range 0.6-6.1 m). In the nursery, 51.5% of 29 nests were in maples, 6.1% were in willows and beech, 3.0% were in alders, and 33.3% were in unidentified cultivars. Mean nest height was 2.5 m (range 1.7-3.7 m). In the suburban area of the city, 81.8% of 34 nests were in maples, 12.2% were in poplars, and 3.0% were in horse chestnut and ash. Mean nest height was 4.4 m (range 1.8-7.1 m). In the natural habitat, 74.1% of nests were in shrubs. A similar choice of shrubs was unavailable in the nursery and city where trees and saplings provided all nest sites. One Guelph nest was in a Japanese yew (Mariani et al. 1993). Dance (2008) reported a nest in a black alder in Oxford County.

Throughout its range, the American Goldfinch nests almost exclusively above ground. Most nests are in deciduous trees and shrubs, but it also nests in conifers and herbaceous species. It is opportunistic and nests in the most abundant tree or shrub species. Presence of suitable food plants within the home range, such as thistles and other members of the aster family, appears to be more important than nest sites. In different studies, the dominant nest species included common elderberry, red-osier dogwood, willows, wild roses, poplar saplings, hawthorn, gray dogwood, and orchard fruit trees (apple, pear, peach, plum, and cherries). Other woody species it has nested in include red oak, red pine, red cedar, tamarack, elm, swamp birch, lilac, ninebark, Manitoba maple, buttonbush, red maple, balsam poplar, bur oak, chokecherry, sugar maple, purple willow, honey locust, staghorn sumac, large-toothed aspen, white birch, silky dogwood, privet, trembling aspen, Osage orange, steeplebush, black locust, wild plum, black cherry, American bittersweet, swamp white oak, red mulberry, nannyberry, wild grape, white poplar, scotch pine, white pine, meadowsweet, sagebrush, Saskatoon, hazelnut, raspberry, white oak, crabapple, alder, cottonwood, black poplar, spruce, fir, walnut, and horse chestnut. It will apparently nest in any species of tree, shrub, or forb that provides good anchorage, proper support underneath the nest, a reasonable height, and concealment. Shrubs appear to be preferred to trees, with scattered trees in shrubby areas rarely, if ever, used. In contrast, most British Columbia nests were in trees rather than in shrubs. Nests are often in shrubs close to a tree that provides a singing perch (Berger 1948, 1968; Campbell et al. 2001; Holcomb 1969; Mousley 1930, 1932, 1935; Nickell 1951; Stokes 1950; Tyler in Austin 1968). Some nests are in herbaceous species. In Wisconsin, 5% of 230 nests were in thistles, 5% were in giant sunflowers, 2% were in asters, 1% were in Joe-pye-weed, 0.5% were in wild lettuce, and 0.5% were in goldenrods. In Ohio, 8.7% of 126 nests were in bull thistles and 1% were in goldenrods. It has nested in Canada thistle and purple loosestrife elsewhere. In Wisconsin, there was a marked increase in the use of forbs as the season progressed. Birds probably wait until forbs mature before nesting in them. Almost all nests in forbs were in rosettes where lateral buds had sprouted in response to insect damage near the top of the plant. In New York, purple loosestrife appeared to be selected as a nest substrate over apparently suitable nearby woody vegetation. Nesting in purple loosestrife allowed goldfinches to nest in marshes that would otherwise be unsuitable for nesting. An analysis of 5,991 nest-substrate records revealed that 87.5% of nests were in deciduous trees and shrubs and only 11.6% were in herbaceous species (mostly thistles). Thirty-two percent of the nest plants were wetland species, 22% were upland species, and the remainder were facultative species (Holcomb 1969; Kiviat 1996; Nice 1939a; Pierce 1922; Stokes 1950). In Michigan, Nickell (1951) described 6 types of nest placement for 147 nests that were mostly in shrubs. Type 1 nests were the

most important (81.6% of nests) and were in an upright fork with an average of 4 evenly spaced vertical branches that were used for attachment and formed a cradle-like support for the nest. Type 2 nests (6.8%) were also in an upright fork, but with all branches on 1 side, leaving the nest unsupported on the other side. Type 3 nests (3.2%) consisted of 2 parallel upright branches between which the nest was built with no support underneath. Type 4 nests (4.1%) consisted of tufts of small twigs growing in an upright position from horizontal branches; the nest was cradled within the twigs. Type 5 nests (4.1%) were saddled over and around horizontal branches and fastened to small horizontal twigs or leaves. Type 6 nests (1.4%) were wedged between horizontal forks and held in place by attaching the nesting materials to the 2 sides. The bottoms of these nests were unsupported and resembled the semipensile nests of vireos. In Wisconsin, 93% of nests in shrubs and forbs were within 60 cm of the top of the plant and 99% were within 90 cm of the top (Stokes 1950). Of British Columbia nests in trees and shrubs, 57% were in the fork of a branch and 31% were saddled on a larger branch. Seven percent were near the end of a branch and 5% were near the top of a shrub or tree (Campbell et al. 2001). Many nests in trees are distant from the trunk on limbs and the goldfinch has been documented nesting on limbs overhanging roads (Tyler in Austin 1968). A Michigan nest was on the ear of a standing corn plant. Another was in a tangle of bedstraw and a fence, with the nest attached to a vertical wire and resting on a horizontal wire. Vines such as bittersweet and grape were used as a nesting substrate only when they were climbing on more rigid plants to which the nest was attached (Nickell 1951). Nests have been reported 0-18 m above ground (Campbell et al. 2001; Tyler in Austin 1968), but these extremes are rare. Nests in herbaceous species are the lowest. Those in purple loosestrife in New York averaged 1.4 m from the ground (range 0.9-1.9 m; Kiviat 1996). In Wisconsin, Stokes (1950) reported that almost all nests in shrubs and forbs were 0.9-1.8 m from the ground; those in trees were usually 2.4-4.6 m up. In Ohio, mean nest height was 1.44 m in July (range 0.77-2.34 m), 1.37 m in August (range 0.60-2.92 m), 1.08 m in September (range 0.80-1.57 m), and 1.39 m overall (range 0.60-7.42 m). Most nests were in shrubs, but a few were in trees and forbs (Holcomb 1969). In Michigan, 71% of 583 nests were in hawthorns at an average height of 1.35 m (range 0.69-2.79 m; Berger 1968). In 3 different habitats in Michigan, nests averaged 5.7, 3.7, and 1.6 m from the ground. Highest nests were in trees along fencerows and at edges of forests. The overall average height of 211 nests was 1.86 m (Nickell 1951). In British Columbia, most nests were 1.8-4.0 m from the ground, with a range of from ground level to 12.0 m (Campbell et al. 2001). The goldfinch has been observed dismantling old Yellow Warbler and Baltimore Oriole nests and using the milkweed fibres in its own nest. Nests may rarely be used to raise a second brood but more commonly to lay a replacement clutch (McGraw and Middleton 2020).

It is most likely that the American Goldfinch defends only a small area around the nest, but there are conflicting reports in the literature. Food resources do not appear to be defended. Drum (1939) reported the most extensive territories in Michigan. Males circled the territory several times, roughly defining their boundaries. All areas defended by males contained at least a few trees and in 2 cases were more than 30 m long and 15 m wide (0.045 ha). The further the nesting area was from the feeding area and the more isolated the nesting area, the larger the territory was. One was at least 300 m long and 150 m wide (4.5 ha); the average territory size was about 0.2 ha. Males did not allow other males to land within their territories and females defended the territory from other females.

Although some of the large areas were defined as territories, it was unknown if these areas were actually defended because no other goldfinches were observed to alight in them. There was little or no defence around the nest site once the male began feeding the female at the nest. Despite the apparently large territories, nests were found as close together as 9 m. In Wisconsin, Stokes (1950) described the same circle flights by males. Males were intolerant of other males that approached their female. He used mounted goldfinches to determine the extent of territories. The greatest distance from the nest that a male defended was 27 m (0.23 ha). The territory consisted of the nest site and immediate area, but did not include sufficient food or water for the nesting pair. Some birds began defending their territory 2 weeks before nest building, but usually only 1 or 2 days earlier. Defence of the nest continued as late as the tenth day of incubation. In 4 cases, females built second nests in a new territory as far as 137 m from the first nests. These territories were vigorously fought for with the neighbouring males, suggesting that the female selects the territory. The goldfinch tends to nest in small aggregations or semicolonially, with each pair defending a small territory within the colony. At Guelph, groups of nesting goldfinches were randomly distributed in some habitats, and these same areas were used regularly from year to year. Coloniality may result from the distribution of some resource other than nest sites (McGraw and Middleton 2020; Middleton 1979). In Ohio, Nice (1939a) reported that 12 of 15 pairs nested in groups: 4 in 0.4 ha, 3 in 0.8 ha, and 5 in 0.8 ha. The grouping of nests was not dependent on nest-site availability because thistles, the nesting substrate, were abundant everywhere. Nickell (1951) saw no evidence of intraspecific aggression and found 3 nests within 0.5 ha. In Michigan, Berger (1957) reported that most nests in hawthorn meadows and swampy habitats were semicolonial, and only the immediate area around the nest appeared to be defended. The average distance between 7 nests in 1 group was 21 m and the minimum was 6.1 m. Isolated nests were more likely to occur along roadsides, in shade trees in towns, or at edges of woods. Feeding areas may be distant from the nest site, so the goldfinch may have a large breeding season home range. Nickell (1951) reported that most feeding areas were within 90 m of the nest site, but some were 180-225 m distant. Drum (1939) reported that the distance between some nest sites and feeding areas was greater than 1.6 km and Fitch (1958) reported separation distances of more than 800 m.

Natal philopatry is very low. Over a 24-year period at Guelph, only 2 nestlings returned to breed in their natal area (McGraw and Middleton 2020). In Michigan, 1 of 1,133 nestlings (0.09%) returned to nest. One nestling was recovered 2 years later in the breeding season in New York (Berger 1968).

Adult site fidelity appears to be fairly low. In Kansas, Verheijen et al. (2017) reported return rates of 6.1% for males and 7.2% for females. In Michigan, Berger (1968) banded 15 adults and the band of 1 female was found in an Eastern Screech-Owl pellet the following year. This was the only recovery, representing a 6.7% return rate. In Guelph, Middleton (1979) observed that returning females usually remained in the same habitat, particularly if they had nested successfully the previous years. A few unsuccessful females switched habitats the following year. Females were significantly more likely to remain in the same area in a subsequent year than males (81.1% compared with 25.0%). Attachment to a nesting area by a female appeared to increase with age and nesting experience. Two returning females in Wisconsin nested 45 and 13.5 m from their previous year's nest. Of 53 females that moved between nests within a breeding season, the longest move was 137 m and almost all remained in the same territory (Stokes 1950). In Michigan, 3 territories had

nearly identical boundaries in a subsequent year and nests were built in the same tree within 1 territory in 3 consecutive years. It was unknown if the same birds were involved each year (Drum 1939).

Limiting Factors

The American Goldfinch is a late breeder. Peck and James (1987) reported eggs in Ontario nests from the second week of June until the end of September, with most present from the last week of July until mid-August. Peck and James (1998b) reported that the earliest egg date in the province was 28 May, and that nests had been observed under construction on 21 and 26 May. In Algonquin Park, nests are under construction from early to late July and eggs are present from mid-July to mid-August (Tozer 2012). In Guelph, the first nests are typically found in late June or early July, with an early nest with an egg reported on 28 May. Over an 8-year period, the date of the first egg ranged from 2 to 10 July (average 6.5 July). The mean egg-laying date was 17.9 July (range 17.1-18.8 July). Old males came into breeding condition about 2 weeks before yearling males and lost their breeding condition slightly before yearlings. Females reached breeding condition in mid-July and it lasted until mid-August. Maximum ovarian development occurred in the latter half of July when all females were in breeding condition. Ovarian activity waned after that and no females had ovaries in breeding condition by September. Old birds built the earliest nests and typically laid the first eggs; yearlings built most of the late August nests. In all habitats at Guelph, most reproductive effort occurred in the last half of July with no difference in timing among habitats. The onset of egg laying was unrelated to temperature and rainfall and is probably regulated by photoperiod. Reproduction is timed to coincide with the flowering and fruiting of plants in the aster family, thereby ensuring maximum food availability (Gissing et al. 1998; Mariani et al. 1993; Middleton 1978, 1979). Similar timing of nesting has been reported in Michigan, Wisconsin, and Ohio. First nests may be 2 weeks later in New York and 2 weeks earlier in British Columbia. Because of the lateness of nesting, nestlings may be present until the end of September or very early October (Berger 1968; Campbell et al. 2001; Holcomb 1969; Nickell 1951; Stokes 1950).

The pair bond is established within prebreeding flocks during May and early June, and possibly sooner. Females select the male and therefore the territory. Brighter-coloured males are preferred because the yellow plumage and pink bill are a result of carotinoids in the diet, suggesting that they are superior at foraging. Most nests are completed in about 6 days, but extremes of 4-15 days have been reported. A longer period is taken to build the nest early in the season than later, and inexperienced birds may take longer than older birds. In Ohio, nests took an average of 8.6 days to complete in July compared with 4.1 days in August. In Wisconsin, it took an average of 13.0 days to build a nest in the first half of July, 10.8 days in the last half of July, 5.8 days in the first half of August, and 5.6 days in the last half of August. Usually some time elapses between nest completion and laying of the first egg. The interval is shorter later in the season, averaging 3.4 days in July and 1.3 days in August. In 1 case, the first egg was laid while down was still being added to the nest. Intervals as long as 27 days have been reported between nest completion and laying. Lengthy intervals were probably due to adverse weather or other unusual events. Eggs are laid at the rate of 1 a day. Incubation begins with the laying of the second or penultimate egg. Incubations periods of 8-14 days have been reported in Ontario, with most eggs hatching in 10-12 days. Elsewhere, incubation periods of 11-15 days have been reported, with most eggs hatching in 12-14 days. Eggs may hatch

either synchronously or asynchronously over a period as long as 4 days. Fledging success is higher in synchronous nests because all nestlings are fed equally. In asynchronous nests, larger nestlings receive a disproportionate amount of the food to the detriment of younger nestlings. Nestling periods of 11-17 days have been reported, with most chicks fledging when they are 13-15 days old. If undisturbed, nestlings rarely leave the nest before age 12 days (Berger 1953; Drum 1939; Holcomb 1969; McGraw and Middleton 2020; Mousley 1932, 1935; Nice 1939a; Peck and James 1987; Skagen 1987; Stokes 1950; Tyler in Austin 1968).

Due to the lateness of its breeding season and the limited time that it is physiologically capable of breeding, the American Goldfinch can raise a maximum of 2 broods a year. Most pairs raise a single brood. In Guelph, 34 of 508 nests (6.7%) were second broods. Most, if not all, were raised by older females who tended to initiate nesting earlier in the season. Their first broods usually fledged in early August, allowing sufficient time to raise a second brood before gonadal recession occurred. Guelph females must initiate their second brood by 16 August at the latest if the second brood is to be successful. Females invariably abandon their first nest before the young fledge, leaving the male to raise the first brood. Only experienced males are capable of this. Raising a second brood is highly advantageous, with those doing so raising a mean of 7.3 fledglings compared with 3.4 for older females raising a single brood and 2.8 for females of unknown age (Middleton 1979, 1988). In Wisconsin, most birds that raised their first brood before 20 August initiated a second clutch. Nine of 60 pairs (15.0%) were double brooded (Stokes 1950). If a nest is lost, a replacement clutch is laid, occasionally in the same nest. As many as 3 attempts may be made to raise a brood. At Guelph, the mean time between nest loss and laying the first egg in the replacement clutch was 6.9 days. Replacement nesting allowed 60% of birds that lost their first brood to raise a mean of 2.8 fledglings (McGraw and Middleton 2020; Middleton 1979). In Wisconsin, laying in replacement clutches started 4-21 days after nest loss, taking longer earlier in the season (Stokes 1950). In Michigan, a new nest was begun the day after the first one was damaged by a storm (Drum 1939). In Ontario, Peck and James (1987) reported clutch sizes of 2-7 eggs, but mostly 4-6 eggs with 5 eggs the most common clutch size (mean 4.89 eggs). At Guelph, clutch size was 2-7 eggs (mean 5.2 eggs); most clutches contained 5 eggs. Mean clutch size may have been somewhat inflated because parasitized nests were not included in the calculations. Mean clutch size of older females (5.3 eggs) was significantly greater than females of unknown age (5.0 eggs). The age classes of females cannot be distinguished, so the sample of unknown-age birds may have included some older females that nested in the area for the first time. Old females laid a higher proportion of 6- and 7-egg clutches than younger birds, who laid a higher proportion of 3- and 4-egg clutches. The mean clutch size of old females mated to old males was 5.6 eggs compared with 5.3 eggs for old females mated to young males. Older males may be more proficient at finding high-quality foods. Clutch size varied by habitat: 5.0 in the natural area, 5.6 in the nursery, and 5.2 in the city. Clutch size decreased significantly with the season in all habitats. The most common clutch size of 5 eggs was not the most productive, with no difference in the comparative success of 4-, 5-, and 6-egg clutches. Six eggs appeared to be the most productive clutch size, producing the greatest number of fledglings (McGraw and Middleton 2020; Middleton 1979). In Wisconsin, Stokes (1950) reported clutch sizes of 2-7 eggs (mean 5.3 eggs in July and 3.7 eggs in August). For 10 females that laid 2 clutches, mean clutch sizes were 4.8 eggs for the first clutch and 3.8 eggs for the second clutch. In Ohio, Holcomb (1969) reported clutch sizes of 3-6

eggs (mean 5.03 eggs). The clutch size of 4.0 eggs in September was significantly lower than in July (5.1 eggs) and August (5.0 eggs). Temperature did not appear to affect clutch size. In Michigan, clutch size was 2-7 eggs with a mean size of 4.89 eggs for 474 nests.

Both sexes are capable of breeding when they are 1 year old and they breed annually thereafter. Yearlings are physiologically incapable of breeding as early as older birds because their gonadal development is slower. The peak of nesting in the latter half of July is due to yearlings nesting. They may further delay nesting until large numbers of plants in the aster family are in bloom, ensuring an abundance of the most desirable nest-building materials and a later abundance of food. Yearlings raise a single brood only and produce few 6-egg clutches. This suggests that rearing young is a difficult task for them or they may be unable to find sufficient food to raise a large brood (McGraw and Middleton 2020; Middleton 1979).

The mating system is predominantly monogamous; all first nests of the season are monogamous. Some females are sequentially polyandrous when they raise a second brood. The female typically remains in the same territory for the second brood, but may switch mates. At Guelph, polyandry occurred at 25 of 508 nests (4.9%); 70.6% of females that attempted a second brood switched mates. In some cases, the polyandrous matings did not persist. The new male was displaced by the original male, who accompanied her at the second nest. Because the new male copulated with the female, some of the young in the nest were extra-pair. Polyandry is a successful strategy because it allows the female to abandon the first brood early and start a second brood. Polyandrous females produced an average of 7.4 fledglings per season, significantly more than for all other females (2.3) within the same time period. Polyandrous females select experienced males and build the first nests of the season (Middleton 1979, 1988). In Wisconsin, 1 of 3 double-brooded females appeared to be polyandrous (Stokes 1950). McGraw and Middleton (2020) concluded that as many as 15% of females were polyandrous, due in part to the male-biased sex ratio. At Guelph, 5 of 16 females (31.3%) and 1 of 8 males (12.5%) were faithful to their mate in a subsequent year (Middleton 1979). Extra-pair copulations are another mating strategy. At 15 Guelph replacement nests, the female was the genetic parent of the offspring in all cases. Ten of 70 nestlings (14.3%) in 4 of 15 broods (26.7%) had DNA profiles that were inconsistent with the attending male. Three of the 4 nests that contained extra-pair young were replacement nests; in the other nest, there was a protracted delay between nest completion and egg laying. Nest disruptions may be a factor in extra-pair paternity, which may result from nesting asynchrony and reduced mate-guarding efficiency (Gissing et al. 1998). Holcomb (1969) reported that 2 eggs were laid in an Ohio nest in 1 day. It is possible that this was a case of intraspecific parasitism.

The American Goldfinch feeds in flocks even during the breeding season, but birds may forage singly at this time. Flocks frequently feed in a rolling leap-frog fashion, especially in winter, thus exploiting food efficiently and maximizing protection from predators. It prefers to take seeds while perched on the flowering head of a plant to feeding on the ground. It hangs upside down from branches or thistle heads and strips bark from terminal shoots. It has a distensible esophagus or rudimentary crop so it can transport food to the nest or store food to meet overnight energy demands. It has been observed plucking winged elm fruits and extracting small larvae about 1 mm in length (McGraw and Middleton 2020; Tyler in Austin 1968). It needs to procure a seed on average

every 100 seconds to meets its daily energy requirements. It was most efficient at consuming the smallest seed sizes (less than 25 mg). It ate seeds ranging in size from 0.1 to 230 mg, but mostly those weighing 10-100 mg. Its low requirement for seed encounter rates and its ability to store food allow it to exploit concentrated food patches rapidly and use patchily distributed resources (Benkman and Pulliam 1988). The only apparent observation of a goldfinch eating fruit was reported by Chapman (1948). In early July in Ohio, birds commonly visited a large smooth juneberry tree heavily laden with ripe fruit. They pulled off the fruits and crushed them in their beaks, apparently eating both the seeds and pulp. Batts (1953) reported a goldfinch visiting a Yellow-bellied Sapsucker boring. It was evidently feeding on sap because it hesitated between pecks, probably waiting for more sap to flow. Prior to this, it had been feeding on the dried fruit capsules of a sweetgum. In spring, the goldfinch may pick caterpillars from their webs and it has been documented eating green algae. It regularly drinks from slow-moving streams, shallow pools, bird baths, and dew, and eats snow in winter (McGraw and Middleton 2020; Tyler in Austin 1968).

The male feeds the female while she is incubating and during the first few days of the nestling period. Older males are more proficient at this and contribute significantly to fledging success by allowing the female to maintain long unbroken periods of incubation. This is particularly important in the first few days after hatching when the male is providing all the food. The male feeds the female sticky semisolid masses of predominantly seeds by regurgitation (McGraw and Middleton 2020; Middleton 1979; Stokes 1950; Tyler in Austin 1968). The young are also fed by regurgitation and are fed the same food items that the adults eat. After the nestlings are a few days old, both adults feed them directly. If the female initiates a second brood, the male may be responsible for feeding the nestlings before they fledge and while they are dependent fledglings (Mousley 1930; Stokes 1950). In Wisconsin, only 1 of 12 nestlings' crops contained animal matter, a single caterpillar 1.9 cm long (Stokes 1950). Skagen (1987) observed adults feeding nestlings seeds of bull thistle, field thistle, Canada thistle, reed canary grass, timothy, moth mullein, and salsify as well as insect larvae and pieces of green vegetation; adults also consumed these food items. In Ohio, the nestling diet consisted of thistle seeds with a few small caterpillars and other insects (Holcomb 1969).

Adult American Goldfinches feed predominantly on seeds with a preference for species in the aster family, notably thistles and dandelions. It also eats seeds of grasses, certain trees and shrubs, buds of deciduous trees, and limited amounts of insects. It has eaten seeds of spotted Joe-pye-weed, giant sunflower, dandelions, several species of thistles (Canada, bull, nodding, and field), cutleaf coneflower (personal observation), blanketflower, sweet clover, black alder and other alders, birch, chickweed, wild lettuce, juneberry, white cedar, elm, pitch pine, catnip, burdock, sweetgum, sycamore, evening-primrose, ragweeds, asters, trumpet creeper, chicory, tulip tree, rough-stemmed goldenrod, cinquefoil, St. John's-wort, and apple. It also consumes seeds of cultivated coneflowers (personal observation). It eats buds of fruit trees, birches, and elms, and has eaten Japanese honeysuckle berries and young leaves of European mountain-ash. Insect foods include those found on oak galls growing on twigs, cankerworms, and aphids; 1 stomach contained 2,210 birch aphids. Illinois birds consumed Canada thistle bud weevils, imported long-horned weevils, and Japanese beetles. All fecal samples contained arthropod DNA (Dance 2008; Drum 1939; Fitch 1958; Garfinkle et al. 2022; Leighton et al. 2002; McGraw and Middleton 2020; Stokes 1950; Tyler in Austin 1968).

The American Goldfinch is usually an acceptor of Brown-headed Cowbird eggs, but it occasionally deserts the nest or builds another nest layer over the cowbird egg. Three-layered nests have been found, with a cowbird egg buried in each of the 2 bottom layers (Berger 1948; Rothstein 1975). At Guelph, parasitized nests had a significantly smaller clutch size (4.4 eggs) than unparasitized nests (5.2 eggs). The number of chicks that hatched and fledged was lower, but not significantly. Parasitism effectively reduced the clutch size by 1 egg, but had little influence on the subsequent success of the remaining eggs (Middleton 1977a). In the east, parasitism rates are low because there is a limited overlap in the nesting cycles of the 2 species. At Guelph, the mean laying date of the last cowbird egg was 14.1 July, approximately 8 days later than the mean laying date of the first goldfinch egg. Because of the short overlap in the breeding seasons of the 2 species, only those goldfinch nests that were initiated early were affected. Most early nests are by older females who produce the largest clutches and have higher nesting success rates, so parasitism may have a greater effect on reproductive success than previously anticipated. Yearlings, which nest later, are not affected by parasitism (Middleton 1977a, 1979). Peck and James (1998b) reported that 101 of 1,221 Ontario nests (8.3%) were parasitized. In Guelph, 47 of 802 nests (5.9%) were parasitized (Middleton 1991). Other eastern parasitism rates include 1 of 230 nests (0.4%) in Wisconsin (Stokes 1950), 1 of 102 nests (1.0%) in Ohio (Holcomb 1969), 0 of 25 nests in New York (Hahn and Hatfield 1995), 1 of 139 nests (0.7%) in Michigan (Nickell 1951), and 11 of 865 nests (1.3%) in Michigan (Berger 1968). In the east, the goldfinch has never been documented fledging a cowbird. Many cowbird eggs do not hatch. When eggs hatch, the cowbird nestling typically dies by the time it reaches 4-5 days of age, or sooner. The failure of cowbird eggs to hatch may be due to low fertility coincident with the end of its breeding season. The low fledging rate is probably due to the goldfinch's granivorous diet. Cowbird nestlings require protein to develop properly and this is mostly lacking in the food supplied by goldfinches (Mariani et al. 1993; Middleton 1977a, 1991). In British Columbia, the goldfinch begins nesting earlier than in the east, so there is much more overlap in the breeding seasons of the goldfinch and cowbird. Parasitism rates are higher there, with 32 of 140 nests (21.9%) parasitized. Two cases of goldfinches feeding cowbird fledglings were reported (Campbell et al. 2001).

It is probable that the amount of suitable breeding habitat for the American Goldfinch has declined, beginning around the 1950s. This is due to several factors including natural succession of old fields to treed habitats, establishment of plantations, fencerow removal, cleaner agricultural practices, roadside mowing, and urbanization. Older suburbs provide habitat, but many new subdivisions have high-density housing and very small lots. In Kansas, the quantity of sunflowers decreased due to natural succession and the goldfinch declined (Fitch 1958).

Some habitat loss may be offset by forest management, but only the heaviest cuts provide habitat, and this habitat is suitable for only a few years. Selective harvesting does not provide habitat for the goldfinch, but it responds positively to clear-cutting. In New York, its abundance increased 2-5 years after clear-cutting and began to decline in the sixth year (Keller et al 2003). In Pennsylvania, 1-ha squares were clear-cut in 4-ha blocks in deciduous forest. It was absent in uncut areas, uncommon when 50% of the squares were cut, and most abundant when 75% of the squares were cut; no 100% cuts were made (Yahner 1993). In Minnesota, it increased in response to timber harvesting (Hanowski et al. 2003).

The goldfinch responds positively to high-intensity burns in forested habitat. Only burns that significantly reduce canopy cover and remove most, if not all, the woody understorey are beneficial. In Georgia, it was most abundant 1-2 years after a severe burn but was still common 3-6 years postfire. In pine-oak forests in Tennessee and North Carolina, it occurred more frequently after a burn only if it was of high intensity. It declined again 25 years after fire (Klaus et al. 2010; Rose and Simons 2016).

Weather may affect nesting success. In Guelph, the year of lowest nesting and fledging success was the coldest and wettest of the study period (Middleton 1979). In Wisconsin, nestlings exposed to cold rainy weather for at least 2 days of their first week grew significantly slower than those not experiencing those conditions (Skagen 1987). In Wisconsin, most mortality was from storms, especially in nests in elderberries. Elderberry branches open up with the weight of the fruit, and this exposes nests to the wind. Fully completed nests are sometimes deserted if rainfall prohibits egg laying for several days (Holcomb 1969). The nest is so tightly woven that it holds water and nestlings sometimes drown after a heavy rainfall (Tyler in Austin 1968).

The goldfinch is susceptible to endocrine-disrupting herbicides and insecticides. Linuran, a broad-leaf herbicide, delays moult and lowers hemocrit levels. Dimethoate, an agricultural organophosphate, reduces daily activity levels (McGraw and Middleton 2020).

The goldfinch is highly tolerant of human disturbance (Middleton 1979; Tyler in Austin 1968). In North Carolina, abundance of the goldfinch within forested habitats was positively correlated with the number of buildings within 200 m (Lumpkin and Pearson 2013). In Illinois, Peak (2003) experimentally clipped all woody vegetation within 1 m of nests. The amount of concealment around nests did not appear to affect predation rates and no nests were abandoned due to disturbance. In Niagara Region, a pipeline was constructed through a shrubby field and 3 goldfinch nests were found on the right-of-way. A 5-m buffer was established around each nest and all other vegetation was removed using heavy equipment. All nests successfully fledged young despite the major disturbance (personal observation).

In Delaware, Tymkiw et al. (2013) reported no difference in goldfinch abundance in areas where white-tailed deer density was low, medium, or high.

In Minnesota, Hanowski et al. (1997) studied the effects of mosquito control in wetlands on the American Goldfinch. They applied Bti and methoprene and found that there were no significant differences in its abundance in control wetlands and wetlands treated with either method.

Status

Prior to European settlement, the range of the American Goldfinch was probably much more restricted than it is now, and it was probably considerably less common. It benefitted from forest clearing and the small agricultural fields surrounded by hedgerows that characterized early agriculture. Prior to settlement, it was probably confined to openings such as prairies, wetlands, and burns. Settlers introduced several nonnative species to the province, such as thistles and dandelions that are important sources of food and nesting material (McGraw and Middleton 2020; Nickell 1951; Stokes 1950). These species grow in the open, disturbed, early successional areas that the goldfinch prefers.

McIlwraith (1894) reported that the American Goldfinch nested throughout the south. In Elgin County, it was a fairly common resident in 1891 and was common in 1954 and 2000 (Lancaster et al. 2004). It was common in the Kingston area in 1864 (Weir 2008). Baillie and Harrington (1937) reported that it was a common summer resident in Ontario north to the transcontinental railway west to Thunder Bay, and that it probably nested throughout this area. The first atlas demonstrated that the goldfinch nested from the Red Lake area east to south of Moosonee, but was absent in the northwest portion of the Boreal Forest Region and the Hudson Bay Lowland. It was most abundant south of the Canadian Shield and less abundant in more northerly forested landscapes. It was absent from the northern portion of Algonquin Park and certain islands in Georgian Bay. These areas are characterized by dense forest cover, bedrock outcrops, and an absence of suitable food plants (Middleton in Cadman et al. 1987). James (1991) considered the goldfinch common north to Sioux Lookout and Cochrane, occasional and rare to James Bay, and a vagrant at Attawapiskat.

The second atlas revealed that there had been no substantial change in the goldfinch's range since the first atlas. It extended its range somewhat northward in the east to include Moosonee in the southern extreme of the Hudson Bay Lowland. Overall, there was a slight but nonsignificant increase in its probability of observation, but there was a significant increase in the Boreal Forest Region. This may have been a result of increased forestry activities. It was most abundant in the Great Lakes–St. Lawrence Forest Region south of the Shield, except in heavily forested areas such as the Bruce Peninsula. Areas of high density also occurred in the Carolinian Forest Region, notably along the south shore of Lake Huron and in Hamilton, Haldimand County, and most of Niagara Region. There is limited remaining shrubby habitat in the intensively farmed areas of the extreme southwest (Leckie and Cadman in Cadman et al. 2007).

Breeding Bird Survey (BBS) data for 1966-2017 indicated a nonsignificant decrease of 0.17% per annum rangewide and a decrease of 0.67% per year in Canada (McGraw and Middleton 2020). For 1970-2021, it decreased at annual rates of 0.771% in Canada and 1.06% in Ontario. For 2011-21, it decreased at annual rates of 1.47% in Canada and 2.8% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Older nestlings are capable of flying 30-45 m as soon as they leave the nest. Young birds fledge after a shorter time in the nest and may simply flutter to the ground below or near the nest. Once the fledglings are accomplished fliers, they follow their parents in a group and family groups range over a wide area. Fledglings begin to feed themselves once they have been out the nest for a week, but are dependent on the adults for about 3 weeks. Once juveniles are independent, they gather in flocks, often with adults. The flocks gradually increase in size and may number in the hundreds in late September and early October (Berger 1968; Drum 1939; McGraw and Middleton 2020; Mousley 1930; Tyler in Austin 1968).

During the postbreeding period, the goldfinch prefers the same types of weedy and shrubby habitats, and they must contain adequate food supplies in the form of seeds from plants in the aster family. Patches of thistles and other food plants attract flocks of goldfinches. Several studies netted goldfinches in young clear-cuts during the postfledging period. In Missouri clear-cuts in oak-hickory-pine forests, it was captured 2-4 years after harvest but not 5-15 years postharvest. In Michigan, it

was significantly more abundant in mature riparian than upland trembling aspen stands. Riparian stands also contained a shrubby layer of alder and honeysuckle that was absent in upland stands (Akresh et al. 2001; Marshall et al. 2003; Porneluzi et al. 2014; Streby et al. 2011b).

MIGRATION

Although the American Goldfinch occurs in Ontario year-round, it is a regular migrant. Banding at Guelph indicated that the breeding population leaves in winter and is replaced by a distinct wintering population. Birds may not migrate until their second winter, but some yearling males have been documented migrating to the southeastern United States. Females winter further south than males and young males winter further north than old males. Migration is presumed to be strictly diurnal. A high proportion of Ontario birds remain in the province for the winter. Others move to the states just south of the Great Lakes and east to the Atlantic coast. Birds banded in Ontario have wintered in most states east of Texas south to the Gulf of Mexico. Some travelled in excess of 1,600 km (Brewer et al. 2018; McGraw and Middleton 2020; Middleton 1978).

Males arrive earlier in spring than females. In Massachusetts, males arrived an average of 3.6 days earlier than females. This may be because males winter further north. Over a 33-year period, neither sex arrived earlier in response to climate change; the interval between the arrival of the sexes did not change (Bauböck et al. 2012). Spring migration may occur from mid-April to June throughout the goldfinch's range (McGraw and Middleton 2020). Birds start to return to the Guelph area in late May (Middleton 1979). At Prince Edward Point, migrants arrive during April and May (Weir 2008). Migrants arrive in Algonquin Park in early to mid-May (Tozer 2012). Autumn migration may extend from late October to mid-December rangewide (McGraw and Middleton 2020), and this is the case in Guelph (Middleton 1978). Most migration in Ontario is in September and October (Mills 1981; Tozer 2012; Weir 2008). There is a noticeable autumn migration along the Lake Erie shoreline in Elgin County when hundreds may be seen daily, especially in late September and early October (Lancaster et al. 2004).

During migration, the American Goldfinch occurs predominantly in open weedy areas that have ample food for large foraging flocks. It may also inhabit small isolated woodlots (McGraw and Middleton 2020; Tyler in Austin 1968). It is most common in farmlands and open fields where there are large patches of food plants. Hydro transmission line corridors, city parks, rural and suburban residential lots, orchards, and nurseries may be frequented (Campbell et al. 2001).

Shrubby areas are selected over treed areas during migration. In Pennsylvania, numbers of spring migrants declined when the viburnum leaf beetle killed most southern arrowwoods and decreased shrub coverage (Smith and Hatch 2017). During autumn migration in New York, mature shrublands were used more than early successional forests (Mudrzynski and Norment 2013). During spring migration in Pennsylvania, significantly more goldfinches were observed on transects and captured in mist nests in shrubs than in forests (Smith and Hatch 2008). During spring migration in Wisconsin and Minnesota, it was significantly more abundant in upland than floodplain forests. Upland forests were often small and dominated by oaks, sugar maple, beech, red cedar, and white pine plantings. Floodplain forests were dominated by silver maple, green ash, white elm, cottonwood, black willow, and Manitoba maple. Kirsch et al. (2013) considered the goldfinch an upland species during spring migration.

During migration, conifers are important for nocturnal roosting by the goldfinch (McGraw and Middleton 2020).

James (1991) considered the goldfinch a common to locally abundant migrant. It is more conspicuous as a migrant in autumn and juveniles are also present at this time, so counts tend to be higher in autumn.

WINTER

Root (1988) concluded that the winter distribution of the American Goldfinch was associated with climate. In the west, it is absent where the average January minimum temperature drops below −12°C. East of the Mississippi River, it appears to survive in areas where the average January temperature drops as low as −15°C. Vegetation and precipitation do not appear to strongly influence its range but may affect local abundance. In the west, all abundance peaks are associated with ecotones between forest and grassland or shrubsteppe. Where it winters in large numbers is strongly influenced by the distribution of feeders. McGraw and Middleton (2020) reported that there had been no major change in its range over time, but more birds overwintered in the north due to feeders.

Winter habitat is more variable than during the breeding season and migration, depending upon whether birds migrate. In the north, it remains in typical habitat until natural food supplies are depleted or covered with snow. Flocks then either move to sites with feeders or wander nomadically to access areas with less rigorous climate or snow cover. Flocks often mingle with Black-capped Chickadees, Pine Siskins, Redpolls, and American Tree Sparrows. Rural and suburban woodlots and riparian woodlands may be frequented, particularly if they have heavy seed crops of birch or alder. In Illinois in 1906-07, highest densities occurred in forests, followed by shrubs of all types, pasturelands, fallow fields, ungrazed grasslands, and cornstalk habitat (Campbell et al. 2001; Graber and Graber 1963; McGraw and Middleton 2020; Tyler in Austin 1968). Smith (2003) summarized the results of Winter Bird-Population Studies for 52 sites in southern Ontario. Densities per km^2 were 0 in row crops and treeless pastures, 9.1 in mixed rural areas, 23 in natural forests in urban settings, 27.3 in urban natural areas larger than 10 ha, 52.3 in urban natural areas smaller than 10 ha, 7.2 in urban areas with open water, and 2.5 in cities. In Arkansas, Kentucky, and Mississippi, it was significantly more abundant in row-crop fields that had a buffer of warm-season grasses and forbs than in fields without buffers. It was more abundant in fields with buffers wider than 23 m than those with narrower buffers, but not significantly (Evans et al. 2015).

Where winters are severe, the goldfinch usually roosts in conifers. In Guelph, it appeared to roost in dense stands of white cedar along river valleys. There is 1 record of a goldfinch roosting in a hole about 30 cm deep under the snow where there was access under a stump (McGraw and Middleton 2020; Prescott et al. 1989; Tyler in Austin 1968).

Some birds exhibit site fidelity between winters but others spend subsequent winters in disparate locations. Of 14 birds banded in Ontario in winter and encountered in another winter, 9 spent both winters in Ontario. The other 5 spent winters in Maryland, New York, Pennsylvania, Kentucky, and Alabama (Brewer et al. 2018). Within winters, the goldfinch may be nomadic, travelling regionally or locally among food sources. One banded in Guelph in January was retrapped in April of the same year 24 km distant in Cambridge. Another Guelph bird banded in December

was captured the following February 50 km distant in Toronto. Much daytime movement occurs between feeders with direct-distance movements of 7 km between feeders common (McGraw and Middleton 2020).

In winter, the goldfinch prefers to forage in sheltered areas or at feeders (McGraw and Middleton 2020; McIlwraith 1894). McIlwraith (1894) reported it feeding on hemlock seeds, the only apparent record of it feeding on this species. In Algonquin Park, it fed on seeds of white birch, grey alder, balsam fir, and a variety of herbaceous species (Tozer 2012). At a Guelph feeder, juvenile males and females arrived earlier in the morning. They may be less capable of overnight fasting than adult males. During snowy weather, the number of adults visiting the feeder was the same as on days when it was not snowing, but fewer juvenile males visited during snowstorms. This suggested that they were less likely to use suburban feeders at this time or that they are excluded from doing so by the dominant adult males (Prescott et al. 1989). In Pennsylvania, Nastase and Linville (1995) provided feeders at heights of 0, 2, 4, and 6 m. Striped sunflowers, niger seed, cracked corn, white millet, and canary seed were provided at each level. Foraging occurred 8.6% of the time on the ground, 52.6% at 2 m, 17.9% at 4 m, and 20.9% at 6 m. Seeds consumed included 17.7% niger, 0.3% canary seed, 1.4% millet, 1.7% corn, and 78.9% sunflowers. At a feeder in Wisconsin, goldfinches pecked at niger seeds and swallowed them, taking 0.1 second or less. It usually took more than 0.4 second to manipulate a sunflower seed, find the crack in the husk, and break it open (Popp 1988b).

In Canada and the United States, 187,892 American Goldfinch feeding observations were documented. It preferred niger seeds but commonly ate sunflower chips. Sixty-four percent of birds ate black oil sunflowers, 23% ate cracked corn, 71% ate 0.3-mm sunflower chips, 73% ate 0.5-mm sunflower chips, 85% ate niger seeds, 23% ate red milo, 26% ate safflower, 26% ate white proso millet, and 22% ate whole peanuts. It was more likely to select seeds with a greater bill to seed volume ratio, without hulls, and greater levels of protein. It was most abundant at tube feeders (Horn et al. 2014; Johansen et al. 2014). Project FeederWatch data indicate that the goldfinch visits feeders in all habitats, but flock sizes are almost 2 times as large at rural than urban feeders. Flock sizes increase in cold weather. Favourite foods include niger seed, canary seed, black oil and hulled sunflowers, and water. Less frequently, it eats mixed seeds, millet, striped sunflowers, safflower, cracked corn, milo, wheat, peanut hearts and peanuts in the shell, canola, peanut butter mixes, bird puddings, baked goods, sugar water, and popped corn (Dunn and Tessaglia-Hymes 1999). In Saskatchewan, niger and canola seeds were preferred at feeders (Leighton et al. 2002).

During a single-day severe winter storm in Guelph that included heavy rain, snow, and wind, goldfinches could not land on the feeder because of the strong winds and were restricted to gleaning seeds below it. They significantly increased their body weight before and during the storm. They may have been able to use the change in barometric pressure, wind speed, and wind chill as indicators of weather deterioration. They responded by rapidly increasing their body reserves. There was no evidence of mortality or a decrease in numbers (Middleton 1982). In Illinois, Graber and Graber (1979) monitored goldfinch populations after an extended period of heavy snow and extremely cold weather. It increased by 66% in bottomland forests after the storm and was found in low density (1 per km^2) in upland forests after the storm; it had been absent in them prior to the storm. It was not detected in urban residential areas before or after the storm. There was no

indication that mortality had occurred, and birds may have moved from habitats they did not survey to forested areas. Dunn and Tessaglia-Hymes (1999) concluded that the goldfinch was not particularly well adapted to extreme weather conditions. It relies more heavily on filling its crop each evening than it does on accumulated fat reserves. When severe snow or ice storms make food inaccessible, it can starve.

The goldfinch is vulnerable to contracting mycoplasmal conjunctivitis, especially from feeding at feeders (McGraw and Middleton 2020). This disease affects the eyes and eventually causes blindness. Birds typically succumb to the disease either from being unable to find food or to being preyed upon.

James (1991) considered the American Goldfinch a common winter resident in the south, north to Georgian Bay and Ottawa, and occasional north to Kenora and Cochrane. Mills (1981) reported that at least some remain in Parry Sound and Muskoka districts each year. It is absent some years in winter in Algonquin Park but is usually present in years when numbers of other finches are high due to plentiful conifer seeds (Tozer 2012).

Freedman and Riley (1980) analyzed Christmas Bird Count (CBC) data for southern Ontario for 1929-77. There was a large overall increase in the wintering population of the American Goldfinch over this period. At Guelph, it regularly overwinters in large numbers now, whereas wintering in the province was not common even by the mid-20th century. CBCs for southern Ontario indicated a significant increase in southern Ontario 1915-75 from 0.12 per party-hour to 1.76 per party-hour in 1966-78. There were significant negative correlations between populations and temperatures and snowfall. From 1969 to 1973, sales of bird seeds by 3 companies increased by 50% wholesale and 131% retail. Probably winter was formerly a period of large mortality in southern Ontario, but there is now no apparent increase in mortality due to snow or ice storms or low temperatures. In the early part of the period, it probably responded to reduced snowfall by greater numbers attempting to overwinter. Winter feeding is probably the reason for its increase and successful overwintering in the province (Middleton 1977b). Following the steady increase on Ontario CBCs from the 1920s to the mid-1970s, there was little change in the winter population 1968-91 (McGraw and Middleton 2020). CBC data for Ontario for 1970-2021 indicate that it increased at an annual rate of 4.9% but it decreased at an annual rate of 3.73% 2009-21 (National Audubon Society 2022).

Lapland Longspur

Calcarius lapponicus

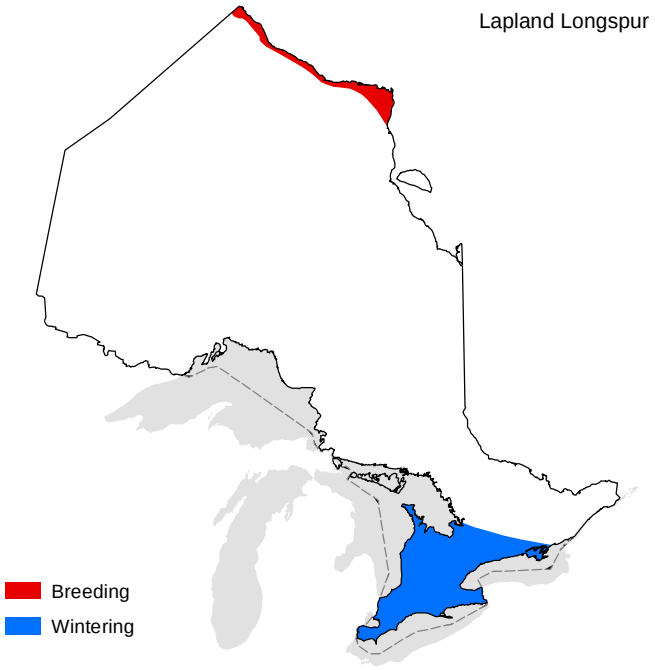
BREEDING SEASON

Habitat Requirements

In Ontario, the Lapland Longspur breeds on open, treeless tundra, usually in dry areas covered with a heath-lichen community, moss, grass, and the occasional arctic willow. One nest was in wet, graminoid tundra (Peck and James 1987).

Typical breeding habitat in Ontario, where it is confined to the strip of tundra along the Hudson Bay coast, is wet, hummocky graminoid tundra interspersed with low, sparsely vegetated gravel beach ridges. Hummocky meadows with good growth of mosses, grasses, sedges, and dwarf shrubs are favoured. It also nests on relict marine beaches with sparse vegetation and exposed gravel and cobblestones that intersect lower-lying, well-vegetated meadows (Hussell in Cadman et al. 2007).

Ontario represents the extreme southern extent of the Lapland Longspur's breeding range in North America. On the continent, it occurs in low-lying tundra and alpine meadows and is predominantly restricted to tundra and grass or sedge meadows in the High Arctic. It is a characteristic bird of tundra and in the far north it is often the most abundant species and only passerine present. Near Churchill, it commonly breeds in wet tundra, thickly vegetated uplands,



sedge margins along streams and ponds, and hummocks and sedges in marshes. Where it coexists with the Smith's Longspur, the Lapland Longspur prefers wetter, more hummocky habitats. Near Churchill, 38% of nests were in graminoid dwarf shrub tundra consisting of 75-100% cover by graminoids and moss, with herbaceous plants and dwarf shrubs on the occasional drier earthen hummocks; 28.6% were in mesic to hydric graminoid tundra with nearly contiguous graminoid cover and occasional dwarf shrubs that were mostly willows; 28.6% were in hummocky tundra that consisted of mounds and ridges supporting herbs, mosses, dwarf shrubs, and some graminoids in lower areas; and 4.8% were in dwarf shrub-lichen barrens that were windblown sites at higher elevations, such as beach ridges, with 25-50% vegetation coverage. No nests were found in wet sedge meadows with nearly continuous sedge cover and often shallow surface water, or in dwarf shrub tundra on moist but well-drained slopes with 50-75% coverage by dwarf shrubs (Boal and Anderson 2005; Jehl and Smith 1970). In Quebec, it nests in open tundra habitat where it uses rocks or shrubs for singing posts (Lanore and Doyon in Gauthier and Aubry 1996). In the Yukon, it nests in open, upland tussock tundra. These habitats range from dry tundra of mountain avens–horsetail terraces to complex wet tundra including both low-centred and high-centred polygons (Sinclair et al. 2003). In Alaska, it exhibited a modest selection for areas of dry and mesic habitat rather than wet habitat. Nesting density was highest on raised ridges or other areas of well-drained tundra. Wet meadows were not used unless they contained more elevated areas such as hummocks or ridges where nests could be placed. Very dry communities such as mountain avens and lichen-clad fell-fields of hills and mountains were avoided. In Alaska, it is most numerous in cottongrass tussocks, meadow-like tundra dominated by sedges, ankle-high areas of willows, and expanses of dwarf birch intermixed with various species of heaths. Areas that are moist support higher densities than areas with standing water. Highest densities are in low-lying flat meadows with dense stands of sedges mixed with herbaceous plants. Moderate densities occur in upland communities dominated by crowberry and lichens, with sedges, grasses, mosses, and shrubby species such as mountain cranberry. Mesic habitats are preferred in Alaska and throughout. Small territories contained significantly less dry and especially wet habitats, and a much larger proportion of mesic habitats. Large territories contained about equal amounts of wet, mesic, and dry habitats; the actual amount of mesic habitat was greater in small territories on average. The main mesic habitats used were gently sloping meadows of water sedge, arctic spear grass, and willows. Low, tidal salt marshes where Savannah Sparrows bred were avoided (Custer and Pitelka 1977; Hussell and Montgomerie 2020; Seastedt and MacLean 1979; Tryon and MacLean 1980; Williamson in Bent 1968). Alpine habitat used in Alaska included rounded

mountains covered with low and dwarf shrubs; wet sedge-graminoid meadows, often with tussocks on wetter substrates; and steep mountain peaks with patches of herbaceous plants or dwarf shrubs among considerable rock rubble and exposed bedrock (Handel et al. 2009). On Melville Peninsula, the northeastern tip of continental Nunavut, nests were mainly in dry mountain avens but occasionally on hummocks in wetter areas (Montgomerie et al. 1983).

Several studies were completed on the Lapland Longspur on Canada's arctic islands (Bylot, Baffin, Banks, Devon, Ellesmere, and Victoria islands). Tundra and graminoid meadows are mostly used for nesting in the High Arctic. It inhabits both extensive level meadows and sloping meadows. Sloping meadows may be only a few metres wide and often border tiny snow-fed streams. When slopes are used for nesting, it usually selects those facing south or east. Flat tundra areas that are inhabited are occasionally associated with shorelines of lakes. Areas that are too well drained, too gravelly, or too bare are not used. Prime habitat is wide, moist tundra intersected by ponds and streams and studded with grassy hummocks. On Banks Island, it was most abundant in hummocky tundra and graminoid–dwarf shrub tundra and least abundant on or adjacent to water bodies, in sparsely vegetated areas with less than 10% cover by vascular plants, and in dwarf shrub–lichen barrens (Drury 1961; Henry and Mico 2002; Hussell and Montgomerie 2020; Parmelee and MacDonald 1960; Parmelee et al. 1967; Soper 1946; Sutton and Parmelee 1955; Wynne-Edwards 1952). The Lapland Longspur also commonly nests in disturbed and settled areas close to roads and buildings (Höhn 1968; Parmelee et al. 1967).

During the nesting period, females roost at the nest. Males roost on their song perches or among hummocks. In the northern portion of the range, there may be almost continuous sunlight so birds may be active for as long as 20.5 hours per day. During cold weather, several pairs may roost together in grass tussocks (Hussell and Montgomerie 2020). On Victoria Island, birds often roosted in grassy, wet tundra areas during the postbreeding period rather than the barren tundra that was used earlier in the season (Parmelee et al. 1967).

Ontario nests were depressions in lichen, moss, and sedge hummocks, and one was near a clump of arctic willow (Peck and James 1987). The first nest found in Ontario, at Cape Henrietta Maria, was sunk in moss in a clump of arctic willow (Baillie 1962).

Nests are invariably in a depression in the ground. On Devon Island, nests were in fairly exposed sites on open ground. In other areas, most nests are well concealed and partially covered by sedges, grasses, small shrubs, or herbaceous material. Most nests are built into the sides of a bank or tussocks of sedges, often cottongrass, but they may also be in clumps of sedges, grasses, or Labrador tea. Almost all nests at Churchill were on the side or top of a pressure ridge (38.1%) or mound (57.1%). Nests averaged about midway (55.1%) up these features. The slope at nests was 30.1%, significantly greater than random (17.0%). Vegetation within of 400 cm^2 of the nest averaged 21.8% willow, 18.9% sedges (mostly water sedge), 10.3% moss, 12.8% litter, 10.6% Lapland rosebay, 7.6% dwarf birch, and 7.3% bog rosemary. Species occurring around nests in low frequency were 2.1% bearberry, 2.0% crowberry, 1.4% mountain cranberry, 2.4% Labrador tea, 0.3% mountain avens, and 0.2% cloudberry. Selected sites had comparatively greater amounts of willow, dwarf birch, and Lapland rosebay and lesser amounts of moss; graminoids were used in proportion to their availability. Nests were well concealed by vegetation, with average coverage of 67.0%. Nest concealment was negatively

associated with the amount of sedges at the nest. In the Northwest Territories, areas near nests had higher coverage of graminoids, shrubs, and forbs than random points, but lower coverage of lichens and mosses. Nests have a distinct entrance that faces away from the prevailing winds. At Churchill, nests had a predominantly southwestern orientation: 48% had a southwest orientation and 33% were oriented south. Further north, nests typically face south. Nesting in the side of hummocks or between hummocks provides shelter from wind that is often accompanied by near-freezing temperatures and rain and snow. On Banks Island, when the wind speed was 15 km per hour, the wind at the bottom of microdepressions was only 5% of what it was 1.5 m above ground and 10% of the wind speed at ground level. In depressions with overhanging vegetation, the wind velocity in the depression was 0.1% of what it was 1.5 m above ground. In Alaska, nests in burned and unburned tundra were placed similarly against or in edges of sedge tussocks. Monocots covered 45.0% of the area 15 cm around the nest in burned areas and 48.1% in unburned areas; these were mostly cottongrass and other sedges. Nests in burned areas were more exposed due to scarcity of shrubs (3% each of deciduous and evergreen shrubs within 15 cm of the nest). Nests in unburned areas had 28.1% coverage by deciduous shrubs (birch and blueberry) and 15.0% coverage by evergreen shrubs (blueberry and Labrador tea). In the arctic, nests may be in drier situations where they are typically more exposed. Near settlements, nests are often on roadsides. An unusual nest on Victoria Island was beneath a tilted, flat rock on a dry slope. Nests and nest depressions may be used in subsequent years, but the frequency of this is uncertain (Beyersbergen 1978; Boal and Anderson 2005; Drury 1961; Grinnell 1944; Henry and Mico 2002; Höhn 1968; Hussell 1972; Hussell and Holroyd 1974; Hussell and Montgomerie 2020; Jehl 2004; Male and Nol 2005; Parmelee et al. 1967; Sinclair et al. 2003; Soper 1946; Williamson in Austin 1968; Wright 1981).

Males establish territories shortly after arrival on the breeding grounds. In the event of a severe snowstorm early in the breeding season, territoriality may temporarily cease and birds may band together in flocks. Territorial defence may be intense and hostile, or almost nonexistent if territories are widely spaced. Some territories have undisputed boundaries along large snow patches that were present when territories were established. The Lapland Longspur does not use all available habitat and many territories do not have a contiguous territory. This is due, in part, because territories are established in snowfree areas so that areas that were initially snow covered are unoccupied. On Bylot Island, singing males appeared to attract other males so that territories were congregated in a small portion of the available habitat. Territoriality becomes much reduced when incubation commences and is essentially absent by the time there are young in the nest. The area that is defended varies greatly from area to area, probably due to differences in the quality of habitat and its abundance. On Bylot Island, there were 10 nests and territories in an area of 1.6 ha. Many territories were 0.2 ha or less; 1 territory was 0.08 ha. At Clyde Inlet on Bylot Island, territories were 2.0-6.1 ha. One Alaskan pair had a territory of 3.38 ha; territories of another 20 males in Alaska ranged from 1.09 to 2.83 ha. In some cases, the female built the nest outside the male's defended area, so the defended area was expanded to include the nest. Because of the variable territory sizes, distances between active nests are highly variable. On Bylot Island, nests in an area with small territory sizes were 91-155 m apart; they averaged 229 m apart at Clyde Inlet. Near Baker Lake, Nunavut, mean territory sizes were 0.40-0.54 ha. The closest distance between nests at Churchill was 183 m in 1 study but 2 nests in another study were only 39.5 m apart. The mean distance between 3 nests in

Alaska was 180 m. Territoriality spaces out birds and minimizes, but does not eliminate, direct competition for food in the first half of the breeding cycle. It also contributes to spacing of nests which provides exclusive use of resources immediately around the nest during the nestling period (Boal and Anderson 2005; Drury 1961; Grinnell 1944; Holmes et al. 2024; Hussell 1972; Seastedt and MacLean 1979; Tryon and MacLean 1980; Wynne-Edwards 1952).

The home range of the Lapland Longspur is larger than its territory. Both sexes forage outside the defended area. One Alaskan pair had a territory of 3.38 ha, a foraging area of 3.74 ha for the female and a foraging area of 8.21 ha for the male. Sixty-five percent of foraging by the male and 83% of foraging by the female occurred within the territory. The area used for foraging was smallest during the prenesting and nestling periods and increased in the fledgling period. During the early stages of nesting through incubation, the peak of adult activity occurred in the area between adjacent nests. Usage became concentrated around the nest in the nestling period but the total area used did not decrease. On Melville Peninsula, adults flew as far as 140 m to collect food for nestlings. Males continue to display after females begin incubation and often fly from their territories to pursue unattached females or females with incomplete clutches. Males have been seen as far as 6 km from their territory during this period (Hussell and Montgomerie 2020; McLaughlin and Montgomerie 1990; Seastedt and MacLean 1979).

Natal philopatry is very low and few, if any, birds return to their natal area to breed. Of banded young, 0 of 56 on Devon Island and 0 of 129 on Melville Peninsula returned. Ten of 382 (2.6%) nestlings returned in Alaska but none were confirmed as breeders. A nestling banded in Alaska was found breeding 6 years later 9.3 km from its natal site. Seven juveniles banded at McConnell River, Nunavut, were recaptured there the next year (Custer and Pitelka 1977; Hussell and Holroyd 1974; Hussell and Montgomerie 2020; McLaughlin and Montgomerie 1985).

When mortality rates are taken into account, adult site fidelity appears to be high. On Melville Peninsula, 47 of 86 adults (54.7%) returned. On Devon Island, only 3 of 22 (13.6%) returned. This may have been in response to high nest predation in marginal habitat near the northern extent of its range (Hussell and Holroyd 1974; Hussell and Montgomerie 2020). An adult banded in 1936 near Churchill was recaptured annually through 1939 (Jehl 2004). In Alaska, 11.6% of males and 23.5% of females returned to breed and 1 male and 1 female returned for all 6 years of the study (Custer and Pitelka 1977).

Limiting Factors

Eggs have been reported in Ontario nests from mid-June until the third week of July (Peck and James 1987). Within populations, nesting is highly synchronized and hatching of young usually coincides with peak emergence of insects. Timing of nest initiation varies annually depending upon snow cover. There is no evidence that timing varies by latitude. In Alaska, the nest-building period may span 17-18 days, but nests can be built within 3 days. Egg laying usually starts as soon as the lining in the nest is adequate, but 2-3 days may elapse before the first egg is laid. Eggs are laid at the rate of 1 a day but a day may rarely be missed. Incubation may begin with the laying of the first egg, but more often with laying of the third egg or later eggs. The incubation period at 1 Ontario nest was 11 days. The overall range of incubation periods for the last egg is 10.5-13 days. Hatching is asynchronous and may occur over 1-4 days. Mean hatching intervals were 27.0 hours at Churchill,

more than 38.8 hours on Devon Island, and 40.8 hours in Alaska. The overall hatching period ranges from 18.5 to 64.0 hours and is dependent upon clutch size but not latitude. Young leave the nest asynchronously over the same period that hatching takes. The nestling period ranges from 6-12 days, but is mostly 8-11 days with shorter periods due to disturbance (Custer and Pitelka 1977; Drury 1961; Grinnell 1944; Hussell 1972; Hussell and Montgomerie 2020; McLaughlin and Montgomerie 1985, 1989a, 1989b; Parmelee et al. 1967; Peck and James 1987; Soper 1946; Sutton and Parmelee 1955; Tryon and MacLean 1980; Williamson in Austin 1968; Wynne-Edwards 1952).

A single brood is raised in a nesting season. Some second clutches have been attempted after successfully rearing a first brood, progressing as far as hatching eggs in the second clutch. All attempts failed. Second nests are unlikely to be successful because the females need to moult, and cold weather and snow typically arrive before the second brood can be raised. Replacement clutches may be laid if the first clutch is lost early. In Alaska, all 4 females that lost nests during the egg-laying phase renested, 2 of 4 that lost nests during days 1-6 of incubation renested, and 0 of 18 that lost nests later in incubation renested. Clutches of 4-6 eggs have been reported in Ontario. In North America, clutches of 1-8 eggs have been reported, but the normal clutch size is 3-7 eggs. Clutch size declines with season; clutches smaller than 3 are typically late or replacement clutches. Overall, nearly all clutches are initiated between 20 June and 6 July and the mean clutch size declines from 6.0 to 4.0 during this period. Clutch size increases with latitude. The most frequent clutch size south of latitude 68°N is 5 eggs. Six-egg clutches are rare at the southern limits of the breeding range but are the most frequent clutch size in many areas north of latitude 68°N. Clutches of 7 eggs have been reported from north of latitude 66°N only. Larger clutch sizes in the north may be due in part to the long days that allow adults to feed the young for more than 20 hours a day. Clutch sizes at individual sites may vary annually depending upon when nesting is initiated and how many replacement clutches are laid. Individuals tend to lay the same number of eggs annually, with no change in performance with age. An exception is that yearling females may initiate nesting later and consequently have smaller clutches (Custer and Pitelka 1977; Drury 1961; Grinnell 1944; Hussell 1972; Hussell and Montgomerie 2020; Lyon and Montgomerie 1987; Parmelee et al. 1967; Peck and James 1987; Sinclair et al. 2003; Sutton and Parmelee 1955; Williamson in Austin 1968; Wynne-Edwards 1952).

Both sexes are capable of breeding when they are 1 year old and it is probable that most yearling females breed. Yearling males are usually unsuccessful in attracting a mate and few breed in their first year. Most populations have a surplus of males, so there are often floating, nonbreeding males present. In Alaska, only males that obtained a territory within an 9-day period (4-12 June) were successful in attracting mates although pair formation was observed as late as 16 June. Six of 28 males (21.4%) that established territories before 12 June and all 3 that established territories later failed to attract mates. The mating system is typically monogamous although bigamy and trigamy rarely occur. During a 13-year study, 96% of males were monogamous. One bigamous male had an unusual and large territory that included a 20-m cliff. One female nested at the bottom and the other at the top, both unaware of the other's existence. Females of polygynous males arrive on the breeding grounds first, nest first, and produce young that exhibit faster growth rates than females mated with monogamous males. There are unusual cases of 2 females laying eggs in the same nest and sharing incubation, even with both birds sitting on the nest at the same time; 2 females have

been observed feeding the same fledgling. Once females begin incubating, males often leave the territory to seek extra-pair copulations, occasionally traveling as far as 5-6 km. Because of intense mate guarding while the female is fertilizable, few attempts at extra-pair copulation are successful. Extra-pair fertilizations account for approximately 12% of nestlings (Beyersbergen 1978; Custer and Pitelka 1977; Hussell 1972; Hussell and Montgomerie 2020; Lyon and Montgomerie 1987; Montgomerie 1988; Seastedt and MacLean 1979; Sedinger 1986; Tryon and MacLean 1980; Wynne-Edwards 1952).

Adults creep, walk, and hop to pick food off the ground. When enough seeds cannot be found on the ground, they pull down plant stems or flutter upward and yank at the stalks with their bills. After a heavy snow, the Lapland Longspur takes seeds directly from emergent plants or shakes them so that the seeds fall on the snow where it picks them up. On Baffin Island, it caught large numbers of insects by snapping at them in the air, but also searched vegetation for insects when cold weather reduced the numbers of flying insects. Adults in 1 area were attracted to a tent where they fed on mosquitoes. Adults may obtain crane fly larvae and pupae by searching and picking through mosses, but are unable to probe wet areas to obtain larvae and pupae of a more aquatic crane fly species. Crane flies may be abundant in subarctic lowlands but unavailable to foraging Lapland Longspurs. Early in the breeding season, it spends a disproportionate amount of time is in areas of partial (0-49%) snow cover than in areas 50-100% snow covered. A large amount of time is spent feeding along retreating margins of snow fields, so foraging areas change day to day. There is a significant negative correlation between prey density and territory size. In Alaska, dry habitats produced more biomass of insects than wet meadows and longspurs selected drier areas for their territories. Territories appeared to be selected on the basis of habitat and not insect abundance. Over 90% of foraging by adults occurs in the territory early in the season when the territory is most actively defended. The percentage of foraging that occurs in the territory declines as the season progresses. The density of food within the territory is important because most food fed to the nestlings is obtained in or near the territory (Drury 1961; Hussell and Montgomerie 2020; Lyon and Montgomerie 1987; McLaughlin and Montgomerie 1985, 1989b; Seastedt 1980; Seastedt and MacLean 1979; Sutton and Parmelee 1955; Tryon and MacLean 1980; Williamson in Austin 1968).

Crane flies or midges are the dominant food provided to nestlings and fledglings, depending on the area. Egg laying is timed so that hatching is synchronous with the emergence of adult crane flies or midges. On Devon Island, food brought to nestlings from 12 to 18 July consisted of 80.9% adult insects, 15.6% other animal prey, and 3.5% plant material. From 20 to 30 July, the diet consisted of 97.1% adult insects, 2.5% other animal prey, and 0.5% plant material. Overall, the food delivered to nestlings was 92.7% adult insects, 6.0% other animal prey, and 1.3% plant material. In total, flies comprised 91.4% of nestlings' diet and 84.3% of these were midges. Other insects included 1.0% hymenopterans and 0.2% lepidopterans. Other animal prey included 1.0% larvae, 0.9% pupae (mostly lepidopterans), 0.1% eggs, 4.0% spiders, and other flies (crane, house, and dance flies). At 1 site in Alaska, over 90% of the biomass fed to nestlings older than 4 days and fledglings was crane flies. These were semiaquatic species associated with low, wetland habitats. At another site, the diet of young was dominated by another crane fly species found primarily in mesic and upland habitats. Sawflies that occurred on willows in mesic areas were secondary in importance (14.9% of diet) at the second site, but were nearly absent in the diet at the first site. Other prey items included a third

species of crane fly, midges (4.8% and 2.3% at the 2 sites), house flies (5.3% and 0.1%), and spiders (4.7% and 3.1%). The amount of dietary overlap as measured by the percent biomass shared in common at the 2 sites was only 12.4%. Both adult and larval crane flies (the species found in dry and mesic habitats) and sawflies occurred in the nestling diet more than their availability. On Baffin Island, crane fly adults were commonly fed to nestlings. Young have also been fed mosquitoes and beetles. In western Greenland, the diets of nestlings inhabiting lowlands and plateaus differed. Seventy-nine percent of the diet on plateaus consisted of adult flies; 76.5% of food items in lowlands were caterpillars. On Ellesmere Island, 1 immature female had eaten buttercup seeds. On Melville Peninsula, there was no difference in the diet of nestling Lapland Longspurs and Snow Buntings, with a 96.9% overlap in diet (Custer and Pitelka 1977; Drury 1961; Hussell and Montgomerie 2020; Lyon and Montgomerie 1987; Parmelee and MacDonald 1960; Seastedt 1980; Seastedt and MacLean 1979; Sutton and Parmelee 1955; Williamson in Austin 1968; Wynne-Edwards 1952).

During the breeding season, adults eat mostly seeds upon arrival and switch to insects in late June and July when they become plentiful. In early spring, the Lapland Longspur may forage on snow to capture springtails. An Alaskan study identified 8,849 food items from 174 stomachs and 61 esophagi. Seeds comprised 70% of the diet in late May, less than 6% in June and July, and 24-30% in mid- and late August. Seeds eaten were mostly those of sedges and grasses, although some herbaceous plant seeds were eaten, such as mountain avens and mouse-ear chickweed. It may consume moss capsules, leaf remains, and wood-rush seeds. Adults eat insect larvae early in the season, switch to adults in June and July then switch back to larvae. Arthropods eaten include crane flies, midges, other nematoceran flies, beetles (including weevils), bugs, spiders, springtails, butterflies, sawflies, and other hymenopterans. There is 1 record of an adult eating a snail and another of it feeding on blow flies on a carcass. Crane flies and midges dominate the diet; adults may feed almost exclusively on these when they are abundant. Sawfly larvae may be important in the diet in late July and August. At Churchill, adults fed on millet put out for them (Custer and Pitelka 1978; Drury 1961; Gabrielson 1924; Grinnell 1924; Hussell and Montgomerie 2020; Wynne-Edwards 1952).

Cold rain during the early nestling period may result in widespread mortality of young. A 5-day cold and rainy period occurred in early July near Churchill. Of 15 nests containing young, all nestlings died in 14 nests. In the other nest, 1 chick died; the other 3 survived. Death was caused by exposure. The nestlings were drenched and chilled while the adults gathered food; brooding failed to dry them. A single nest contained 4 eggs during this period and all hatched. Mortality from rain has been reported from other locations and this is probably a common event (Hussell 1972; Jehl and Hussell 1966; Seastedt and MacLean 1979; Austin in Bent 1968). Even if adverse weather does not result in direct death of nestlings, their growth rates may be inhibited in summers that are colder and wetter than normal. Adverse weather resulted in lower arthropod abundance. Rain appeared to be the primary environmental limitation to nestling growth, although growth was adversely affected by prolonged periods of low temperatures (Pérez et al. 2016).

Nests may experience high predation rates. On Melville Peninsula, the average rate of nest predation over 4 years was 51%. The decline of an Alaskan population was attributed to 3 consecutive years of high predation rates. High predation rates occurred when small rodent

populations were low, forcing jaegers, owls, weasels, and foxes to shift their prey bases (Custer and Pitelka 1977; Lyon and Montgomerie 1987). There was no difference in predation rates during the nestling and fledgling stages. Brood dispersal does not reduce predation risk and its main function appears to be to facilitate feeding of the young by adults (McLaughlin and Montgomerie 1989a; Wynne-Edwards 1952).

Wild fires can decrease habitat suitability and result in lower nesting densities. A fire in tundra habitat in Alaska consumed almost all above-ground vegetation, except for the cores of sedge tussocks and scattered small patches of moss. Density of longspurs in the burned area was one-third that of the unburned area. The fire may have deterred birds from settling into the area, and they may have required larger territories (Wright 1981). In habitats where there is dense shrub growth, fire could potentially improve habitat.

Overgrazing by geese may make sedge meadows less suitable for nesting by the Lapland Longspur. At Churchill and La Pérouse Bay, lower densities occur in grazed than ungrazed areas. Goose grazing is unlikely to be a major problem unless it is severe and occurs over a widespread area (Boal and Anderson 2005; Jehl 2004; Sammler et al. 2008).

Climate warming is likely to result in massive habitat loss in the Low Arctic and southern breeding areas. Gains are possible at higher elevations further north, but these are unlikely to compensate for losses in the south. The significant local contraction near Churchill may be due to climate change, but positive evidence for this is lacking (Hussell and Montgomerie 2020). Ontario represents the most southern area of the Lapland Longspur's breeding range, so the Ontario breeding population is at high risk of extirpation if global warming continues.

Oil, gas, mining, transportation, and urban development in the breeding range may result in small-scale, local loss of breeding habitat. The disappearance of this longspur near Churchill was a result of roads and drainage ditches. The current levels of disturbance are very low and will have little impact on population levels (Hussell and Montgomerie 2020; Jehl 2004).

Male and Nol (2005) investigated the impacts of roads associated with a diamond mine in the Northwest Territories. There was no evidence that Lapland Longspurs avoided placing their nests near roads and there was no difference in the success rates of nests near and distant from roads. Sites near roads supported significantly more invertebrates than those distant from roads. A maximum of 1,000 trucks per day created anthropogenic noise for 14% of the day. The truck noise overlapped with the lower range of longspur song. It may be tolerant of human disturbance but long-term changes in vegetation could occur that might affect nest-site selection.

Status

The first nest was found at Cape Henrietta Maria between 20 and 24 July 1947, and a juvenile not quite able to fly was collected; 41 were seen on this trip. A juvenile was taken at Little Cape west of Cape Henrietta Maria in 1947. In 1948, additional nests and young were observed at Cape Henrietta Maria and 100 were seen on 5 July 1948. It was considered likely that the Lapland Longspur bred all along the Hudson Bay coast (Baillie 1962; Manning 1952). Peck (1972) considered it an abundant breeder at Cape Henrietta Maria. Although earlier ornithologists speculated that it nested from Cape Henrietta Maria west to the Manitoba border, there was no positive evidence of this. During the first

atlas, breeding evidence was documented near the Manitoba border and from Winisk to Cape Henrietta Maria in the east. There was a distinct gap in its distribution that may have been partially due to lack of coverage, but there is considerably less suitable habitat in the intervening area. It was locally abundant in the Cape Henrietta Maria area (Hussell in Cadman et al. 1987). James (1991) considered the Lapland Longspur a common breeder in the Tundra Region. Wilson and McRae (1993) reported that it was a common breeder at Brant but apparently absent at Shagamu, supporting the evidence that there was a gap in its distribution.

The second atlas revealed a similar distribution with concentrations of breeding Lapland Longspurs at the Manitoba boundary and from Winisk to Cape Henrietta Maria. There were 2 breeding records from the intervening area, but only 7 squares were investigated in the central area of the Tundra Region. It was recorded in 23 squares during the second atlas and 18 squares in the first (Hussell in Cadman et al. 2007).

POSTFLEDGING PERIOD

As soon as the young leave the vicinity of the nest, brood division occurs with each adult taking 2 or 3 chicks. There is no difference in the number of chicks cared for by each adult or the age of chicks led by either sex in Alaska. On Baffin Island, males appeared to take charge of the oldest chicks. Adults forage around the chicks and feed each individual several times before making a long flight to feed the next chick. One of the main functions of early nest departure by young and brood division and dispersal appears to be to reduce distances that adults must travel to find food for young. Young are gradually led to prime foraging areas so that they are in good habitat once they begin feeding on their own (Hussell and Montgomerie 2020).

Young stay within their parents' territory for 3-5 days until they can fly at age 12-15 days, then drift through other territories to gather in damp areas. They begin to try and feed themselves at age 17-18 days, and are independent after age 23 days. Chicks are fairly immobile at this time and hide among hummocks, in crevices, or beside rocks. The distance between chicks in brood groups cared for by an individual parent increases from 0 m at nest departure to 200-325 m at independence. Young disperse from the nest with time. Just prior to independence, female-tended broods average 1 km from the nest compared with 250 m for those tended by males. During this dispersal process, adults lead the chicks closer to feeding areas. By age 18 days, chicks within a sub-brood averaged 132 m apart and 264 m from the closest chick in the other half of the same brood. At this time, the average distance of each chick to a feeding area was only 8.6 m. The strategy of young leaving the nest early before they can fly, brood division, and leading chicks toward parental feeding sites greatly reduces the amount of flying that adults have to undertake to raise young to independence. Young move to shrubby areas by ponds and streams once they become independent and strong fliers. Juveniles remain scattered until at least mid-August when they form flocks that presumably include adults. Flocks concentrate in wet, grassy tundra and less often on barren tundra. These flocks remain intact until autumn migration (Drury 1961; Hussell and Montgomerie 2020; McLaughlin and Montgomerie 1985, 1989a, 1989b; Sutton and Parmelee 1955; Tryon and MacLean 1980).

MIGRATION

The Lapland Longspur migrates both diurnally and nocturnally. Some birds observed during migration and winter in Ontario may breed in Greenland. During spring migration, birds migrate in

flocks. Individual birds remain in a given flock for as long as 3-5 days. Marked birds migrating to Alaska gradually disappeared from individual flocks but were replaced by other birds. Flocks remained at the same location and approximately the same size. Males migrate northward before females and arrive at the breeding grounds before they do. Early migrating flocks are dominated by males, later flocks have approximately equal numbers of the sexes, and late flocks are mostly females. Males arrive on the breeding grounds in flocks of 10-100 birds. In most areas, males arrive 3-6 days prior to females, but the differential in arrival times may range from 1 to 14 days. Males remain in small flocks initially and females may flock together upon arrival prior to pair formation. In 1 year on Victoria Island, males arrived in flocks 1 day, flocks containing equal numbers of males and females arrived the next day, and flight singing occurred the following day. Northward migration may be slowed by inclement weather and this may affect the timing of arrival of the sexes and how long they remain in discrete flocks before pairing (Brewer et al. 2018; Drury 1961; Freeman 1970; Hussell 1972; Hussell and Holroyd 1974; Hussell and Montgomerie 2020; Irving 1961; MacPherson and McLaren 1959; Manning et al. 1956; Parmelee et al. 1967; Soper 1946; West et al. 1968a; Williamson in Austin 1968; Wynne-Edwards 1952).

Northward movement may begin in the southern wintering range in late February or early March. The peak of migration in southern Canada is from late March until early May. The Lapland Longspur arrives at Churchill in mid-May with peak numbers in late May and early June. Arrival in the High Arctic is in late May or early June. In southern Ontario, numbers often increase in March as migrants move through from further south. Most leave in late March or early April, but stragglers may persist until mid-May. In Algonquin Park, average spring arrival is in late April, average departure is in late May, and some remain until early June. Late spring migrants occurred at Longridge on 6 and 8 June, on 14 June at Ekwan, and on 24 and 28 June at Shagamu, although the latter birds may have been failed breeders (Black and Roy 2010; Curry 2006; Jehl 2004; Jehl and Smith 1970; Hussell and Montgomerie 2020; Lancaster et al. 2004; Tozer 2012; Weir 2008; Williamson in Austin 1968; Wilson and McRae 1993).

In Alaska, Ward et al. (2016) compared spring arrival dates of migrants over a 50-year period. Warming during this period resulted in the transition from winter to summer occurring weeks earlier than it did previously. The Lapland Longspur arrived significantly earlier with time at a rate of 0.11 day per year or 0.8 day per 1°C increase in temperature.

Autumn flocking on the breeding grounds may begin in mid-July but is not prevalent until early August. Mixed flocks of Lapland Longspurs and Snow Buntings may be common at this time, and also during autumn migration and winter. Longspurs typically leave the northern portion of the breeding range from mid-August to early September, with some remaining into late September or early October. At Churchill, autumn migration begins in late August and peaks in September, with some remaining until mid-October. At Thunder Cape on the northern shore of Lake Superior, migrants pass through from mid-September to late October, peaking in the first half of October. Autumn migrants were observed at Ekwan 3-13 September and 4-13 September at Longridge. In the southern Shield, the Lapland Longspur may occur in late September but is more likely in October; some remain until late November. Some arrive in the south in mid-September, but most arrive in mid- to late October. Along the northern Lake Erie shoreline, numbers peak from late

October to mid-November (Black and Roy 2010; Curry 2006; Hussell and Montgomerie 2020; Jehl 2004; LaForest 1993; Lancaster et al. 2004; Lyon and Montgomerie 1987; MacPherson and McLaren 1959; Mills 1981; Parmelee and MacDonald 1960; Parmelee et al. 1967; Soper 1946; Sutton and Parmelee 1955; Tozer 2012; Weir 2008; Wilson and McRae 1993).

During migration, the Lapland Longspur occurs in flocks, occasionally only with conspecifics, but usually in the company of Snow Buntings or Horned Larks, and less frequently with American Pipits. This longspur avoids forested and treed habitats. In forested regions, it concentrates along coastlines; shorelines of lakes, rivers, and reservoirs; and on roadsides. In extensively forested landscapes, it makes greater use of human-created habitat including gravel pits, roadside clearings, sewage lagoon dykes, airstrips, utility corridors, recent clear-cuts, and settlement areas. In agricultural settings, where it is most common during migration, it prefers fields of grain stubble. It is attracted to fields with standing water, sloughs, small ponds, water-filled ditches, shorelines, sewage lagoons, and wetlands where flocks gather to drink. Autumn migrants in Davis Strait and the Labrador Sea were attracted to a ship 75 km off the Baffin Island coast. Birds circled and landed on the ship (Campbell et al. 2001; Crins 2004; Curry 2006; Hussell and Montgomerie 2020; LaForest 1993; Lanoue and Doyon in Gauthier and Aubry 1996; Leighton et al. 2002; Mills 1981; Orr et al. 1980; Sinclair et al. 2003).

West and Peyton (1980) collected 280 gizzards of Lapland Longspurs during spring migration in British Columbia, the Yukon, and Alaska. Twenty-seven types of seeds were eaten and they comprised 39.3% of the total dry weight of the gizzard contents. Fragmented material, estimated to be more than 90% plant material, comprised 60.3% of the gizzard contents. Squirrel-tail grass, bluejoint, bentgrass, and sedges comprised more than 77% of the identifiable food items. Unknown seeds of 2 types comprised 1.6% of the weight of food items. Larval, pupal, and adult insects constituted only 0.4% of the diet. Other foods included seeds of white spruce, fescues, smooth brome, wood-rushes, white birch, grey alder, lamb's-quarters, chickweeds, sandworts, buttercups, golden corydalis, geraniums, phlox, mints, and members of the aster family. Overall, the diet consisted of 59.7% grasses and 20.6% sedges. It preferred seeds of squirrel-tail grass and also selected seeds of chickweeds, sandworts, and bearberry more than their availability. Sedge seeds were taken in proportion to their availability. Bluejoint, bentgrass, and lamb's-quarters were taken slightly less than their availability. Brome grass, cinquefoils, and fescues were taken less than their availability. Some abundant plant species were not eaten at all including wheat grass and mustards. Crins (2004) observed one feeding on the seeds of ensheathed dropseed during autumn in Algonquin Park. The seeds of this grass are enclosed. The bird used its bill and tongue to separate the overlapping leaf sheaths to eat the grains. In agricultural areas, it feeds on waste grain seeds and a variety of other plant seeds. In New York in early October, Hoyt (1961) observed an adult feeding a young bird, apparently the only record of young being fed during autumn migration.

Seeding of agricultural crops and application of pesticides often coincide with spring migration, making the Lapland Longspur vulnerable to these chemicals. In 1984, at least 300 and probably more than 2,000 died in a Saskatchewan field that was recently planted to canola and treated with carbofuran. Although carbofuran has since been banned in Canada and the United States, the alternative pesticides currently in use are also toxic (Hussell and Montgomerie 2020).

Due to its habit of foraging along roadsides and flushing at close range, the Lapland Longspur is vulnerable to vehicle collisions (Campbell et al. 2001; Mills 1981).

The Lapland Longspur occasionally strikes tall structures during migration. One was killed at an unlit forestry tower during spring migration at Parry Sound (Mills 1981). Mass destruction of migrating flocks may occur at lighted structures, especially during periods of poor visibility due to snowstorms (Hussell and Montgomerie 2020).

On the prairies, the Lapland Longspur is an abundant migrant and often occurs in flocks larger than 5,000 (Hussell and Montgomerie 2020), but in Ontario it is an uncommon to locally abundant migrant (James 1991).

WINTER

The Lapland Longspur tends to avoid snow in winter. Snow cover variability is an important predictor of its presence, with it selecting areas where there are frequent changes between presence and absence of snow (Keyser et al. 2023).

In winter, the Lapland Longspur usually occurs in mixed flocks with Snow Buntings and Horned Larks. In southern Ontario, it is most frequent in large, windswept fields, particularly those where manure has been spread. Areas south of Hamilton, Wolfe Island, Amherst Island, Hay Bay, and Prince Edward County are favoured wintering areas. It is most frequent in agricultural fields, especially those with retained grain stubble, but also occurs in grazed pastures. In Oklahoma, it preferred sites with vegetation 0-10 cm tall with little to no litter cover. At an Oklahoma airport, it occurred in greatest numbers in grassy areas between the runways where it was associated with agalinis, panic grass, and ragweed. In another winter study, it preferred fields planted to winter wheat to grazed grasslands. In Massachusetts and Maine, it inhabits ocean sand dunes where the vegetation is sparse. In inland areas, it frequents fields where ragweed and other weed stalks protrude above the snow. In winter in British Columbia, it occurs mostly along the southern coast in open grassy or sparsely vegetated areas including cultivated fields, grazed pastures, roadsides, estuaries, rocky shorelines and islets, beaches, lagoons, jetties, causeways, sedge wetlands, golf courses, playing fields, and airports (Black and Roy 2010; Campbell et al. 2001; Curry 2006; Hussell and Montgomerie 2020; Weir 2008; Williamson in Austin 1968).

The Lapland Longspur does not maintain any particular home range in winter and is largely nomadic. Flocks forage in a given area for a few minutes to more than an hour and then fly to another location. Large-scale movements may occur in winter in response to food supplies and snow depths. When snowstorms cover plants, birds fly to areas with less snow cover. North of latitude 50°N, it may be abundant some years and absent in others (Hussell and Montgomerie 2020; Williamson in Bent 1968).

The degree of site fidelity that Lapland Longspurs exhibit for wintering areas is uncertain. One banded in October 1961 in North Dakota was recovered elsewhere in North Dakota in January 1963 indicating fidelity to the same general region. Another bird banded in North Dakota was recovered in California indicating a lack of winter fidelity (Hussell and Montgomerie 2020).

Gabrielson (1924) analyzed the contents of 600 stomachs of wintering birds. More than half were collected in January and February in Kansas under very similar conditions which may have

given undue prominence to millet and crabgrass in the diet (75% of the January food and 65% of the February food). Only 4.0% of the winter food was animal matter and almost half of this was taken by 4 birds in April that had fed exclusively on ground beetles. The remaining animal food consisted of leaf beetles, weevils, fly larvae, caterpillars, and spiders. Grass seeds dominated the diet and comprised 61.7% of the food: 30.6% foxtails, 10.0% cultivated millet, 8.7% hairy crabgrass, 2.3% panic grasses, and 10.5% other grasses such as smooth crabgrass and barnyard grass. Sedge seeds comprised 10.3% of the diet, taken mostly by birds in Montana, Ontario, and the Northwest Territories. Seventeen birds had eaten 64.4% sedge seeds in October but this food item was only 8% of the April and May diet. Seeds of purslane were common in the diet but were only 0.8% of the volume because they are so small. Amaranth seeds comprised 6.0% of the diet and miscellaneous seeds were 6.5%, of which lamb's-quarters and ragweed were most common. Wheat was eaten every month except October and represented 8.3% of the diet. It also ate timothy seeds and oats (1.4%). Most cultivated seeds were waste from crops, but it may also pick up newly sown grain or grass seeds. Judd (1901) summarized the contents of 113 stomachs collected in winter in the United States. The diet consisted of 94% plant material and 6% animal material. Waste oats, wheat, barley, and millet consumed in fields constituted 27% of the diet. The Lapland Longspur also ate large quantities of seeds of foxtails, crabgrasses, and panic grasses. Other seeds consumed included those of amaranths, lamb's-quarters, smartweeds, and ragweeds. Insects occurred only in stomachs of birds collected in Texas and included weevils, ground beetles, leaf beetles, and grasshoppers. Other winter foods commonly taken include seeds of bluegrasses, marram grass, and orache, and it may also eat snow (Hussell and Montgomerie 2020; Williamson in Austin 1968). The Lapland Longspur rarely visits bird feeders, usually when snow storms cover natural food supplies (Campbell et al. 2001; Curry 2006; Lancaster et al. 2004).

There has been no large-scale habitat degradation in the Lapland Longspur's winter range. Agriculture may have enhanced winter habitat and overwinter survival through increased availability of seeds (Hussell and Montgomerie 2020).

Until the 1960s, massive kills of the Lapland Longspur occurred almost every winter on the prairies. Most kills were associated with farmyards and other rural structures with less than 10 lights. Kills occurred during falling snow or foggy conditions around isolated groups of lights which disoriented birds. Many were killed by hitting human structures, but most flew into the ground or frozen lakes. On the night of 13-14 March 1904, 1-5 million were killed over an area of 3,800 km² in southwestern Minnesota, northwestern Iowa, and southeastern South Dakota. Approximately 10,000 were killed over an area of 9,000 km² in northwestern Iowa on 5-6 January 1939; 10,000 were killed in north-central Texas 19-23 February 1978 following snowfall; and on 22-23 January 1998, 5,000-10,000 were killed near 3 communication towers and a natural gas pumping station in Kansas. There have been no recent major kills associated with prairie towns, probably because of brighter and more general lighting than was present previously (Hussell and Montgomerie 2020; Williamson in Austin 1968). In Wyoming, Ramirez et al. (2015) reported a kill of 251 at an oil drilling rig. They attributed this to the birds entering the area illuminated by the drilling rig lights in fog and repeatedly circling until they fell to the ground in exhaustion, subsequently perishing.

The Lapland Longspur is the most abundant terrestrial bird wintering in northern North America. Flocks as large as 4 million occur in winter in the Great Plains from southern Canada to northern Texas. In eastern North America, it is uncommon in winter (Hussell and Montgomerie 2020). James (1991) considered it an uncommon to locally common wintering species in the south, north to Kingston.

Freedman and Riley (1980) examined Christmas Bird Count (CBC) results in southern Ontario. Numbers were extremely irregular dating back to 1929, with major peaks in 1939 and 1951 and minor peaks in 1936 and 1960. At the time of their publication, the Lapland Longspur was an irregular winter visitor. CBC data for Ontario indicate that the Lapland Longspur decreased at annual rates of 3.17% 1970-2021 and 14.67% 2009-21 (National Audubon Society 2022).

Smith's Longspur

Calcarius pictus

BREEDING SEASON

Habitat Requirements

In Ontario, the Smith's Longspur breeds on open, treeless tundra. It prefers grassy and somewhat wetter tussock tundra rather than the dry heath-lichen areas selected by the Lapland Longspur. The Smith's Longspur occasionally nests on raised, dry tundra areas and beach ridges (Peck and James 1987). Peck (1972) concluded that the Smith's Longspur preferred wetter habitat than the Lapland Longspur at Cape Henrietta Maria. Prime breeding habitat in Ontario consists of hummocky graminoid tundra with scattered stunted spruces interspersed with low gravel ridges. It may occur in suitable transition habitat 40-60 km inland from the Hudson Bay coast, but is absent from exposed treeless tundra near the coast (Hussell in Cadman et al. 2007).

Throughout its limited range, the Smith's Longspur is predominantly a bird of the more northern part of the transition zone between the Boreal Forest Region and the treeless tundra. In Alaska, southern Yukon, and northern British Columbia, it also breeds in alpine meadows and tundra. Suitable breeding habitat in tundra tends to be patchy in distribution, isolated from other suitable habitats by spruce forests or bedrock outcrops. Near Churchill, it nests most commonly in dry sedge meadows with scattered, isolated clumps of black spruce, but a few pairs breed well out into the tundra. It is found mostly where tongues of spruce forest extend out into the tundra. Nesting may occur on grassy eskers at Churchill. It nests most frequently where drier sedge meadows dominated

by tufted bulrush and dwarf birch are interrupted by low hillocks or small beach ridges bearing scattered, isolated clumps of black spruce or, less frequently, tamarack. These hillocks are dominated by heaths, predominantly Lapland rosebay, bog rosemary, bearberry, bog bilberry, and mountain cranberry. Other common species include mountain avens, crowberry, net-leaved willow, and reindeer lichen. In the Yukon, it inhabits open sedge tussock tundra, often in areas with scattered low willow or birch shrubs. In the north, it occurs in relatively bare tundra; it is restricted to high-elevation areas in the south. In British Columbia, it nests in subalpine tundra with shrub cover of willows, dwarf birches, and shrubby cinquefoil and a ground cover of sedges, mosses, lichens, and perennial forbs. In Alaska, it nested on hummocks in wet grassy areas; in tussock-heath tundra; in waterlogged sedge-grass marsh dominated by water sedge with scattered cottongrass; in a wet area with low willows, marsh horsetail, cottongrass, and water sedge; in a cottongrass tussock tundra by a small lake; in a sunken summit plateau bog with higher ground forming the rim; and in a well-drained site dominated by hummocks of mountain avens and Lapland rosebay. It selected wetter habitats than those used by the Lapland Longspur (Briskie 2020; Campbell et al. 2001; Jehl 1968, 2004; Jehl and Smith 1970; Martin et al. 1981; Sage 1976; Sinclair et al. 2003).

Wild et al. (2015) examined the distribution of the Smith's Longspur at landscape and microhabitat levels in Alaska. At the landscape level, it inhabited river valleys within the tundra-forest transition zone, large tundra valleys, areas along the front of a mountain range, and the edge of a river. It was positively associated with sedge and shrub ecotypes and negatively associated with barrens, water, and forest ecotypes. At the microhabitat scale, occupied and unoccupied habitats were composed of the same ground-cover species, but at varying levels of percent cover. It was most frequently associated with willow shrubs, dwarf willow, mountain avens, non-tussock sedges, and mosses. It was also associated with greater moss cover and, to a lesser degree, cover of lichens and heather. These habitats were closer to the northern coastline and at higher elevations. It was negatively associated with greater cover by birch, willow, and alder shrubs. At both scales, it was associated with a heterogeneous land cover of sedge and shrub habitats. Landscape heterogeneity may be an important habitat variable, but this was not tested. Large patches of closed shrub coverage appeared to be avoided, yet foraging occurred in some shrubby areas.

In Alaska, habitat at nests and random points was very similar, but shrubs tended to be taller at random sites than at nest sites. Mean shrub height at nests was 26.8 cm and nests were never found in tall shrubs. General nesting habitat consisted of open low-shrub tundra. Nest habitat selection

was weak with the shorter height of erect willows at nest sites being the best predictor (McFarland et al. 2017).

At night, the Smith's Longspur roosts on the ground, either singly or in pairs (Briskie 2020).

Ontario nests were on the ground in both tall and short sedges and grasses, sometimes with mosses and lichens near the nest. One was in a clump of rhodendrons; 1 was under a small dwarf birch; 1 was well hidden in tall, dead grass clumps; and another was on a hummock (Peck and James 1987). Most nests are in grass tufts on or beside hummocks or between frost boils (Hussell in Cadman et al. 2007).

Nests are invariably in a small depression in the ground or in the sides of tussocks of vegetation. In Alaska, 47.7% of nests were in the tops of hummocks, 24.4% were in the sides of hummocks, and 27.9% were on level ground. Of 86 nests, 44.2% were directly under clumps of graminoids, 33.7% were under shrubs less than 30 cm tall, and 22.1% had no overhead cover. Common shrubs associated with nests were willows, followed by bog bilberry, rhododendrons, and dwarf birches. Low shrubs (1.7-20.8 cm) were present at 88% of nests. Many nests are completely exposed from above; others are concealed at the base of a small shrub, in Labrador tea, or in graminoids (Briskie 2020; Campbell et al. 2001; Jehl 1968, 2004; Kemsies in Austin 1968; Martin et al. 1981; McFarland et al. 2017; Sage 1976; Sinclair et al. 2003).

The Smith's Longspur does not defend a territory but males compete for copulation. Males are aggressive with other males only when copulating with a female and may chase other males over several 100 m for several minutes. Males guard females by following them closely on the ground while they are foraging. Mate guarding by alpha males is most intense on the day before and the day of clutch initiation, when the first and second eggs are available for fertilization. Guarding by beta males is greatest after the third egg is laid, when the fourth egg could be fertilized. Mate guarding is most prevalent in the morning and evening, but nonexistent in the afternoon. Males sing from treetops, boulders, hummocks, or other conspicuous perches to attract females. Males are completely nonterritorial while advertising, with as many as 3 singing from the same tree at once without conflict. Male home ranges overlap extensively with 2-5 other males. Female home ranges overlap with 3-6 males and 2-5 other females. Populations tend to be distributed into discrete neighbourhoods delineated by the patchy nature of suitable habitat. At Churchill, each neighbourhood contained 4 to more than 20 birds, with larger areas supporting more birds. Neighbourhoods were separated by 100 m to several kilometres. The area used by 2 pairs during the incubation period at Churchill was 1.7 and 2.4 ha. Home ranges of 12 males at Churchill averaged 16.3 ha (range 9.4-30.9 ha). Home ranges of 8 females averaged 10.4 ha (range 5.4-19.5 ha; Briskie 1992; Jehl 1968).

Natal philopatry appears to be very low. Only 1 of 90 chicks (1.1%) returned to nest at Churchill, and it nested 3 km from its natal site (Briskie 1992, 2020). In Alaska, 4% of 431 juveniles were sighted in subsequent years. Nests were located for 3 returning males and 3 females. The mean distance between their natal and breeding nests was 1,674.4 m, significantly further than for returning adults. One of 6 returning birds nested within its natal neighbourhood (Craig et al. 2015).

Adult site fidelity is high. At Churchill, 13 of 15 adult males (86.7%) and 10 of 11 females (90.9%) returned to breed the following year. Birds that did not return were not seen in neighbouring populations and had likely died. In 1 case, a nest was placed in the same location in 2 consecutive years suggesting high fidelity, but it was unknown if the same birds were involved (Briskie 2020; Jehl 1968). In Alaska, return rates were 53% for males and 37% for females. Most returning adults nested within the same neighbourhood as in previous seasons. Four individuals (17%) returned to breed in a different neighbourhood; these were all females. The mean inter-annual nest distance was similar for the sexes: 325.2 m for females and 300.9 m for males. Dispersal rates of females were unrelated to reproductive success the previous year (Craig et al. 2015).

Limiting Factors

Eggs have been reported in Ontario nests from the last third of June until mid-July (Peck and James 1987). Nesting in populations is highly synchronized, with only 5, 6, and 8 days between the initiation of the first and last clutches at Churchill over 3 years. Timing varies annually depending upon weather conditions, with first clutch initiation ranging from 9 June in a warm spring to 21 June in a cold, late spring at Churchill. Fledging occurs over 6-14 days for entire populations. Pairing occurs as soon as males leave flocks and begin to sing from perches. Females begin to search for a nest site a few days to a week after this. In Alaska, nest building was initiated almost immediately upon arrival or as soon as temperature and snow conditions allowed. The length of the nest initiation period was 7-19 days, with longer periods occurring in years with warmer temperatures and fewer snow and rain events. The female begins to gather nest material as soon as the site is selected and completes building the nest in 3 or 4 days. Nests are not reused, with a new nest built for each clutch. Eggs are laid at the rate of 1 a day. Incubation begins with laying of the penultimate or final egg. The incubation period is 11-13.5 days (average 11.5 days). Nests may be temporarily abandoned during cold, wet weather, but eggs in these nests usually hatch once incubation is resumed. Hatching occurs over 11-36 hours (average 22 hours). Young begin to stray short distances from the nest by age 6 days and leave it completely when they are 7-9 days old. In Alaska, the mean nestling period was 7.0 days (Briskie 1992, 2020; Jehl 1968, 2004; Jehl and Smith 1970; McFarland et al. 2017).

A single brood is raised annually; renesting is rare if a clutch is lost. At Churchill, renesting occurred in only 2 of 6 years and in only 3 of 11 nest failures (27%). Clutches of 3-5 eggs have been found in Ontario, with most containing 4 or 5 eggs. Overall, clutches of 1-6 eggs have been reported, but those with 1 or 2 eggs may have suffered partial losses. Most clutches contain 4 or 5 eggs; 4 eggs is the most frequent clutch size. Mean clutch size in Alaska was 3.7 eggs (range 1-5 eggs); 1 nest contained 9 eggs. This nest was attended by a single female and hatched 6 young and fledged 4 (Briskie 1992, 2020; Campbell et al. 2001; Jehl 1968; Jehl and Hussell 1966; Martin et al. 1981; McFarland et al. 2017; Sinclair et al. 2003).

The age at first breeding is 1 year. Nonbreeding birds have not been detected in any populations, so it is likely that most, if not all, yearlings breed. The Smith's Longspur has an unusual mating system termed polygynandry and it is 1 of only 3 passerine species to exhibit this behaviour. Each female copulates with 1-3 males and each male copulates with 1-3 females. Females actively solicit copulations and copulate an average of 365 times per clutch (range 214-629 times). Of 13 females at Churchill, 77% were biandrous, 8% were triandrous, and 15% were monogamous. Of

males, 62.5% mated with at least 2 females, 12.5% with 3 females, and 25% with 1 female, but the level of polygyny may have been underestimated. The alpha male of 1 female might be the beta male of another female. Seventy-five percent of broods had mixed paternity. Alpha males fathered about 67% of the chicks and beta and gamma males fathered the rest. Alpha males fertilize most of the first-, second-, and third-laid eggs and beta and gamma males fertilize some of the third- and all of the last-laid eggs. All mating behaviour occurs in a 5-8-day period which centres on clutch initiation and usually ceases by the laying of the penultimate egg. Alpha, beta, and gamma males have all been observed feeding young, so polyandry may result in recruitment of males to assist in raising the young (Briskie 1992, 2020). Despite high site fidelity, only 1 pair reunited in a subsequent year in Alaska. There were 2 cases of males attending the same nest in 1 year and they were associated with each other again in subsequent years (Craig et al. 2015).

Birds walk rapidly over drier regions of tundra while foraging, peering and pecking for seeds and invertebrates. The Smith's Longspur does not scratch the substrate with its feet, but occasionally digs through moss clumps, lichen mats, and soil with its bill to capture ants or beetles. Later in the breeding season, it often hops or makes short flights to catch flying insects. Males and females forage solitarily except when mate guarding and copulating. After laying is complete, males and females do not associate closely until hatching, when most males return to assist the female in feeding. At 10 Churchill nests, chicks at 5 nests were fed by 1 male and 1 female, those at 4 nests were fed by 2 males and 1 female, and those at 1 nest were fed by 3 males and 1 female. All males that fed at nests had earlier copulated with the female, but not all males that copulated with a female later fed her brood (Briskie 2020; Jehl 1968).

The most conspicuous food items brought to nestlings are caterpillars, grasshoppers, and adult flies and lepidopterans, but many other items are provided to the young. Jehl (1968) examined the stomachs of 29 nestlings, but results may have been biased. They died of exposure during adverse weather, so adults may not have been able to secure some items that were normally fed to chicks. Spiders were found in 7 of 29 stomachs but otherwise there was no difference in the diet of nestlings and adults 1-20 July. Entire leaves of plants commonly occurring in the area were found in stomachs of 5 nestlings, but not in those of adults. Foods taken by adults and nestlings included spiders, damselflies, grasshoppers and locusts, earwigs, leafhoppers, geometer moth larvae, owlet moth larvae and pupae, crane flies, anthomyiid flies, soldier beetles, leaf beetles, ants, and spider wasps. Vegetable matter consumed included cinquefoil seeds; leaves of net-leaved willow, mountain avens, and bearberry; and reindeer lichen stem fragments. Jehl (1968) analyzed the stomach contents of 39 adults and 2 juveniles and found that they fed opportunistically on a wide variety of organisms through much of the summer. In the first 10 days of June, more than 90% of the volume of food was plant material, predominantly seeds. Invertebrates were taken when available, mostly ants, spiders, beetles, and caterpillars. In mid-June, when invertebrates are more abundant, the Smith's Longspur switches to a largely animal diet dominated by flying insects. After 20 June, the diet is comprised of more than 85% animal material, predominantly terrestrial species or immature stages of flying insects. Ants and spiders are taken frequently in early June but not in July; these are ignored once larger prey becomes available. Snails were found in 5 of 14 stomachs collected 11-20 July, reflective of the drying of small tundra pools. From late June through July, adults of flying insects comprised less than 25% of the diet.

The most significant limiting factors to the Smith's Longspur are predation and severe weather. During a cold and rainy period in early July, all young died in 18 nests near Churchill. Death was caused by exposure, with nestlings becoming drenched while adults searched for food. Subsequent brooding failed to dry them and all perished. One nest contained 4 eggs during this period, and 3 hatched (Briskie 2020; Jehl and Hussell 1966). Nest loss occurred in Alaska due to hail storms and unusually hot days (McFarland et al. 2017).

Human disturbance does not appear to be a significant factor. The Smith's Longspur is fairly tame and tolerant of humans and will nest in moderately disturbed habitat. Some declines occurred in the Churchill area due in part to habitat succession. Areas previously open along roads and airport runways have grown up with tamarack and are now unsuitable breeding habitat (Briskie 2020; Jehl 2004).

Drastic changes associated with climate change are predicted for Alaska, including advance of the treeline, increased shrub abundance and growth, decreased moss cover, and decreased soil moisture. Shrubs are already becoming larger and more abundant. Open tundra habitats may be lost which could affect the Smith's Longspur. How it responds will depend upon patterns of shrub growth and the persistence of mosses and sedges in the understorey. Increased shrub growth in sedge tundra could create the sedge-shrub tundra that it prefers; reductions in soil moisture and moss cover could drastically reduce habitat suitability. The extent to which Smith's Longspur will persist in increasingly shrubby sites or occupy new sites is uncertain (Wild et al. 2015). It had high nesting success in Alaska and the ability to delay nest initiation during inclement weather. This suggests that it may be resilient to predicted changes in weather, but the potential loss of low-shrub habitats is a significant threat (McFarland et al. 2017).

Status

Nesting was first confirmed in the province on 22 June 1940 when a nest was found at Fort Severn, and juveniles were collected at Little Cape and Cape Henrietta Maria in 1947 and 1948, respectively. More than 100 Smith's Longspurs were seen at Cape Henrietta Maria in 1948 and 2 nests were found that year (Baillie 1961; Manning 1952). Peck (1972) observed Smith's Longspurs daily near Radar Site 416, but they were less abundant than the Lapland Longspur and found in wetter areas of tundra. Schueler et al. (1974) considered the Smith's Longspur abundant at Winisk in 1965 and common in suitable habitat in 1971, with evidence of breeding obtained in both years. They saw it along the Sutton River in 1962, but no breeding evidence was obtained. During the first atlas, the Smith's Longspur was more abundant than the Lapland Longspur at Cape Henrietta Maria. Breeding evidence was found along the entire strip of tundra along the Hudson Bay coast, but it was absent from the more exposed outer coast at Cape Henrietta Maria and at West Pen Island (Hussell in Cadman et al. 1987). James (1991) considered it a common summer resident in the Tundra Region. Wilson and McRae (1993) found it nesting at Shagamu and Brant, seeing an average of 3-5 per day at Shagamu and 2-12 at Brant.

The second atlas demonstrated that the breeding distribution of the Smith's Longspur had not changed since the first atlas. The main areas of concentration were near the Manitoba border and inland from Cape Henrietta Maria (Hussell in Cadman et al. 2007).

POSTFLEDGING PERIOD

At fledging, young can run rapidly through the grass; by age 12 days, they can fly short distances but several more days are required before they can fly well. Brood division occurs as soon as the young leave the nest. Nest mates may be separated by 400 m a day after fledging. Some family groups disappear quickly from the vicinity of the nest; others remain nearby for as long as 3 weeks. The chicks are fed for about 3 weeks after they hatch (Briskie 2020; Jehl 1968).

MIGRATION

Most migration by the Smith's Longspur occurs through the Prairie Provinces and Great Plains states west of Ontario. It is regularly noted in small to moderate numbers in the Midwest in spring, mostly in central Illinois and Missouri, with smaller numbers from western Indiana. It may also occur in central and northern Ontario in April en route from Texas to Alaska. The autumn migration route may be further west although there are a number of autumn records from Thunder Bay and Duluth, Minnesota. It is uncertain if birds breeding in Ontario use the Thunder Bay area as a flyway to the plains or if these birds are strays (Briskie 2020; Dunn and Beadle 1998; Ryff 1987; Will et al. 2024). Wilson and McRae (1993) observed an autumn migrant on 12 September at Ekwan, south and a bit east of the breeding area.

The Smith's Longspur migrates by day and night, and may arrive at the breeding grounds at any hour. Birds usually travel in small flocks of 10-30 birds, but flocks as large as 250 have been seen. Flocks tend to be comprised solely of Smith's Longspurs. It is rarely seen in the company of the Lapland Longspur and Snow Bunting, typically only when forced to by crowding. Individuals at an Ohio airport remained for 6-19 days (Briskie 2020; Dunn and Beadle 1998; Jehl 1968; Sinclair et al. 2003).

Depending upon weather conditions, males usually arrive on the breeding grounds a few days before females. Most years, males remain in small flocks of 3-5 birds for several days after their arrival prior to establishing home ranges. If females arrive while the males are still in flocks, they may join the flocks but show no evidence of being attracted to the males. In years of colder weather when males arrive later, flocks disband almost immediately. Females that arrive after male flocks have disbanded immediately take up residency on males' home ranges. After spring arrival, only 10-12 days are available for pairing and mating before clutch initiation. At Churchill, birds arrive in the first days of June. In typical springs, most males have arrived by 6 June but in cold springs they may not appear until 18-20 June. Spring migration records from the north shore of Lake Superior range from 24 April to 19 May and there is an accepted spring migration record for southern Ontario on 20 April (Briskie 1992, 2020; Jehl 1968, 2004; Jehl and Smith 1970; Ryff 1987).

In the Churchill area, adults leave the young in late July and congregate in flocks. Migration there begins as early as mid-August some years and all are gone in the first week of September. Birds leave the Yukon in late July and August, occasionally into September. In British Columbia, birds start leaving in mid-August with 3 September the latest record from the northern breeding grounds. Late records for Ontario include 12 September at Ekwan, 29 September at Thunder Bay, and 31 October to 2 November at Long Point (Campbell et al. 2001; Jehl 1968; Jehl and Smith 1970; Ryff 1987; Sinclair et al. 2003; Wilson and McRae 1993).

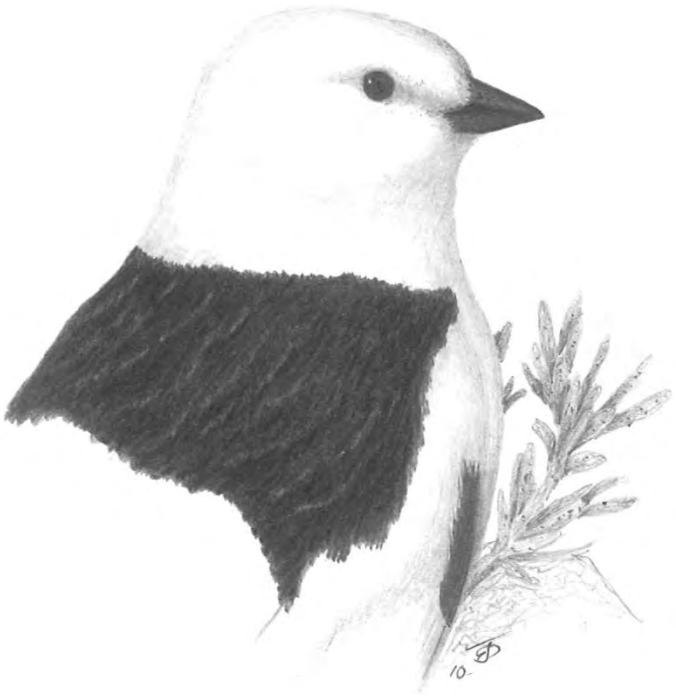
During spring migration in Alaska, the Smith's Longspur often occurred in wet, grassy areas and did not frequent dry areas. Near the breeding grounds in northern British Columbia, it fed in large flocks on open, grass-herb slopes or flats vegetated with dwarf birches, forbs, grasses, and sedges at subalpine sites. It also occurred in patches of dry grasses and weeds in logged areas, along gravel roads, in field verges, perched in shrubs in clear-cuts, and in grassy meadows bordering a lake. In agricultural landscapes, it is most often seen in stubble fields, pastures, and open, grassy fields and at airports (Briskie 2020; Campbell et al. 2001; Kemsies in Austin 1968).

Limited data are available on the diet of the Smith's Longspur during migration and winter. Ryff (1987) observed an autumn migrant at Thunder Bay capturing and eating a grasshopper. The stomachs of 9 birds collected in May at Fort Simpson, Northwest Territories contained insects almost exclusively. The diet of 21 birds collected in Illinois in April was composed of 37.1% animal matter and 62.9% vegetation. The predominant animal food consisted of beetles (mostly ground beetles with lesser numbers of click beetles and other beetles), comprising a total of 25.9% of the diet. Other animal foods included caterpillars (7.5%), other insects that were mostly grasshoppers and crickets (3.5%), and spiders (0.3%). Important grass seeds included those of tall dropseed (28.7%), foxtails (12.1%), witch grass (7.3%), wheat (4.7%), barley (0.7%), and small amounts of timothy, crabgrass, wiregrass, and millet. It also ate seeds of ragweeds, clover, and sedges. It eats cracked corn when it is available (Briskie 2020; Gabrielson 1924; Kemsies in Austin 1968). The diet of the Smith's Longspur is very similar to that of the Lapland Longspur (Gabrielson 1924).

The Smith's Longspur is an infrequent and rare migrant in the north. In the south, it is a rarely observed vagrant. There are only 4 accepted records for southern Ontario, including 3 migrants and 1 wintering bird (Curry et al. 2002).

Snow Bunting

Plectrophenax nivalis

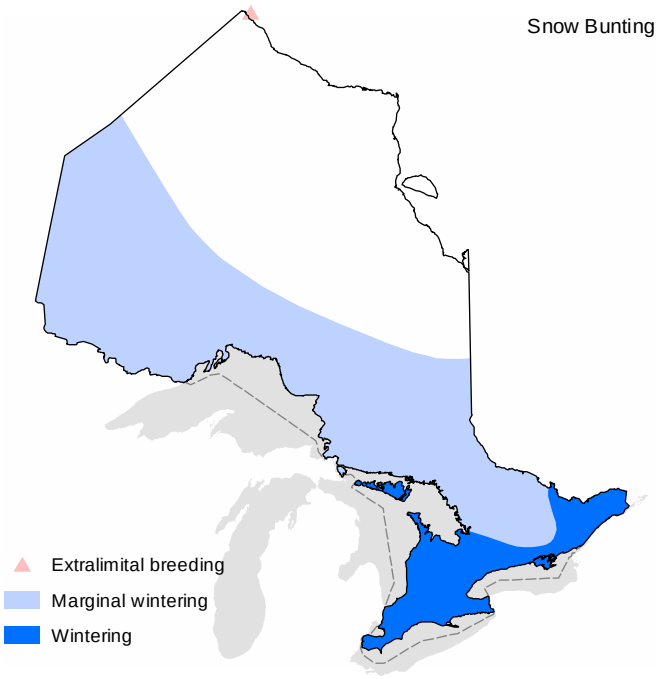


BREEDING SEASON

Habitat Requirements

In Ontario, breeding of the Snow Bunting has been confirmed only at West Pen Island on the Hudson Bay coast near the Manitoba border. The habitat there is not rocky, but piles of driftwood along the beach may have provided suitable nesting habitat (Hussell in Cadman et al. 1987).

The Snow Bunting nests in treeless areas, typically north of the treeline, but also in alpine areas in northern British Columbia, the Yukon, and Alaska. It prefers rocky terrain for nesting that is in or near vegetated areas that are used for feeding. Preferred habitats include stony beaches, cliffs along oceans, rocky outcrops in inland areas, rock piles, rock debris near remnant snowbeds, talus slopes at the base of cliffs, slumping benches along streams, and walls of steep ravines. It is attracted to outposts and villages where it may nest in a variety of artificial structures. Highest breeding densities may occur in disturbed areas. High densities often occur near seabird colonies because these birds transport nutrients into areas that would otherwise be nutrient-poor. Higher nutrient levels enhance conditions for aquatic insects that are critical to the diet of the Snow Bunting. In the Yukon, it nests on beaches strewn with driftwood. It is one of few species that inhabits nunataks, tundra islands on ice caps as far as 60 km from the edge of caps. In Greenland, it often nests in association with cliff-



nesting birds, particularly alcids. Lowest breeding densities occur in grassy tundra with little broken or rocky ground. It is mostly absent in marshes, grassy tundra devoid of rocks, higher areas of talus slopes and cliffs, and areas perpetually covered with snow (Bray 1943; Campbell et al. 2001; Drury 1961; Freedman and Svoboda 1982; Macdonald and Love 2012; Manning et al. 1956; Montgomerie and Lyon 2020; Montgomerie et al. 1983; Parmelee in Austin 1968; Parmelee et al. 1967; Sinclair et al. 2003; Smith and Marquiss 1994; Soper 1946; Vincent in Gauthier and Aubry 1996; Wynne-Edwards 1952).

Upon arrival on the breeding grounds, both sexes roost together in eroded snowbanks. Throughout the breeding season in the arctic, birds roost when the sun is low. Most roost in shadowy niches, but some sleep in direct sunlight. Some on Ellesmere Island roosted in a lumber pile. In natural areas, most roosted in shallow niches in sandstone outcrops and gullies. Even at −31.6°C, birds did not huddle together in roosts. After territories were established, few roosted in gullies; those that did used the same spots. Once territories are established, males roost alone in a crack or hole in their territory. In August, family groups roosted among rocks on steep banks, in nearly dry streambeds, or under huge snow banks undercut by running water. In September, large flocks roosted in open tundra where the ground was eroded or hummocky. In Greenland, birds roost in loose aggregations in cracks and holes in cliffs in spring (Montgomerie and Lyon 2020; Parmelee and MacDonald 1960).

In natural habitat, the Snow Bunting places its nest in a cavity under a boulder or rock, in a crevice in a rock, or in some similarly protected site. Nests, with rare exceptions, are not visible from above and are almost always in the shade, although some may be exposed to the sun for as long as an hour a day. Most nests are under rocks, but they may be in lemming burrows in banks, in holes on bare ridges, in piles of boulders, in vertical rock crevices, in cracks in cliffs, in earthen cavities created by slumping benches along streams, in shallow crevices in sandstone outcrops, and on or near the ground in piles of driftwood on beaches. Nests are usually well back from the cavity entrance and completely invisible. On Melville Peninsula, nests averaged 27 cm from the cavity entrance (range 10-60 cm); average distances of 30 cm have been reported elsewhere. Occasionally nests are hidden only under moss. Unusual nests include between 2 hummocks in open tundra, flat against a rock wall on a ledge 7.5 cm wide, and on a ledge of a sandstone outcrop. All these nests were completely exposed from above, but exposed nests are exceptional. Where rocks or artificial nest sites are lacking, it will nest in cracks or holes in soft ground, particularly where the earth is frost-heaved into piles of mud. Nests in soft mud are in depressions that are presumably scratched out by the birds. Nest cavities and old nests are frequently reused, occasionally for as many as 4 years,

because suitable nest sites are often limited. Of 56 nests found on Melville Peninsula, 9 were on top of an old nest, 2 were in the same cavity as an old nest, and 1 nest was used in 3 different years. On Ellesmere Island, all nests that were closely examined had been used in previous years. There is no clear orientation of nests. On Melville Peninsula, 59% of nests faced southward between 90° and 270°. The Snow Bunting readily uses artificial nest sites. It has nested in stone walls of buildings, old barrels, derelict buildings, tin cans, metal and wooden boxes, construction rubble, barrels filled with rocks, in the eaves of a building, on steel beams 3 m above the ground, under a piece of plywood, in skulls, in a coil of wire, under an oil drum, and in an old engine block (Bray 1943; Campbell and Van Der Raay 1985; Campbell et al. 2001; Drury 1961; Freedman and Svoboda 1982; Geale 1971; Höhn 1968; Hussell 1972, 1985; Hussell and Holroyd 1974; Kukal and Pattie 1988; Lyon and Montgomerie 1987; Montgomerie and Lyon 2020; Montgomerie et al. 1983; Parmelee in Austin 1968; Parmelee and MacDonald 1960; Parmelee et al. 1967; Sinclair et al. 2003; Soper 1946; Wynne-Edwards 1952).

Males may remain in flocks upon arrival on the breeding grounds. Once territories are established, they are vigorously defended by males. Females also challenge trespassing females. Territorial defence peaks in early June and gradually declines, ending in early July. During the period when the female may be fertilized, the male guards her from extra-pair copulations, rarely straying more than 3 m from her. Early on, males may leave their territory in midday to forage elsewhere, but remain and feed within the territory more as the season advances. After pairing, females occasionally leave the territory, but the male seldom does. In Canada, where males feed females on the nest during incubation, territorial defence wanes by the incubation period. In Greenland, where incubation-feeding does not occur, males continue to be territorial until hatching. Not all suitable habitat is used and males may forage together in undefended areas. By mid-July, some males abandon the territory and flock in common defence of the young. In Greenland, territory size shrinks with the season. Territories are initially 300-400 m in diameter (approximately 28-50 ha) but later shrink to 50-100 m (0.8-3 ha). A similar pattern was noticed on Melville Peninsula but the distances were not quantified. Adult home ranges are as large as 50 ha during the breeding season, depending upon the distribution of food. Nests are usually well dispersed, but 2 nests were found within 4.6 m of each other in a stone wall of a house on Bylot Island. On Devon Island, nearest-neighbour nests averaged 115 m apart with a range of 44-438 m (Drury 1961; Montgomerie and Lyon 2020; Nethersole-Thompson 1966; Parmelee in Austin 1968; Vincent in Gauthier and Aubry 1996).

The Snow Bunting exhibits very low natal philopatry. On Melville Peninsula, 1 of 53 nestlings (1.9%) returned to breed the following year; 0 of 135 returned to Devon Island. Adult site fidelity also appears to be low. On Melville Peninsula, 2 of 9 (22%) adult males and 0 of 10 adult females returned. On Devon Island, 2 females and 1 male of 32 adults (9.4%) returned. Although adult site fidelity is low, some adults return to the same general area, sometimes to the same home range, and rarely to the same nest site (Hussell and Holroyd 1974; Montgomerie and Lyon 2020).

Limiting Factors

The Snow Bunting is the earliest passerine to arrive in arctic breeding grounds, but it does not initiate nesting earlier than other species. Birds may remain in flocks for as long as a month before initiating

nesting. Nesting is highly asynchronous: by 6 July on Baffin Island, some nests were well incubated, other eggs were still fresh, and some birds were still building nests as late as 2 July. It is uncertain if the timing of nest initiation is related to snow melt or so that the peak of hatching coincides with insect emergence. Timing of nesting is independent of latitude but is related, at least in part, to disappearance of snow. Many crevices and cavities become filled with ice over winter and birds have to wait until it melts before nesting can be initiated. Nests are usually initiated 1 or 2 days after the appearance of large snow-free patches. The female may start several nests and abandon them before choosing the one that she finishes. Most nests take 3-4 days to build (range 1-8 days); 1 Alaskan nest was built in 14 hours. The first egg is usually laid on the day of nest completion or the following day. The first egg may be laid on bare substrate before nest building even starts; the nest is built around it while the clutch is completed. One egg is laid a day, although a day may rarely be skipped. Incubation usually starts before the clutch is complete. On Melville Peninsula, incubation began with the laying of the third or fourth egg; incubation started with laying of the first egg on Baffin Island; and incubation does not start in Greenland until the clutch is complete. The incubation period is usually about 12 days (range 10-15.5 days). Longer incubation periods (13-15.5 days) are often by females that are not being fed by males. These females are less attentive to their nests because they are forced to feed themselves. Nesting cavities have a harsh microclimate where eggs quickly become cool, thereby prolonging the incubation period and reducing hatching success when the female is absent. Because incubation begins before the clutch is complete, hatching is asynchronous and takes place over 3-5 days. The age of young within a brood may vary by as much as 3 days. On Devon Island, mean hatching intervals were 30.25 hours for 4-egg clutches (range 17-55 hours), 43.06 hours for 5-egg clutches (range 30-59 hours), 53.00 hours for 6-egg clutches (range 37-69 hours), and 55.00 hours for 7-egg clutches (range 24-80 hours). Young tend to remain in the nest cavity until they are about 13 days old, but are capable of leaving when they are as young as 9 days; some remain in the nest for 17 days. They may be almost ready to fly at age 10 days. Occasionally, the young leave the nest at the same time, but asynchronous departure is more common. On Melville Peninsula, 1 brood fledged over a 24-30 hour period. Fledging occurred over less than 15 hours in 2 other broods. Chicks may return to the nest cavity for 2 days after fledging. When the brood fledges asynchronously, the male feeds the first chicks to fledge while the female continues to attend to the nestlings. On Victoria Island, the interval from laying of the first egg to fledging of the last chick was 26 days for a 5-egg clutch and 28 days for a 7-egg clutch (Drury 1961; Hussell 1972, 1985; Lyon and Montgomerie 1985, 1987; MacDonald et al. 2014; Montgomerie and Lyon 2020; Montgomerie et al. 1983; Parmelee in Austin 1968; Parmelee and MacDonald 1960; Parmelee et al. 1967; Soper 1946; Wynne-Edwards 1952).

A single brood is raised in Canada and Alaska, although there is time to raise 2 broods. In 1 case, a female deserted half the first clutch as soon as some young left the nest and started raising a second brood. Therefore, she did not successfully rear 2 broods. The habits of Canadian Snow Buntings of incubation feeding and brood division make raising second broods difficult. Replacement clutches have not been confirmed in Canada or Alaska, but may occur in Greenland. Clutches contain 2-9 eggs, but mostly 4-6 eggs. Clutch size increases with latitude and is larger earlier in the season. There is little variation in the amount of day length at different latitudes and no difference in the amount of time that buntings are active. Other factors correlated with latitude may

influence clutch size. Clutches of 7 eggs were reported as far south as Iqaluit, where 5 eggs is the most frequent clutch size. On Victoria and Jenny Lind islands, 7 eggs was the most frequent clutch size. Clutches of 8 eggs have been found in the northern part of Ellesmere Island (latitude 80°N) and on Prince Patrick Island (latitude 76°N) where clutch size ranged from 5 to 8 eggs, but 6 eggs were most common. On Devon Island, average clutch size declined from 6.0 to 4.8 eggs between 20 June and 6 July. Similar declines in clutch size with season have been reported elsewhere. There are frequently significant differences in clutch sizes from year to year that may be related to timing of snow melt and when clutches can be initiated. On Devon Island, clutch-manipulation studies revealed that adults with broods of 7 could raise more young than those with any lower brood size, suggesting that 7 was the most productive brood size. Decline in food supply did not contribute to the decline in clutch size with season (Hussell 1972, 1985; Lyon and Montgomerie 1985, 1987; Montgomerie and Lyon 2020; Nethersole-Thompson 1966; Parmelee in Austin 1968; Parmelee and MacDonald 1960; Parmelee et al. 1967; Soper 1946).

Many first-year males breed, but some in Greenland are unable to obtain territories. Many or most yearling females breed if they can find a mate. In most populations, there is an excess of males resulting in unmated territorial males or small flocks of unmated males after the peak of nest initiation. On Melville Peninsula, the sex ratio was female biased. Unpaired females visited paired males but were chased off by resident females. Unpaired females formed small flocks once all males were paired. Once a bird has bred, it continues to do so annually. The Snow Bunting is typically monogamous, but polygyny occasionally occurs. On Melville Peninsula, 1 of 16 males (6.25%) was polygynous and polygyny was suspected in a second case. In Greenland, 1 male attracted a second female after his first female started incubating. In populations where incubation feeding occurs, widows were able to fledge only about 60% of the number of young raised by pairs and these were lighter and in poorer condition. Females benefit from monogamy because males feed the female during incubation, the nestlings, and half the brood (Lyon and Montgomerie 1987; Lyon et al. 1987; Montgomerie and Lyon 2020; Nethersole-Thompson 1966; Parmelee in Austin 1968).

Upon spring arrival, the Snow Bunting seeks snow-free patches for foraging, such as edges of barren beaches, wind-swept ridges, and steep slopes. At Resolute, flocks occurred at the town landfill. In early spring, it prefers to forage on newly exposed vegetation at the edge of melting snow and also forages on snow, gleaning insects that are immobilized by the cold. As more areas become ice-free, it prefers to feed in vegetated areas such as wet sedge meadows and well-vegetated dry tundra. On Bylot Island, where the Snow Bunting coexists with the Horned Lark, Lapland Longspur, and American Pipit, buntings and larks forage in drier areas and longspurs and pipits feed in thick, moist vegetation. The Snow Bunting forages on the ground by creeping through sparse vegetation, especially clumps of grasses, sedges, and rushes. It takes most food from the bare surface of the soil, but also picks at last year's grass heads to obtain seeds. On warm, sunny days, it captures basking spiders by darting around rocks. In July, it becomes a proficient flycatcher, rising every few seconds to snap at a passing insect. Large crane flies are frequently caught using this technique and butterflies are occasionally caught. Birds may fly as far as 500-700 m from the nest to obtain food for nestlings (Drury 1961; Freedman and Svoboda 1982; Freeman 1970; Geale 1971; Lyon and Montgomerie 1987; Montgomerie and Lyon 2020; Nethersole-Thompson 1966; Smith and Marquiss 1994; Wynne-Edwards 1952).

On Devon Island, more than 90% of food brought to nestlings was adult insects and more than 80% of food items were midges. Midges comprised only 56% of food items before 20 July, but constituted 87% in later samples. The percentage of all insects in the diet increased during this period from 93% to 98%. There was a close correspondence between the peak period of hatching and the initial emergence of adult insects. The nestling diet consisted of 97.0% adult insects, 2.1% other animal prey, and 0.9% vegetable matter. The adult insects were predominantly flies (95.9%), including 82.2% midges, 6.6% crane flies, 3.5% dance flies, 2.7% house flies, and 0.9% unidentified. Other animal foods included 0.4% lepidopteran adults, 0.5% sawflies, 0.2% ichneumonid wasps, 0.4% larvae (mostly lepidopterans), 0.4% pupae (mostly lepidopterans), and 1.5% spiders. Nestling diet in Greenland consisted of 57% spiders, 17% caterpillars, 2% adult lepidopterans, 9% larvae and pupae of crane flies, 7% adult crane flies, and 4% mosquitoes. On Melville Peninsula, the diet of nestling Snow Buntings and Lapland Longspurs overlapped by 96.9%. The food of adult Snow Buntings consists mainly of seeds, especially grass seeds. In summer and fall, they eat a mixture of insects (mainly beetles, lepidopterans, bugs, and flies), spiders, and buds. It eats marine crustaceans, especially sand fleas, and these may be locally important in the diet of birds nesting near coastlines; sand fleas may also be fed to nestlings. On Devon Island, the adult diet was restricted to seeds until mid-June followed by a rapid switch to 2 spider species, with another switch in late June to insects. Adults eat fruits of crowberry in mid-May on the Belcher Islands. On Ellesmere Island, adults ate toasted whole wheat cereal that was put out for them (Drury 1961; Freeman 1970; Hussell 1972; Lyon and Montgomerie 1987; Montgomerie and Lyon 2020; Parmelee in Austin 1968; Parmelee and MacDonald 1960; Sinclair et al. 2003). Gabrielson (1924) analyzed 43 stomachs collected in summer mainly from the Hudson Bay shoreline and the Pribilof Islands in Alaska. The diet consisted of 29.3% animal matter and 70.7% vegetable matter. The animal matter consisted of 3.8% beetles, 25.5% other insects (fly eggs, pupae, and adults, particularly those of crane flies), and 0.02% spider fragments. The vegetable matter consisted of 28.6% grass seeds, 7.0% sedge seeds, 0.2% smartweed seeds, 0.9% goosefoot seeds, 4.4% ragweed seeds, 1.2% grain seeds, and 28.4% of a variety of other seeds. Miscellaneous food items included bushy pondweed, crabgrass, barnyard grass, quack grass, switch grass, timothy, ensheathed dropseed, overlooked dropseed, marram grass, red fescue, campions, purslane, buttercups, cinquefoil, blackberry, clover, crowberry, Virginia creeper, Labrador tea, blueberry, vervain, lousewort, beggarticks, froghoppers, ground beetles, water-scavenger beetles, clown beetles, dung beetles, and leaf beetles.

Availability of suitable nest sites is a limiting factor for many populations. In many areas, there are few suitable nesting cavities close to good foraging areas. Consequently, many nest sites are used for multiple years. Although the Snow Bunting readily accepts artificial nest sites, these are usually present only near human settlements and reproductive success is lower in artificial than natural sites (Montgomerie and Lyon 2020). On Devon Island, Kukal and Pattie (1988) observed 2 cases where arctic bumble bees colonized active Snow Bunting nests and displaced nesting females. Both instances occurred within the same nest cavity so it is unknown how prevalent competition for nest sites by buntings and bumble bees is. Nest-seeking queen bees select well-insulated and isolated nest sites protected from predators, so Snow Bunting nests provide suitable sites for bees.

Spring snowstorms may cause widespread mortality due to starvation. Birds that do not starve may become weakened and become easy prey for predators. Food shortages are more likely during periods of inclement weather (Montgomerie and Lyon 2020; Parmelee in Austin 1968).

Smith and Marquiss (1994) identified a potential impact of climate change on the Snow Bunting. Reduced snow cover may result in decreased productivity, possibly due to effects on invertebrate food supply. This may be of broad conservation and biological significance.

Status

No Snow Bunting nests have been found in Ontario. The only confirmed breeding record in the province is an observation of a family of 2 adults and 2 or 3 fledglings on 20 July 1985 on West Pen Island. There is no other suitable nesting habitat for this species along the Hudson Bay coast except at Cape Henrietta Maria. It has been observed at Cape Henrietta Maria during the breeding season, but without any evidence of breeding (Hussell in Cadman et al. 1987). Wilson and McRae (1993) observed 25 on 21 August and 11 on 27 August at Brant, well before the usual start of migration. These may have been early migrants from an established breeding area, but it was possible that they were family groups raised nearby.

Ontario is at the extreme southern limit of the Snow Bunting's breeding range. The nearest regular breeding site is on the Belcher Islands in southern Hudson Bay (Freeman 1970), approximately 160 km northeast of Cape Henrietta Maria and 550 km east of West Pen Island (Hussell in Cadman et al. 1987). It also breeds on the Nastapoka Islands in Hudson Bay, northeast of the Belcher Islands near Quebec. On the west coast of Hudson Bay, the nearest regular breeding area is about 600 km from the Pen Islands (Godfrey 1986).

No evidence of breeding was obtained for the Snow Bunting during the second atlas, although there were some observations of nonbreeding birds. The 1985 observation remains the only record of breeding in Ontario (Sutherland in Cadman et al. 2007). The single record may represent an unusual extralimital nesting.

POSTFLEDGING PERIOD

The brood scatters soon after leaving the nest cavity, often beyond the male's territory, but some juveniles remain in the vicinity of the nest until they are 60 days old. Brood division occurs with each adult feeding a discrete portion of the brood. The adults continue to feed the young 8-12 days after they leave the nest, although the chicks are capable of catching flies 3-5 days after fledging. Shortly after becoming independent, most juveniles join together in flocks but a few remain with their parents. Fledglings may inhabit boulders in bare scree areas, stony creek beds, and slopes of fiords. A high proportion of juveniles are attracted by large bodies of water, especially oceans. They forage among large driftwood on beaches or on edges of ponds adjacent to the ocean. Premigratory flocking and wandering may occur as early as 30 June and most juveniles leave the parents in late July or early August to form flocks (Campbell and Van Der Raay 1985; Drury 1961; Montgomerie and Lyon 2020; Montgomerie et al. 1983; Parmelee in Austin 1968; Parmelee and MacDonald 1960; Parmelee et al. 1967; Sinclair et al. 2003).

MIGRATION

Birds that winter in Ontario may breed either in the Canadian arctic or in western and southeastern Greenland. Populations breeding in these areas of Greenland migrate across the Davis Strait in autumn, down the coast of eastern North America, and west along the St. Lawrence River. There are numerous spring sightings of birds crossing the Davis Strait from Canada to Greenland. Birds that breed in eastern Greenland winter in Europe. One bird banded in Canada presumably bred in Greenland and was recovered in Scotland. Some migratory populations appear to follow coastlines and concentrate along shorelines of oceans and rivers. Birds wintering in Ontario migrate along the St. Lawrence River to the Gulf of St. Lawrence and then along the Labrador coast to breeding areas in western Greenland. Birds breeding on East Bay Island adjacent to Southampton Island in Hudson Bay appear to winter in the prairies. These birds migrate along the western coast of Hudson Bay. Migration occurs during the day and at night with birds moving in small, loose flocks containing as many as 30 individuals. From 13 to 20 November 1987, approximately 500 per hour arrived at Niagara-on-the-Lake as if they had just crossed Lake Ontario, then crossed the Niagara River and flew west along the south shore of Lake Ontario. During migration, the Snow Bunting occasionally occurs in mixed flocks with Horned Larks, Lapland Longspurs, and Smith's Longspurs. The average staging period is about 10 days (Black and Roy 2010; Macdonald and Love 2012; Montgomerie and Lyon 2020; Orr et al. 1980; Parmelee in Austin 1968; Parmelee and MacDonald 1960; Vincent in Gauthier and Aubry 1996).

The Snow Bunting is the first landbird to arrive in the arctic in spring and the last to leave in autumn. Arrival dates of first spring migrants may vary by as much as a month, with birds arriving later in springs with late snowstorms or persisting snow cover. Adult males arrive on the breeding grounds 4-6 weeks in advance of females, the longest time lag recorded for any passerine species. The early arrival of adult males is probably related to competition for limited or high-quality nest sites. Juvenile males arrive later than adult males and may arrive with the females. Spring arrival even in northern locations may be prolonged over 30-46 days. In Canada, the first spring migrants arrive in the Low Arctic (latitude 60-65°N) in March and in April in the High Arctic (latitude 75-80°N). At this time, temperatures may drop to –30°C and food resources are largely covered with snow. Because of the extended spring migration and differential timing of migratory males and females, average departure dates in southern Ontario are not a good indicator of arrival times on the breeding grounds. In southern and central Ontario, most migrants move through in March with average departure in late March or early April, with some remaining until mid-May. At Shagamu, migrants were observed 28 May to 9 June but not afterwards. On the Belcher Islands, the first bird was observed on 31 March and flocks of about 2 dozen birds were seen occasionally from 29 April to 10 May; pair formation occurred by 12 May. On the Twin Islands in James Bay, spring migrants occurred from 8 May to 6 June. Arrival times in the arctic are the first week of April on Baffin Island with the peak in mid-May; mid-April on Victoria Island with peak numbers throughout May; early April on Banks Island, with most males appearing near the end of that month; on Ellesmere Island, as early as 13 April with the peak in late May; in mid-April on Cornwallis Island; and first migrants in the Yukon appear in late February and early March with the peak in the last half of April (Black and Roy 2010; Curry 2006; Freeman 1970; Geale 1971; LaForest 1993; Lancaster et al. 2004; Manning 1981; Manning et al. 1956; Mills 1981; Montgomerie and Lyon 2020; Parmelee in Austin 1968; Parmelee and

MacDonald 1960; Parmelee et al. 1967; Sinclair et al. 2003; Soper 1946; Tozer 2012; Vincent in Gauthier and Aubry 1996; Weir 2008; Wilson and McRae 1993).

In Alaska, Ward et al. (2016) compared spring arrival dates of migrants over a 50-year period. Warming during this period resulted in the transition from winter to summer occurring weeks earlier than it did previously. The Snow Bunting arrived significantly earlier with time at a rate of slightly over 0.15 day per year or 0.8 day per 1°C increase in temperature.

Flocks of adults and juveniles begin to congregate on the breeding grounds in August. Southward migration begins in August with peak departure from northern breeding grounds from mid- to late September, with stragglers remaining until early November. Females migrate earlier than males and move further south; juveniles leave the breeding grounds after adults. At Churchill, most autumn migrants pass through in early October and large flocks assembled on the coast of the Belcher Islands on 21 September. In southern and central Ontario, the first migrants usually appear in the last half of October with a peak in late October or early November. Migrants may occur from late September to late November (Black and Roy 2010; Curry 2006; Freeman 1970; Jehl and Smith 1970; LaForest 1993; Lancaster et al. 2004; Montgomerie and Lyon 2020; Mills 1981; Sinclair et al. 2003; Tozer 2012; Weir 2008).

The Snow Bunting uses a variety of open habitats during migration. In Muskoka and Parry Sound districts, it frequents beaches, rocky shorelines of lakes, gravel pits, and fields. In Algonquin Park, spring migrants occasionally occur on frozen lakes where they feed at the edge of melting ice. In the south, autumn migrants are initially found on beaches; rocky shorelines of large lakes, rivers, and islands; and occasionally in fields, gravel pits, and on roadsides. Once water freezes or the ground becomes snow-covered, it moves to open fields. During spring migration, it occurs along roads and in typical winter habitat such as old fields and agricultural lands, particularly where manure has been spread. During migration and winter in British Columbia, it occurs in almost any type of exposed habitat such as grasslands, windswept fields, sandspits, extensive lakeshores, and roadsides. It may also occur at airports, cattle feedlots, stockyards, areas of extensive mine tailings, golf courses, jetties, sewage ponds, and rock-strewn islets. Twenty-nine percent of nonbreeding records were from grasslands, 14% at airports, 14% along roads, and 10% at coastal jetties. It occasionally occurs on lawns and expanses of pavement. In the Yukon, some birds inhabit high altitude alpine areas during migration and in the far north it may be common in villages during spring migration (Campbell et al. 2001; Curry 2006; LaForest 1993; Mills 1981; Sinclair et al. 2003; Tozer 2012; Weir 2008).

At La Pérouse Bay in Manitoba, spring migrants fed on leaves of creeping alkali grass. This species and Hoppner's sedge are the dominant plant species in this area and along many subarctic coasts. The leaves of salt-marsh grass contain high concentrations of nitrogen suggesting that it may be an important source of nutrients for spring migrants. There are few records of the Snow Bunting eating vegetation other than seeds, and these include buttercup leaves, moss fragments, and leaves of bog bilberry and mountain avens (Bazely 1987). During autumn migration, Sutherland et al. (2016) reported it foraging in wild rice beds in Pigeon Lake, Peterborough County. The wild rice was approximately 500 m offshore in open water 1-3 m deep. A flock of 30 buntings landed in the tops of wild rice, bending them down to within a few centimetres of the water. Several times

the flock arose, shifted location, and repeated the process. They appeared to be gleaning rice grains or possibly invertebrates.

Montgomerie and Lyon (2020) suggested that the Snow Bunting could be exposed to agricultural pesticides during migration and winter but acknowledged that no studies had been done on this and that no data were available. In Quebec, overwintering birds sampled in March had no detectable amounts of atrazine, clothianidin, or imidacloprid in the blood and liver and there were no detectable amounts of glyphosate or aminomethyl phosponic acid in the liver. Wintering bunting may not be exposed to these chemicals during their presence in agricultural fields or be exposed to doses below detection levels (Ruhs et al. 2021).

James (1991) considered the Snow Bunting a common to locally abundant migrant in the province. Wilson and McRae (1993) noted that it was an abundant spring and autumn migrant along the Hudson and James bay coasts. Flocks of 1,000 birds may be seen with some regularity in most areas south of the Canadian Shield, but flocks on the Shield are much smaller and limited in distribution.

WINTER

In winter, the Snow Bunting typically occurs in flocks, often with Horned Larks and occasionally with Lapland Longspurs. It inhabits open weedy and grassy fields; grain stubble; shorelines, especially where the wind has piled up driftwood and debris or where there is little bluestem; tidal flats; manure-covered fields; and pastures. When snow is deep, it may occur along roadsides and railway lines and selects fields where herbaceous plants and grasses protrude through the snow. Females tend to winter further south than males. Near Ottawa, winter flocks are comprised of 90-95% males. Flocks in Windsor, Long Point, and Cayuga are dominated by females. Males exhibit higher cold tolerance than females because of their larger body size and can inhabit areas further north in winter. In alpine areas, adults winter at higher elevations than juveniles and adult males winter higher than adult females. When these areas are snow-free, they provide vast areas of open ground with seed-producing plants, a habitat that is largely unexploited by other bird species (Black and Roy 2010; Gabrielson 1924; Leighton et al. 2002; Macdonald and Love 2012; Macdonald et al. 2016; McIlwraith 1894; Montgomerie and Lyon 2020; Smith et al. 1993; Vincent in Gauthier and Aubry 1996; Vincent and Bédard 1976; Weir 2008).

In New York, the Snow Bunting occurred more frequently in fields with corn stubble than in pastures. Its probability of occurrence increased with increasing amounts of open habitat within 500 m (Rosenblatt and Bonter 2018).

The Snow Bunting is highly gregarious during the day, but just before sunset flocks break up into smaller groups of 7 or 8. These fly back and forth between feeding areas and recently preselected roosting sites. Roosts are in sites offering greater surface microrelief than normally found at foraging sites. Near Quebec City, birds made no attempt to select protected areas when night temperatures were above –7°C except under very windy or sleety conditions. Under colder conditions, birds settled individually on the leeside of snow drifts, but did not sleep in holes or under overhangs. The average distance between individual roosts was 2.5 m and seldom closer than 30 cm. Birds did not huddle together even under extreme conditions of –27°C with 45 km per hour winds. In Massachusetts, a flock of 150-200 buntings sought shelter from a temperature of –37°C

accompanied by winds by digging themselves into soft snow under the leeward edges of shallow snowdrifts in an open field. Temperatures remained below –29°C 1 day, and birds remained in these holes, leaving only occasionally to feed nearby. When the snow is frozen hard, flocks sleep in the open, protected from the wind only by some slight rise in the ground, by sand dunes, or by a stone wall. On windy days, birds attempt to find shelter on the leeside of irregularities in the snow and on exceptionally cold days, they withdraw 1 leg into the plumage and hop around. Although the Snow Bunting spends almost all its time on the ground, on warm days it may occasionally perch in trees or even on overhead wires (Bagg 1943; Leighton et al. 2002; Parmelee in Austin 1958; Vincent in Gauthier and Aubry 1996; Vincent and Bédard 1976).

Winter flocks near Quebec City followed a regular daily feeding pattern over an area of about 4 km². Flocks occasionally stayed in 1 location for 1-2 weeks where goldenrods and asters protruded through the snow. At less ideal sites, birds may remain for only a few hours, but flocks may remain for several weeks in fields where manure has been spread (Montgomerie and Lyon 2020; Vincent in Gauthier and Aubry 1996; Vincent and Bédard 1976).

The Snow Bunting may exhibit site fidelity to wintering areas. In Michigan, 51 of 596 birds (8.6%) returned in subsequent years; 1 bird was trapped in 9 different winters. Some birds wander during the winter. Birds banded in December or January have been recaptured the same winter 133-241 km further south (Brewer et al. 2018).

In winter, the Snow Bunting forages by walking on the snow and collecting seeds from stems of protruding tall plants. Occasionally, it reaches up or leaps to take seeds from taller stems, jumps against a stem to scatter seeds, or bends a stem over by stepping on it. It also feeds on seeds that are blown over the surface of the snow. As spring approaches, it may move to exposed ground in plowed fields or open terrain at margins of melting snow patches. Seeds and possibly insects accumulate in snow layers over winter and are transported by melt water and sought for in pools near snow patches. It is particularly attracted to fields where manure has been spread where it presumably feeds on undigested seeds in the manure. In maritime areas, it forages on open beaches, following waves in a manner similar to sandpipers. In open habitat, it occasionally visits winter bird feeders. It carries large fat stores even at its lowest winter weight and can survive 2-3 consecutive days of complete food deprivation (Black and Roy 2010; Lancaster et al. 2004; Montgomerie and Lyon 2020; Vincent in Gauthier and Aubry 1996; Vincent and Bédard 1976). McIlwraith (1894) reported that it fed on bare, sandy areas near Lake Ontario where it ate seeds of little bluestem. Near Quebec City, Vincent and Bédard (1976) observed it feeding on the seed heads of asters, goldenrods, and goosefoots. At feeders, it usually feeds on corn and millet and has been documented feeding on a pile of grain (Lancaster et al. 2004; Leighton et al. 2002). Parmelee (in Austin 1968) reported it feeding on seeds of ragweed, amaranth, goosefoot, locust, and oats. Gabrielson (1924) examined 418 stomachs collected from October until April. He reported on an earlier examination by Judd (1901) of 46 stomachs collected in New York, Michigan, Wisconsin, and Ontario that found that the dominant foods were seeds of ragweed, amaranth, and grain. In winter, 3.4% of the diet was comprised of animal matter and 96.6% was vegetable matter. Animal food was taken only in March, October, and November, possibly only during migration. Animal food included clover root weevils, other beetles, fragments of caterpillars and bugs, spiders, and isopods. The diet

of 2 Ontario birds consisted of 60% caterpillars. Of 24 birds collected in October, 7 had eaten animal matter, 13.5% of the total diet for that month. Of 27 November birds, 12 had eaten animals, including beetles (0.9%), other insects (mostly caterpillars, 6.3%), spiders (1.0%), and miscellaneous animals, for a total of 8.1%. The vegetable matter consumed during winter consisted of a variety of seeds. Wisconsin birds all fed extensively on seeds of foxtails, ragweed, goosefoots, and amaranth. Elsewhere, it also ate seeds of sedges, other grasses, and wheat that consisted of waste grain. Overall, grass seeds comprised 31.2% of the winter diet, including 11.8% yellow and green foxtail, plus 4.4% sand grass in New York. Other food items included 8.5% sedges, 3.7% smartweed (mostly pale smartweed and black bindweed), 5.5% goosefoot (mostly lamb's-quarters), 5.6% amaranth, 11.5% miscellaneous seeds, 9.4% ragweed, 13.1% wheat, and 4.7% other grain taken as waste (corn, oats, and barley). Miscellaneous seeds consumed included those of paspalum, meadow fescue, and yellow rocket. In April, 56.4% of the diet consisted of grain, predominantly wheat. This figure was inflated because 37 of the 64 birds were taken while feeding on stacks of grain.

James (1991) considered the Snow Bunting a common to abundant winter resident in the south and rare in the west in the Thunder Bay area. There are occasional winter records from Muskoka and Parry Sound districts, but most leave by the end of November as deep snow forces them further south (Mills 1981).

Freedman and Riley (1980) reported that numbers on southern Ontario Christmas Bird Counts (CBC) were variable, but they had increased since 1929. The Snow Bunting was abundant but exhibited an irregular cycle with periods between peaks ranging from 2 to 5 years. Montgomerie and Lyon (2020) noted that CBC results suggested that the Snow Bunting was in serious decline in North America. It is 1 of 20 species whose population has declined by more than 50% over the past 4 decades based upon CBC results. CBC data indicate a 64% decline in 40 years, with an annual decline of 2.5% per year. The CBC does not survey this species accurately because much of the population winters north of or outside local areas covered by this survey (National Audubon Society 2022).

Grasshopper Sparrow

Ammodramus savannarum

BREEDING SEASON

Habitat Requirements

Ontario Grasshopper Sparrow nests were in areas with short and tall grasses, hayfields, and pastures that were often overgrown with shrubs and small trees (51.5% of nests); in Christmas tree and other conifer plantations in grassy fields (33.8%); on road and railway rights-of-way (11.8%); a grass- and cedar-covered island near a gull colony (1.5%); and in a beach savannah (1.5%; Peck and James 1987).

There are a few breeding records from the southern Canadian Shield, but the Grasshopper Sparrow is predominantly limited to the area south of the Canadian Shield and the Rainy River area. In the Great Lakes–St. Lawrence Forest Region, it occurs mostly on droughty sand, till moraines, and alvars or areas of shallow soils over limestone. These areas are often pastures but others on moraines may consist of sparse grasslands where slopes are too steep to farm. In old-field habitats, it is often associated with common mullein stalks. These may be 0.9-1.5 m tall and are frequently used as

singing perches. Historically, the improved pastures and hayfields that it used were planted to a mix of clovers, alfalfa, and timothy. In the Great Lakes area, it prefers anthropogenic habitats such as pastures, hayfields, recently abandoned fields, grassy fields at airports, and young conifer plantations. Occupied sites are often dominated by plant species adapted to poor dry soils such as bluegrass, quack grass, poverty oat grass, wild strawberries, timothy, and silverweed. It also nests in alvars dominated by little bluestem and poverty oat grass. It rarely uses old fields with dense shrubs or tall vegetation, dense hayfields, or heavily grazed pastures with few perches. It prefers moderate vegetation height (25-50 cm), moderate amounts of bare soil (mean 17%), and a moderately thick litter layer (mean 4 cm; Earley in Cadman et al. 2007; Hope 1946; Savignac 2013; Speirs and Orenstein 1967).

In the Carolinian Forest Region, the Grasshopper Sparrow nests predominantly on moraines and drumlins, on alvars, and on sand plains and other areas where soils are poor with sparse grassy vegetation. In the Hamilton area, it may occur in grassy fields and meadows but prefers stony pastures where mullein stalks provide perches (Curry 2006). It nested in a Christmas tree plantation on the Flamborough Plain where the coverage of woody vegetation was higher than typically documented for this species (personal observation). It formerly nested in a weedy field in an industrial area in Cambridge, but the habitat was subsequently converted to a parking lot (personal observation). In Niagara Region, it is most abundant in fallow fields south of Welland created when the Welland Canal was diverted (Black and Roy 2010). Near Dain City in Niagara Region, it nested on a hill constructed of spoil from the excavation of the Welland Canal. The clay subsoil is nutrient-poor and results in sparse vegetation and patches of bare soil, preferred habitat (personal observation). On the Norfolk Sand Plain, it nests in fields planted to winter wheat and rye that produce grassland-like habitat early in the season. Even the mature crop is sparse because it is growing on sand and therefore provides suitable habitat (Earley in Cadman et al. 2007). In Elgin County, most nesting occurs in pastures and grassy meadows (Lancaster et al. 2004).

The Grasshopper Sparrow is a grassland species, occupying a wide range of grassy areas throughout its range. It is a fairly uncommon species, probably due to its microhabitat requirements. It requires a mix of clumped vegetation and bare soil and tends to avoid areas that do not have these characteristics. Bare soil facilitates movement by the birds and provides good foraging habitat. Denser vegetation provides concealment from predators and cover for the nest. Vegetation of intermediate height is preferred and it avoids areas with tall or dense grasses. Areas of uniform short

or sparse grass are also avoided. It avoids grasslands with a significant woody component. A small proportion of grasslands provide habitat that is suitable for the Grasshopper Sparrow.

In the northeast, the Grasshopper Sparrow nests predominantly in anthropogenic habitat such as pastures, old fields, and hayfields. It may nest on capped landfill sites and, further south, on reclaimed surface mines. It occasionally uses row crops for nesting, but at much lower densities. In Quebec, it shows a marked preference for fallow fields and old pastures where the soil is sandy and well drained. It is partial to areas with grasses such as timothy and quack grass along with other plants that thrive on poor acidic soils such as tufted vetch, viper's-bugloss, and common milkweed. It selects sites with few shrubs and is partial to fields with milkweeds, which it uses as song perches. In Maine, it nested in fields of lowbush blueberry that were commercially harvested; these areas were burned and mowed on a regular basis. Natural habitats used in the east include prairie remnants, oak savannahs, pine and oak barrens, and coastal sand dunes. In the Prairie Provinces and Great Plains, it nests in tallgrass and mixed-grass prairies and fields planted to nonnative grasses. Native grasses that are often in prairies that it inhabits include little and big bluestem, switch grass, broomsedge, Indian grass, native wheat grasses, grama grass, and wiregrass. Planted warm-season grasses that it may use include Kentucky bluegrass, smooth brome, timothy, quack grass, nonnative fescues, wild rye, Virginia wild rye, orchard grass, creeping bentgrass, and crested wheat grass. Conservation Reserve Program (CRP) and Dense Nesting Cover fields planted on marginal lands may be used. Lands that are maintained idle, grazed, or cut for hay may be used. Corn and small grain fields may be used for nesting, but it typically selects no-till fields where there is year-round crop residue. It rarely inhabits fields managed with conventional tillage. It occasionally nests in cottonwood forest. In the west and southwest, it nests in sparse grasslands and is less likely to nest in burned, cut, or grazed areas than in the lusher grasses of more mesic sites. The Florida subspecies of the Grasshopper Sparrow nests in dry prairie grasslands that are maintained by burning. Habitat for this subspecies is different from other locations within its range, although it still nests in sparse cover with a mix of clumped vegetation and bare ground. Other habitats it may occasionally nest in include grassed waterways in grain fields, airports, military bases, and road and railway rights-of-way (Ahlering et al. 2009; Askins et al. 2007; Campbell et al. 2001; Chapman et al. 2004; Dechant et al. 2002b; Delany et al. 1985, 1993; Dieni and Jones 2003; Giocomo et al. 2008; Graber and Graber 1963; Grant et al. 2004; Graves et al. 2010; Hainault in Gauthier and Aubry 1996; Herkert 1994a; Hill and Diefenbach 2013; Jones and Bock 2002; Mossman et al. 1991; Patterson and Best 1996; Renfrew and Ribic 2008; Rotenberry and Wiens 1980; Smith in Austin 1968; Smith and Smith 1992; Swanson 1996; Vickery 2020; Vickery et al. 1994; Walcheck 1970; Whitmore 1981; Wiens 1969, 1973; Wilson and Belcher 1989; Wray et al. 1982).

Several studies examined Grasshopper Sparrow habitat at the landscape scale, often with conflicting results. In Michigan, Minnesota, and Wisconsin, its abundance was positively correlated with coverage by grasslands within 800 m (Murray et al. 2008). Thogmartin et al. (2006) used Breeding Bird Survey (BBS) data and point counts to determine that its abundance was most influenced by climatic variables (wetness and temperature) rather than environmental variables. Models that included the proportion of the landscape that were in grassland or grassland patch area were not among the best models. It was negatively affected by the amount of forest cover within 800 m suggesting that it was more abundant in landscapes with greater herbaceous cover. In the

United States Great Plains at the 400-m scale, it selected drier sites with short or sparse vegetation. It increased significantly with the amount of grassland in the landscape. Probability of occurrence was low with less than 20% grassland within the sampling area and high at 80-100% grassland coverage (Niemuth et al. 2017). In South Dakota, it was unaffected by the amount of grassland in the landscape (Greer et al. 2016). In Quebec, occupied areas had more perennial crops (grasslands, pastures, and old fields) and less forest within 200 m than unoccupied areas. Around occupied areas, there was 59.1% coverage by perennial crops and 31.8% forest cover compared with 42.5% perennial crops and 16.0% forest around unoccupied sites. Male density was not affected by patch size but was positively correlated with the surrounding perennial crop coverage and negatively correlated with forest coverage (Jobin and Falardeau 2010). In Wisconsin, landscape composition was important at the 1,200-m scale, particularly the amount of grassland within this area. Percent grassland coverage was important at the 200-, 700-, and 1,200-m scales. Birds may respond, at least in part, to the landscape at a broader scale as they make settling decisions. Landscape composition may be more important than habitat fragmentation for grassland birds. In this area, grassland fragmentation is more related to a reduction in grassland quality by conversion of native grasslands to areas planted with nonnative grasses (Renfrew and Ribic 2008). In the same area, abundance of the Grasshopper Sparrow was associated with cover-type diversity within 200 and 400 m, the area of grassland within 400 m, and distance to hedgerows. Densities were higher when there was low cover-type diversity within 200 and 400 m; low cover-type diversity landscapes were dominated by hay and grassland. Densities were higher when there were more hedgerows in the landscape or when hedgerows were closer. Although effects as far away as 800 m were studied, it was associated only with landscape variables within 200 m, indicating a more local effect (Ribic and Sample 2001). In Pennsylvania, landscape characteristics did not affect occupancy in the largely forested landscape where grasslands constitute only 8% of the landscape. Hill and Diefenbach (2014) considered it landscape insensitive. Forests were not a barrier to its dispersal and colonization, even when more than 80% of the landscape was unsuitable habitat. In Nebraska and Iowa, the degree of urbanization within 1,600 m did not affect its occurrence, but density declined with the intensity of urbanization. Urbanization at the landscape scale may indirectly decrease the quality of grasslands for Grasshopper Sparrows even if vegetative characteristics do not change. Nonetheless, grasslands in suburban and urban areas may provide conservation value (McLaughlin et al. 2014). In Missouri, its abundance declined with increasing amounts of hayfields within 400 m, but only in hayfields; abundance increased with the amount of hayfields surrounding pastures (Davis et al. 2016). It preferred landscapes with 0-15% tree coverage in North Dakota (Cunningham and Johnson 2019).

The amount of woody vegetation within grasslands may affect suitability for the Grasshopper Sparrow. In the east, it tends to prefer areas with minimal shrub coverage; some shrub coverage may be essential in certain western habitats. Even within small geographic areas, the coverage of shrubs that it prefers or will tolerate may vary considerably. In New York, pastures it inhabited contained as much as 36% coverage by shrubs and trees, and hedgerows were frequent within the habitat (Smith and Smith 1992). In mixed-grass prairie in North Dakota, coverage by shrubs taller than 1 m and the amount of aspen within 100 and 500 m were significantly lower at sites where it was present compared with unoccupied areas. It reached its maximum occurrence of 80% in open treeless grassland. Its probability of occurrence dropped to 50% at 25% tree coverage. It also

declined with increasing abundance of tall shrubs. It was a woodland-sensitive species whose incidence dropped to 0% at about 65% woodland cover. It was negatively affected as woody plant height increased from shrubs shorter than 1 m to tall shrubs and trees (Grant et al. 2004). Arnold and Higgins (1986) surveyed transects with shrub coverage (30-80% coverage by snowberry and wolfberry) and transects with less than 10% coverage by these shrubs. Its density was approximately 3.2 times higher on the shrubless plots. Density of the Grasshopper Sparrow was strongly inversely related to the amount of woody cover in North Dakota and Saskatchewan (Ahlering et al. 2009). In mixed-grass prairie in Oklahoma, its abundance was strongly negatively correlated with coverage by red cedar and was consistently near 0% at 25% coverage by red cedar. Despite this, red cedars were frequently used as song perches. Chapman et al. (2004) suggested that its upper tolerance to woody vegetation was 25-35% coverage. In Georgia, densities were similar in 0% and 10% shrub coverage but it was absent when shrubs covered 35% of the field even though more than 50% of the total area had good grass coverage (Johnston and Odum 1956). In Florida, territories were devoid of trees and the Grasshopper Sparrow avoided areas of even widely spaced trees at densities of less than 1 tree per ha. Territories near trees were 75 m or more from edges of plantations. Singing perches were in shrubs 0.9 m or less in height (Delany et al. 1995). Shrub coverage was 19.9% in occupied territories and only 1.6% in territories abandoned in a declining population; this difference was significant. The range of shrub coverage in territories was 0-33.9% (Delany and Linda 1994; Delany et al. 1985). On reclaimed surface mines in West Virginia, shrub coverage was 0.7% in occupied territories, significantly less than in unoccupied areas (31.1%). It was 10 times more abundant on sites dominated by grasses than in areas with shrub coverage interspersed by small trees (Margenau et al. 2019; Whitmore 1981). On Ohio surface mines, woody vegetation negatively affected its abundance, nest placement, and nest success. Nest sites had 2.5 times less woody vegetation (1.5%) than random sites (4.0%) and daily nest survival rate was negatively affected by the amount of woody vegetation surrounding nests (Graves et al. 2010). In British Columbia, it avoided areas of dense sagebrush. Where shrubs are present, it appears to select patches of grasses among them (Campbell et al. 2001). In Maine, the Grasshopper Sparrow nested in meadows dominated by lowbush blueberry, a short shrub. The site supported lesser amounts of graminoids, forbs, and other shrub species (Vickery et al. 1994). In Nebraska and Iowa, its occurrence was positively correlated with shrub density per m^2. Probability of occurrence was approximately 55% at 0 shrub density, 75% at 0.25 shrub density, and 100% at 0.6-1.0 shrub density. Sparrow density per km^2 increased from 5 at 0 shrubs per m^2 to 10 at 4 shrubs per m^2 (McLaughlin et al. 2014) In Montana, it nested in a cottonwood forest with a subcanopy layer of green ash and Manitoba maple. The ground flora consisted of moderate to heavy thickets of snowberry and rose with a heavy litter accumulation, and limited amounts of forbs and grasses; wheat grass was the most common grass species (Walcheck 1970).

Several studies compared Grasshopper Sparrow usage of different grassland types. In Oklahoma, its density in nonnative bluestem grasslands was approximately 1.8 times higher than in native grasslands. Planted grasslands provided larger tracts of homogeneous habitat with little shrub coverage, less vertical cover, and shorter vegetation. These habitat characteristics were all favourable for it. The biomass of invertebrates that were suitable prey was lower in nonnative fields, suggesting that prey abundance was not a limiting factor (George et al. 2013). In Manitoba, its

abundance was significantly correlated with Kentucky bluegrass and negatively correlated with June grass (Wilson and Belcher 1989). In Missouri, it was more abundant in planted grasslands than in native grasslands (Davis et al. 2016). In North Carolina, there were no significant differences in its abundance in native and nonnative grasslands that were grazed or cut for hay, although it tended to be more common in nonnative grasses. It was absent in fields managed to maintain a mix of native grasses and forbs, possibly due to the lack of bare ground (Moorman et al. 2017). In Illinois, it prefers shorter, more open vegetation typical of grazed or hayed grasslands, or even croplands, to the dense cover of CRP fields. Highest density occurred in unplanted crop fields grown up with annual weeds. Fields of no-till soybeans with grassy residual vegetation supported good numbers, but the Grasshopper Sparrow was absent in conventionally tilled fields (Walk et al. 2010). In Iowa, nest success in CRP fields was twice that in alfalfa fields. It was an infrequent nester in grassed waterways and was not found in roadside habitats (Patterson and Best 1996). In Michigan, it preferred hayfields and avoided permanent pastures, but was more common in grazed than mowed fields (Dechant et al. 2002b). In Ohio, densities were higher in meadows than in corn and small grain fields. In Wisconsin, row crops were avoided during the breeding season. In the northeastern United States, densities in CRP fields are more than 40 times greater than in adjacent cropland (Swanson 1996). In Wisconsin, it occurred at higher densities in dry pastures and dry prairies than in alfalfa and nonnative cool-season grasses, where it was absent. Density in Kansas was higher in pastures than in CRP lands (Ribic and Sample 2001). In Pennsylvania, Smith (1963) attributed a sharp decline in population to a change in species cultivated for hay. Early crops consisted of timothy, alfalfa, and red clover. Later crops consisted of heavy growths of alfalfa and brome grass. Once dense hayfields were established, most of the population occurred in hay and abandoned fields that supported less vigorous growth. In Washington, it was more abundant in CRP fields than in native shrubsteppe vegetation; there was no difference in its abundance in old or newly established CRP lands. Its abundance was negatively correlated with shrub and perennial forb abundance (Vander Haegen et al. 2015).

Several studies compared vegetative structure at nest sites to the remainder of the territory or features within territories to those in unoccupied areas. The Grasshopper Sparrow tends to occupy habitat with moderate vegetation density and height with areas of bare ground. In Quebec, there were no significant differences in vegetation characteristics, structural heterogeneity, and perch-site density between occupied and unoccupied sites. Sites were all grasslands, ranging from young abandoned fields located on poor sandy soil to regularly mowed hayfields lacking prominent perch sites. The lack of difference between occupied and unoccupied areas may have been because they only studied sites that appeared to be suitable habitat (Jobin and Falardeau 2010). On reclaimed mine surfaces in West Virginia, nest sites had more bare ground, greater vegetation height-density, taller grass at the nest, and shorter grass 5 m from the nest than areas without nests. Vegetation height-density and maximum grass height increased with age after reclamation and the amount of bare ground decreased. The Grasshopper Sparrow used grasslands with a mix of native and nonnative grass and forb species interspersed with bare ground. Habitat suitability decreased with time after reclamation. Nest success was 30% higher in grasslands 3-10 years old than in those 11-20 or more than 20 years old (Wood and Ammer 2015). In North Dakota, coverage by live vegetation, shrubs taller than 1 m, aspen within 100 and 500 m, and Kentucky bluegrass and smooth brome

was significantly less where it was present than where it was absent. Occurrence was greatest on plots dominated by Kentucky bluegrass intermingled with native grasses and forbs (Grant et al. 2004). In Kentucky, nest sites had fewer shrubs (48.85 compared with 52.96 in a 0.04-ha circle), more tree coverage (3.96% compared with 0.78%), less vertical cover 0.5-2 m from the ground, and greater foliage coverage 0.5-1 m from the ground (0.70 compared with 0.33 stems within 10 cm) than random sites in territories (Sutter and Ritchison 2005). In Florida, most vegetation characteristics did not differ significantly between nest sites and non-nest sites within territories. Vegetation density at non-nest sites was significantly lower than within 1 cm of the nest and significantly higher than at 1 and 2 m from the nest. Vegetation density was the most important nesting parameter. The availability of small clumps of dense vegetation slightly larger than the nest diameter within more open patches 4 m or less in diameter was an important factor influencing nest selection. Features of occupied territories compared with those of territories abandoned by a declining population were strikingly different. Values for occupied and abandoned territories respectively included: grass cover, 36.7% and 83.1%; shrub cover, 19.9% and 1.6%; forb cover, 7.7% and 2.0%; litter cover, 10.2% and 12.7%; bare ground cover, 25.6% and 0.2%; and vegetation height, 21.4 cm and 11.0 cm. All parameters except for forb and litter coverage were significantly different. Sparrows selected areas with taller vegetation but less vegetative cover and more bare ground (Delany and Linda 1994, 1998a). On West Virginia reclaimed mines, Whitmore (1981) also reported differences between territories and unoccupied areas, with differences significant for all variables except vertical density and percent forb cover. Values for territories and unoccupied areas respectively included: grass cover, 25.7% and 84.1%; shrub cover, 0.7% and 31.1%; litter depth, 2.4 cm and 6.6 cm; horizontal diversity, 1.2 and 1.5; vertical density in hits by live vegetation per 10 cm, 4.2 and 3.8; bare ground cover, 21.9% and 3.6%; vertical diversity, 0.8 and 1.2; total vegetation density in hits per transect, 339.4 and 504.8; effective vegetation height, 43.8 cm and 56.5 cm; forb cover, 24.7% and 28.7%; and litter cover, 72.5% and 93.3%. Territories were more sparsely vegetated, with higher values for bare ground and lower values for all variables related to vegetation height and grass, forb, and shrub coverage. It typically inhabited open areas dominated by grasses that grow in clumps rather than those that form continuous sod. Sod-forming grasses create a mat of dense vegetation that inhibits foraging; clump-forming grasses leave openings. In Montana, nest sites differed significantly from random sites for four parameters. Values for these parameters for nest and random sites respectively included: bare ground, 0.4% and 1.5%; visual obstruction, 1.3 and 0.9; plant height, 32.5 cm and 24.1 cm; and vertical density, 5.5 and 3.5. In addition, 31.0% of nests were associated with grama grass compared with 12.0% of random sites and 4.8% of nests were associated with western wheat grass compared with 29.2% of random sites. It selected for vertical vegetative characteristics at the immediate nest site rather than at the nest-patch scale. Unlike many other areas, nest patches were devoid of any significant amounts of bare ground. For nesting substrate, western wheat grass was avoided and grama grass was selected (Dieni and Jones 2003). On reclaimed surface mines in Indiana, height of the dominant vegetation within 1 m of the nest was positively correlated with nest success (Galligan et al. 2006). In Wyoming, Montana, and South Dakota, the Grasshopper Sparrow greatly preferred sites where black-tailed prairie dogs were absent and vegetation had not been altered. Sites without prairie dogs had a higher percentage of grass cover, higher visual obstruction, and less bare ground (Augustine and Baker 2013). In Wisconsin, coverage by forbs and grasses was similar in territories and unoccupied areas. Forb density was lower in unoccupied areas;

these forbs were significantly taller than in territories. Vegetation density was significantly less in territories: total vertical vegetation density and mean effective height were significantly less, light penetration to the ground was increased, and coverage by lawn-like vegetation was greater. Vegetation density in the 0-10-cm height interval was significantly greater in territories. Litter was slightly less compact and significantly shallower than in unoccupied areas. Vertical vegetation density about nests did not differ significantly from the entire territory, but the mean effective height of vegetation was significantly higher at the nest. Forbs at nests were significantly taller than those in the entire territory (Wiens 1969). In desert grasslands in Arizona, it selected territories in areas of sparser vegetation structure with more shrubs taller than 2 m than in random plots. Some taller shrubs were preferred for song posts. Even in these sparse grasslands, grass structure can be too high and dense. Males selected territories with a maximum of 10 cm of visual obstruction and 7 vegetation hits in 40 cm for vertical vegetation density. The proportion of area covered by nonnative grasses did not influence territory selection. There was limited evidence for territory selection based on litter depth or amount of bare ground. Females selected nest sites in areas with low densities of shrubs 1-2 m tall and preferentially selected areas with native grasses to build nests under. Suitable habitat for territories and nests consisted of visual obstruction readings of 4-14 cm for territories and 5-12 cm for nest sites, vertical vegetation density of 4.8-7.8 hits on a 40-cm pole for territories and 5.0-7.6 for nest sites, more than 40% native grasses at the nest site, 0.2-0.5 shrubs 1-2 m tall per ha (slightly lower for nests), and 0.2-0.3 shrubs taller than 2 m per ha (Ruth and Skagen 2017).

Microhabitat preferences of the Grasshopper Sparrow were identified in several studies. In Quebec, mean coverage of live vegetation was 47%, coverage by dead vegetation was 33%, and bare soil coverage was 19%. The mean vegetation height was 23 cm and the litter depth was less than 4 cm. Plant species present at more than 50% of occupied sites included bluegrass, quack grass, silver cinquefoil, creeping cinquefoil, poverty oat grass, wild strawberry, and timothy (Jobin and Falardeau 2010). In Wisconsin, it occurred at highest densities in the driest habitats with relatively short vegetation (Ribic and Sample 2001). It is typically associated with dry soils and often with nutrient-poor or shallow soils that inhibit dense growths of vegetation. Mean habitat characteristics in Florida included 25.5% grass cover, 19.2% shrub cover, 4.5% forb cover, 14.4% litter cover, 36.2% bare ground, 30.7 stems per m^2, 0.7 cm litter depth, and 27.8 cm vegetation height (Delany et al. 1985). At 2 other Florida sites, mean grass height was 56 and 58 cm. Nest sites had more grass cover and less bare ground (Larned et al. 2020). In North Dakota on both shrubby and non-shrubby transects, highest density occurred in areas with the highest vegetation-height densities. These areas were subjected to light grazing. Grazing intensity was more important than shrub coverage in defining habitat quality. In West Virginia on 3 reclaimed mines, optimal conditions included 73.1% litter cover, 24.1% bare ground, and 27.8% grass cover. Habitat selected at all sites did not vary significantly from the optimum values. Choice of territories was dictated by the overall density of ground cover. There must be enough open or bare ground (a minimum of 24% in this case) to allow free movement but provide adequate cover for nest sites. Density at each site was related to the proportion of habitat that provided conditions similar to the optimal variables (Whitmore 1979). In Pennsylvania, ground cover at nests averaged 6% bare ground, 30% forbs, and 64% grass. Height of vegetation at nests was 28 cm for forbs, 54 cm for grasses, and 6 cm for thatch (Hill and Diefenbach 2013). In North Dakota grazed mixed-grass prairie, abundance of the Grasshopper Sparrow was

positively correlated with grass cover, litter depth, visual obstruction, density of low-growing shrubs, vegetation density, and communities dominated by shrubs with smooth brome, Kentucky bluegrass, and quack grass; and those dominated by Kentucky bluegrass, wiregrass, grama grass, and Indian grass. It was negatively correlated with clubmoss. The strongest predictors were decreasing clubmoss cover, decreasing bare ground, and increasing litter cover. In Missouri tallgrass prairies, it decreased with increasing vegetation height and amount of woody cover (Dechant et al. 2002b). In shrubsteppe vegetation, it was positively correlated with grass cover, litter cover, total hits by live vegetation, maximum interval containing hits, effective height, and litter depth. It was negatively correlated with bare ground, litter depth, and litter height. The abundance of tallgrass species (Grasshopper Sparrow, Dickcissel, and Eastern Meadowlark) was associated with dense grass and deep litter, but these species had a strong negative association with bare ground and other variables associated with increasing horizontal heterogeneity (Rotenberry and Wiens 1980). In Kentucky and Tennessee, its abundance was positively correlated with a 30-70% grass mixture of native warm-season grasses, cool-season grasses, and herbaceous cover. Its abundance was not affected by distance from low-traffic roads (Lituma and Buehler 2016). In Missouri, it was associated with planted grasslands with higher cover by bare ground (Davis et al. 2016). Swanson (1996) reported that it was negatively correlated with legume cover. Mean habitat characteristics in Wisconsin were 3% woody cover, 76% herbaceous cover, 16% litter cover, 8% bare ground, 57 cm maximum vegetation height, and 14 cm vegetation-height density. Mean characteristics in Arizona included 5% woody cover, 72% grass cover, 4% forb cover, 23% bare ground, and 30 cm mean grass height. In Iowa, its abundance was negatively correlated with the vertical cover of vegetation. It was most abundant in fields with grass height less than 0.5 m and moderate vertical cover of 0.3 m. Thick stands of brome grass did not appeal to it even when the grass was optimum height. Mean vegetation characteristics included: 24 cm vertical cover, 45 cm height of living vegetation, 95% grass cover, and 7% forb cover. All parameters were significantly different from those for the Ring-necked Pheasant, Dickcissel, and Red-winged Blackbird, but similar to those for the Western Meadowlark except that grass coverage was significantly greater for the Grasshopper Sparrow than the meadowlark (Patterson and Best 1996). In summary, excluding data for the Florida Grasshopper Sparrow, territories have 3-5% woody cover, 28-95% grass cover, 8-24% bare ground, and 4-76% herbaceous cover with vegetation height of 28-54 cm.

Singing perches are an important habitat component for the Grasshopper Sparrow. In Wisconsin, 60% of territories contained posts, 53% a fence line, 20% a wire bale or tangle, and 10% trees. Nonetheless, the supply of singing perches appeared to be limited. There was considerable overlap in their usage, with some used by as many as 4 species. This did not lead to excessive competition and was usually resolved quickly through the hierarchy of species (Wiens 1969). In Pennsylvania, grass clumps, alfalfa stalks, tall forbs, small shrubs, fence posts, utility wires, trees, hay bales, grain shocks, and farm equipment left in fields were used as song perches. Perches were 50-125 m from the nest. It appeared to select the tallest available perches. When a stake 60 cm taller than the grass was provided, it was claimed within minutes. The next day a taller perch was provided and the first artificial perch was immediately abandoned for it. Singing was confined to grassy areas even if the territory contained row crops. Consequently, singing areas may be separate from nesting areas (Smith 1963; Smith in Austin 1968). Harrison (1977) provided artificial perches 1.5 and 2.0 m

tall in Michigan alfalfa fields. Grasshopper Sparrows preferred the shorter perches. If birds selected perches randomly, 13 of each height class would be used. Twenty-three of the 1.5-m perches were used compared with 3 of the 2.0-m perches. In Ontario and Quebec, common mullein and common milkweed are frequently used as perches.

Some studies compared the habitats of sympatrically nesting grassland birds. In Pennsylvania, the Grasshopper Sparrow preferred shorter vegetation and was more tolerant of woody vegetation than the Henslow's Sparrow (Hill and Diefenbach 2013). In Wisconsin, areas initially settled by the Grasshopper Sparrow were characterized by significantly lower grass cover, somewhat less litter depth, and greater forb height than areas initially selected by the Savannah Sparrow. These differences disappeared as the season progressed and territories of the 2 species were quite similar by mid-June. The earliest Savannah Sparrows settled on areas that later developed deeper and more variable litter, greater grass cover and density, and shorter forbs than early Grasshopper Sparrow territories. The Grasshopper Sparrow foraged more frequently in open unvegetated areas. Savannah Sparrows concentrated their foraging around the perimeter of grass clumps. The Grasshopper Sparrow nested in somewhat more open situations and had considerably less litter associated with its nests. Both species used forbs for singing perches; the Grasshopper Sparrow showed a distinct tendency to sing from higher perches than the Savannah Sparrow. Habitat usage by the Grasshopper and Savannah sparrows was very similar. The average height of forbs in Grasshopper Sparrow territories was less than in those of the Bobolink and Henslow's Sparrows, but exceeded those in Vesper Sparrow and Western Meadowlark territories. The general vegetation density and coverage by bare ground and low vegetation was similar for Grasshopper and Savannah sparrows and the Eastern Meadowlark. Vertical vegetation density and density in the 0-10-cm height interval in Grasshopper Sparrow territories differed significantly only from those of the Henslow's Sparrow. Mean effective vegetation height in Grasshopper Sparrow territories was similar to the Savannah Sparrow, greater than for the Vesper Sparrow and Western Meadowlark, and less than for the Bobolink, Eastern Meadowlark, and Henslow's Sparrow. Litter depth, coverage, and composition in Grasshopper Sparrow territories were intermediate; litter depth varied significantly only from the Henslow's Sparrow. Grasshopper Sparrows used grass slightly less than the Savannah Sparrow. Vegetation density at Grasshopper Sparrow nest sites was somewhat less than at nests of other species. Litter was shallower and forbs were somewhat taller near Grasshopper Sparrow nests than at nests of other species. The species could be arranged in order of increasing habitat richness (vegetation density and height, litter coverage and depth): Western Meadowlark, Vesper Sparrow, Savannah Sparrow, Grasshopper Sparrow, Eastern Meadowlark, Bobolink, and Henslow's Sparrow. The difference in rankings was small, especially between the Grasshopper Sparrow, Savannah Sparrow, and Eastern Meadowlark. Each species avoided competition by performing their activities in slightly different manners by differentially using the various substrate types or by using different strata in the same substrate (Wiens 1969).

In some areas, the Grasshopper Sparrow appears to avoid edges of grassland patches or be affected by patch shape; in other areas, these features have no effect on it. In South Dakota, it was negatively associated with increasing amounts of wooded edge surrounding a grassland patch. Its probability of occurrence was greater than 75% when no wooded edge was present but fell to less than 15% when wooded edge surrounded more than 75% of the patch. Patch shape had no effect

on occupancy (Greer et al. 2016). In North Dakota, fewer nests were within 45 m of aspen woodland than further away (Grant et al. 2004). In Wisconsin, mean distances of territory boundaries from edges were: 82.8 m for cultivated fields (range 10-240 m), 24.5 m from fence lines (range 0-130 m), and 207.8 m from woods (range 10-340 m; Wiens 1969). Also in Wisconsin, there was a significantly lower density of nests within 50 m of edge than more centrally in fields. The type of edge (wooded or open) was not a significant predictor of nest density within 50 m of edge (Renfrew et al. 2005). In Nebraska, only 1 of 31 territories (3.2%) had more than 50% of its area within 50 m of edge but 17 territories (54.8%) had more than 50% of their area within 100 m of edge. The average distance from edge of 10 nests was 119 m; no nests were found within 50 m of edge (Dechant et al. 2002b). In Pennsylvania, Hill and Diefenbach (2014) detected the Grasshopper Sparrow in grasslands with perimeter-to-area ratios as high as 0.25 km to 1 ha. They concluded that it was more likely to occupy grasslands with a small perimeter-to-area ratio. Density was not consistently related to the perimeter-to-area ratio, suggesting that habitat selection is less influenced by edge effects than for certain other species. The probabilities of occupancy related to the perimeter-to-area ratio in km per ha were 95% at 0.05, 80% at 0.15, and 20% at 0.25. In Saskatchewan, its probability of occurrence was not affected by patch shape (Davis 2004). In Nebraska and Iowa, McLaughlin et al. (2014) used an edge-to-interior ratio in their models to explain its abundance and density and concluded that the ratio was not important.

Some studies concluded that the Grasshopper Sparrow is area sensitive. Other studies found no relationship between occupancy and patch size. Vickery et al. (1994) considered it area sensitive in Maine. This study was done where the population is declining and in meadows dominated by blueberries, an atypical habitat. It was detected on only 14 of 235 point counts (6.0%). Its incidence rose sharply with patch area and reached 50% at approximately 100 ha. Herkert (1994a) considered it area sensitive in Illinois. Its probability of occurrence was 10% at 1 ha, 20% at 10 ha, and 60% at 100 ha with 50% occupancy attained at approximately 30 ha. It occupied 82% of transects in suitable habitat in grasslands larger than 100 ha compared with 36% in grasslands smaller than 100 ha. In Ohio, 8 fields that were used averaged 16 ha and inhabited CRP lands averaged 11 ha (range 1-21 ha). It was considered area sensitive in the CRP lands because density increased with patch size (Swanson 1996) but a correlation between density and area is not a true measure of area sensitivity. In Saskatchewan, Davis (2004) concluded that it was area sensitive because its density increased with patch size. The minimum size of field it occurred on was 15 ha, suggesting some degree of area sensitivity. The increase associated with patch size may have interacted with other variables such as shrub density. Its occurrence appeared to be influenced predominantly by vegetation parameters. It was concluded that area sensitivity in this study may be a local phenomenon that may not be evident in other areas with different landscape compositions or regional abundances of this sparrow. It was suggested that it was area sensitive but its actual size requirements were unknown. In Pennsylvania, Hill and Diefenbach (2014) found that grassland area itself was insufficient to explain occupancy patterns and concluded that shape complexity needed to be considered. It was less likely to occupy small grasslands, particularly those with complex shapes. The smallest field it was detected in was 4.6 ha. This study also found that shrub density affected occupancy and this may have been a confounding influence. In Nebraska, the smallest patches it occurred in were 8-12 ha (Dechant et al. 2002b). Johnson and Igl (2001) studied its area sensitivity in Montana, South Dakota,

and North Dakota. At 2 sites, it was positively correlated with grassland size; it was negatively correlated with size at the other 7 sites. Results indicated that there were regional variations in area sensitivity. Walk and Warner (1999) studied area sensitivity in 9 grasslands 7-120 ha in area in Illinois. It occurred regularly on all sites except for the 7-ha site where it occurred in only 1 of 4 years. There was no significant relationship between its occurrence and patch size. Fifty percent occurrence was attained at 12 ha, the least of all species studied. In New York, the smallest pasture that supported the Grasshopper Sparrow was 10.9 ha, but this was the smallest available pasture (Smith and Smith 1992). In Quebec, it nested in fields as small as 6.4 ha but fields with sparrows averaged 15.9 ha compared with 7.6 ha for unoccupied fields (Jobin and Falardeau 2010). In New York, it nested in fields 1.8-13.2 ha. Populations in large grasslands persisted better than those in small fragments and adult return rates, proportion of successful nests, and number of fledglings produced per female tended to be higher in larger fields. Balent and Norment (2003) concluded that small fields were unlikely to support persistent populations. In Missouri, its density was not influenced by patch size but was affected by vegetation characteristics. The smallest grassland they studied was 31.2 ha, however (Winter and Faaborg 1999). Field size has been determined to have no effect on the Grasshopper Sparrow in Wisconsin, Missouri, South Dakota, Nebraska, and Iowa; 1-10 ha was considered sufficient to maintain a viable population in Missouri (Dechant et al. 2002b; Greer et al. 2016; McLaughlin et al. 2014; Ribic and Sample 2001; Swanson 1996). In Quebec, where the Grasshopper Sparrow is uncommon and local, it nests on sites as small as 6 ha (Savignac 2013) suggesting that it is not particularly area sensitive there. Prior to European settlement, the eastern subspecies of the Grasshopper Sparrow probably nested in small natural openings in the extensive forest cover. As late as the 1940s, it nested in forest openings only a few hectares in size in Michigan (Smith in Austin 1968). This subspecies may be adapted to nesting in smaller habitat patches than the western subspecies. Coleman et al. (2000) considered the Grasshopper Sparrow area sensitive in Ontario and concluded that it required grasslands larger than 10 ha. No actual studies on area sensitivity of the Grasshopper Sparrow have been conducted in Ontario so it is uncertain if this conclusion is correct. The evidence for area sensitivity by the Grasshopper Sparrow is weak and it is not universally area sensitive. It has nested in grasslands as small as 1 ha.

All but 1 Ontario nests were in a depression in the ground, in or under dead or occasionally living clumps of grasses or other plants. The exception was a nest 7.6 cm above ground in the crotch of the lowest branch of a 0.6-m red pine. This appears to be the only elevated nest that has been reported. Some nests were near trees or logs and 8 (minimum of 10.5%) were under small trees or dead branches. Most nests were partially domed by nearby grasses and other vegetation (Peck and James 1987).

All nests reported elsewhere were on the ground in a shallow depression that the female may excavate. The rim of the nest is either flush with the ground or as much as 1.3 cm above it. Most nests are domed with nesting material that is woven into overhead grasses and they are typically very well concealed; some nests may be open above. In Kentucky, the mean concealment at nests was 88.9% and there was no difference in the concealment of successful and unsuccessful nests. The Grasshopper Sparrow prefers to build its nest at the base of grass species that form clumps. In Iowa, nests were found exclusively in smooth brome or orchard grass litter even though it avoided dense stands of brome. Nests may have 1 or 2 trails leading to them under the vegetation. In Florida,

orientation of nest entrances was random, probably because they were positioned toward areas of low vegetation density and bare ground. Most Wisconsin nests faced north or northeast; nests in Kansas and Oklahoma faced northwest. In these areas, the directions of prevailing winds and nest openings both shifted seasonally. Mean nest orientation was not directly downwind and shifts in orientation were not completely in concert with changes in wind direction. Although avoidance of wind was important, it was not the only factor in determining nest orientation. Shading from the sun may also be important. In 1 area of Kansas, nests were normally oriented east to northeast. During a drought year, nests were oriented southward. This diminished morning solar radiation and increased cooling due to the prevailing southerly winds. Nests are not reused (Corimanya et al. 2024; Delany and Linda 1998a, 1998b; Long et al. 2009; Patterson and Best 1996; Smith in Austin 1968; Vickery 2020; Whitmore 1981; Wiens 1969).

Males establish territories immediately upon arrival on the breeding grounds. Almost all activities are conducted within the territories, but females occasionally fly considerable distances outside the territory to obtain food for nestlings. Both mated and unmated males defend territories. Boundaries are rigidly maintained during territory establishment, nest building, and incubation. Once the young hatch, territorial defence wanes and considerable movement occurs among territories. Movement is often initiated by young birds that are just able to fly. Territorial defence increases sharply for 2-3 days prior to second nestings. In some areas, territory sizes and boundaries are stable throughout the season but these may change considerably in other areas. Near Ottawa, Grasshopper Sparrows nested in an alvar grassland and a lightly grazed pasture. The 95% kernel territory estimates were 0.5-2.21 ha (average 1.05 ha). Home range sizes were 0.86-5.79 ha (average 2.24 ha), significantly larger than territories. Territories overlapped home ranges an average of 54.7% (range 25.0-95.9%). Home ranges were significantly larger on the alvar (4.96 ha) than the pasture (1.32 ha). The average amount of territory overlap was 3.3% at the alvar and 29.9% at the pasture. The home ranges overlapped by 8.1% at the alvar and 50.1% at the pasture. In Florida, territories were stable throughout the season but densities were low and territories were not contiguous, often separated by 30 m or more. In Pennsylvania, territorial boundaries often shifted considerably in response to habitat changes or disturbances related to mowing. In Montana, territory sizes remained constant throughout the year but varied annually, probably in response to density. In Wisconsin, where territories were contiguous, their size and shape fluctuated throughout the breeding season. Territories were significantly smaller when first established than later in the season during the peak of the breeding season. Birds continued to arrive into early June and forced themselves in among the existing territories until all habitat was occupied. As a result, territory sizes shrank again and considerable modifications were made to boundaries. There was no difference in the size of territories at the periphery of the field than in its centre, with territories averaging 0.81 ha in both locations (range 0.53-1.34 ha). In 1 Wisconsin study, early territories averaged 0.36 ha but expanded and contracted as described above. In another Wisconsin study, territory sizes increased throughout the season with the latest established territories significantly larger than the earliest. Territories averaged 0.73 ha 1-10 May, 0.77 ha 15-25 May, and 0.93 ha after 25 May. In Georgia, territories were 0.4-0.8 ha. In Florida, 30 territories averaged 1.8 ha (range 0.6-4.8 ha). Mean territory size of mated males was 1.55 ha compared with 1.01 ha for unmated males. Twenty-two Pennsylvania territories averaged 0.82 ha (range 0.49-1.34 ha). Twenty-six Montana territories

averaged 0.43 ha (range 0.16-1.87 ha). Seventy-three Wisconsin territories averaged 0.85 ha (range 0.32-1.74 ha). Territory sizes averaged 0.37 ha in California, 1.38 ha in Iowa prairies, 0.81 ha on a West Virginia farm (range 0.49-1.34 ha), 0.19 ha in Pennsylvania, and 0.66 ha and 0.78 ha in Connecticut in 2 years (Delany et al. 1995; Hannah et al. 2024b; Johnston and Odum 1956; Jones 2011; Smith 1963; Vickery 2020; Wiens 1969, 1973).

Limited information is available on natal philopatry. Return rates vary from 0% to 12%. In Montana, 0 of 138 nestlings returned. In New York, 1 of 43 nestlings (2.3%) returned; it established a territory that overlapped with its natal territory. In Florida, where the Grasshopper Sparrow is resident year-round, only 1 of 50 nestlings and 6 fledglings (1.8%) were resighted in a subsequent year. One Florida male moved 2 km from his natal site. In Maine, 2 of 19 juveniles (10.5%) returned (Balent and Norment 2003; Delany et al. 1992, 1995; S.L. Jones et al. 2007; Perkins and Vickery 2001; Savignac 2013; Vickery 2020).

Adult site fidelity rates vary and are considerably higher in the east than the Midwest. In Montana, 4 of 45 adults (8.9%) returned and 3 returned to the same location where they were banded; the fourth bird could not be individually identified. In Kentucky, 6 of 39 adults (15.4%) returned, including 5 males and 1 female, and all returned to territories near those occupied the previous year. Other return rates include 22 of 111 (19.8%) in Kansas, 5 of 10 (50.0%) in Connecticut, 15 of 42 (35.7%) in California, 0 of 85 in Nebraska, 20% in another California location, 33% in New York (29% for males and 27% for females), 15 of 42 (35.7%) in Maine, and 57% in Maryland. In New York, 3 fields that were only 20 m apart appeared to function as separate local subpopulations, with no evidence of movement among them and no defence of territories that included more than 1 field. There were no significant differences in return rates of birds from small and large fields and for birds that bred successfully or unsuccessfully the previous year. In resident populations in Florida, annual return rates of males were 52.1-66.7% but 0 of 15 females returned. Eighty-four percent of returning males occupied the same territory as in the previous year. Three moved 183, 366, and 570 m from the previous year's territory. In Maine, 70% of returning males occupied the same territory (Delany et al. 1992, 1995; S.L. Jones et al. 2007; Kaspari and O'Leary 1988; Savignac 2013; Vickery 2020). Higher fidelity rates in the east may be due to the limited areas of suitable habitat.

In Kansas, Williams and Boyle (2018) determined that male Grasshopper Sparrows dispersed between breeding sites within individual breeding seasons. They based this on 3 factors: seasonal changes in density, turnover of males within plots, and direct observations of individuals defending 2 or more territories in succession within seasons. The mean turnover rate of males among years was 52%, indicating that over half of territory holders changed every month. Seventy-five percent of males changed territories some time during the breeding season. Birds dispersed out of plots that had very low and especially very high territory densities and dispersed into plots with intermediate densities. Nine of 19 males (47.4%) established new territories 120-1,229 m from their initial territories; 7 (36.8%) remained in their original territory. Of 647 males, 33% were observed defending territories more than 100 m from their initial territory; 42% remained on the original territory. Dispersal distances ranged from 101 m to 8,940 m (median 197 m). Over half of dispersal distances were less than 400 m; 4% moved more than 5 km. Seven females dispersed 144-1,321 m. Four

females were detected at subsequent nests, 2 of which divorced their mates and dispersed following nest failure. One pair dispersed together to a new territory.

Limiting Factors

Eggs have been reported in Ontario Grasshopper Sparrow nests from the beginning of May until mid-August, with most present in the first 3 weeks of June (Peck and James 1987). Pairs are formed as soon as the females arrive and nest building begins almost immediately. The nest is usually built within 2-3 days. It is unknown when egg laying begins in relation to nest completion; presumably 1 egg is laid per day. The timing of the onset of incubation is uncertain, but may be with the laying of the penultimate egg. The incubation period at 4 Ontario nests was 11 days. Incubation periods of 7-13 days have been reported elsewhere but most eggs hatch in 11-13 days in the eastern subspecies. In Montana, the incubation period for 86 nests averaged 10.9 days (range 7-13 days). The nestling period for the eastern subspecies is typically 8 or 9 days. Nestlings may fledge when they are as young as 7 days if they are disturbed. In Montana, the average nestling period was 9.7 days (range 7-12 days). In Nebraska, nestlings fledged at age 6-8 days (S.L. Jones et al. 2010; Kaspari and O'Leary 1988; Peck and James 1987; Smith 1963; Smith in Austin 1968; Vickery 2020).

Ontario egg dates suggest that 2 broods may be raised, but this has yet to be confirmed. In most of its range, the Grasshopper Sparrow raises 1 or 2 broods. It appears to be single-brooded in Wisconsin and Montana and double-brooded in Florida, West Virginia, and Nebraska. In Oklahoma and Maryland, 2 and sometimes 3 broods are raised. Under favourable conditions, it is likely that it can raise 2 broods even in the northern portions of its range. Yearlings typically raise only a single brood. It readily renests if a nest is lost and 3 or 4 attempts may be made to raise a brood. Clutches of 3-5 eggs have been reported in Ontario (average 4.39 eggs); 5-egg clutches are most frequent. Throughout its range, clutches of 2-6 eggs have been documented and there is a single case of a 7-egg clutch. The normal clutch size range is 3-5 eggs, with 2- and 6-egg clutches rare; most clutches contain 4 or 5 eggs. Mean clutch sizes reported elsewhere are 4.1-4.5 eggs. Clutch size declines with season. The decline with season was not significant in Montana and West Virginia but significant in Kentucky and Tennessee at a rate of 0.5 egg every 62 days. At this rate, the second clutch would be reduced by about 0.5 egg; later clutches often have only 3 eggs. In another Kentucky study, mean clutch sizes were 4.79 eggs in May, 4.06 eggs in June, and 3.71 eggs in July. Clutch sizes were significantly larger in ungrazed (4.48 eggs) than grazed (3.91 eggs) areas (Danner et al. 2018; Delany et al. 1993; Giocomo et al. 2008; Jones 2011; S.L. Jones et al. 2010; Kaspari and O'Leary 1988; Peck and James 1987, 1998b; Smith 1963; Smith in Austin 1968; Sutter and Ritchison 2005; Vickery 2020; Wiens 1969; Wray et al. 1982).

Both sexes are capable of breeding as yearlings and presumably breed every year thereafter. In Florida, some territories were defended by unmated males that were probably yearlings (Delany et al. 1995; Vickery 2020). The Grasshopper Sparrow is typically monogamous but Small et al. (2009) reported 4 cases of polygyny in Maryland. These represented only 1.2% of the 337 males that were studied. Three cases involved 1 male and 2 females; another male may have had 3 females breeding simultaneously, but this could not be confirmed. The average distance between polygynous nests was 60.6 m. In 2 cases, both nests were within 20 m of each other and in the other 2 cases they were more than 90 m apart. In 2 cases, one of the nests was outside the male's territory; in 1 case, both

nests were in the territory; and in another case, both nests were outside the territory. Polyterritoriality was not documented.

In Maryland, 77 of 124 broods (62.1%) contained at least 1 extra-pair young; 165 of 448 nestlings (36.8%) were the result of extra-pair mating. There was substantial annual variation in the extent of extra-pair paternity. Over 6 years, 43-76% of broods contained at least 1 extra-pair young and 26-60% of nestlings were a result of extra-pair mating. The probability of extra-pair paternity increased with the number of neighbours. Eighty-one percent of extra-pair copulations were with neighbours. Males that were not cuckolded had the highest number of genetic offspring, both within- and extra-pair. These males were better at mate guarding or were perhaps of greater quality. Cuckolded males failed to sire many offspring, including extra-pair young. Males of lower quality can pair with a female and be social fathers but not necessarily genetic fathers. This suggests that females paired with low-quality males actively seek extra-pair copulations whereas those paired with high-quality males have little need to seek matings outside the pair bond (Danner et al. 2018).

The Grasshopper Sparrow forages exclusively on the ground and presence of bare ground is critical for effective foraging. In Wisconsin, most foraging was done in grass 0-5 cm tall, but it used grasses 6-10 cm and 11-15 cm tall more than the Savannah Sparrow. All 7 grassland species there foraged in grass, but there were differences in their patterns of foraging that may have been sufficient to bring them into contact with different foods. In agricultural lands in North Carolina, soybeans and other monoculture crops were important foraging areas (Swanson 1996; Vickery 2020; Wiens 1969).

Adults remove chitinous material from prey before it is fed to nestlings, particularly from grasshoppers. This increases room in the gut for more prey, and increases the proportion of nutrients in the food. Small prey often has a higher proportion of chitin by weight than large prey. A diet of small prey would fill the gut more quickly with less nutritious food. Birds reduce the amount of chitin ingested by avoiding small prey and removing chitin from large prey (Adler and Ritchison 2011; Kaspari and Joern 1993). In Nebraska, the diet of nestlings differed from that of adults. Nestlings consumed significantly larger (15-31 mm) prey than adults (12-15 mm). The diet of adults contained 3-61% seeds, but nestlings were fed arthropods exclusively. Nestlings received more grasshoppers and caterpillars and fewer beetles and bugs than adults ate (Kaspari and Joern 1993). Grasshoppers were the most important food items in the stomachs of 2 Florida nestlings. They constituted 63% of food items and 71% of arthropod prey. They also consumed click beetles, ground beetles, spittle bugs, deer flies, braconid wasps, spiders, and flatsedge seeds (Delany et al. 2000). In Kentucky, grasshoppers constituted 68.1% of food items fed to nestlings. They were also fed 22.6% orthopteran larvae, 5.6% crickets, and 1.9% moths; overall, the diet consisted of 96.3% orthopterans. The mean length of grasshoppers fed to nestlings was 24.4 mm and the mean length of crickets was 21.8 mm. Other nestling prey items included bees, beetles, and spiders (Adler and Ritchison 2011). In Wisconsin, prey items brought to nestlings consisted of 22 unidentified caterpillars, 7 geometer moth caterpillars, 4 damselflies, 2 adult lepidopterans, and 1 each of orthopteran, bug, beetle larva, fly larva, spider, and oligochaete. In this small sample, lepidopterans constituted 75.6% of the diet and orthopterans represented only 2.4% of the diet (Wiens 1969). Judd (1901) reported that nestlings were fed mostly grasshoppers.

Judd (1901) analyzed the contents of 170 stomachs. They contained 63% animal matter and 37% vegetable matter. Fifty-seven percent of the diet consisted of insects and the remaining 6% of the invertebrates consisted mostly of spiders with occasional myriapods, snails, and earthworms. The insects consisted of 23% grasshoppers, 14% caterpillars, 11% ants, 8% beetles (click, leaf, and dung beetles and weevils) and 1% bugs (leafhoppers, assassin bugs, and soldier bugs). In June, 60% of the diet consisted of grasshoppers. Caterpillars were more dominant in the diet in May when they constituted 33% of the diet. More than half the caterpillars were owlet moths (cutworms). The vegetable matter in the diet consisted of seeds, including 17% foxtails, panic grasses, and a few other miscellaneous grasses; 11% other plants, including smartweeds, purslane, plantain, and sedges; 5% wood-sorrel; and 2% waste grain. No fruit was consumed other than a few blueberries in 1 stomach. The Grasshopper Sparrow fed on vegetable matter much less than other sparrows, including the Savannah Sparrow. Insects were the staple of the diet and grasshoppers, caterpillars, and beetles were most important. In Florida, Smith (in Austin 1968) reported that 10 birds had eaten 69% insects and spiders and 31% seeds. The most frequently consumed insects were grasshoppers and crickets, beetles and weevils, and moths and moth larvae, along with a few flies and bugs. The vegetation consisted predominantly of sedge seeds with some seeds of grasses and yellow stargrass. Vickery (2020) stated that the summer diet consisted of 61% invertebrates and 39% seeds compared with 29% invertebrates and 71% seeds in autumn. The summer diet consists predominantly of insects, mostly grasshoppers. Major taxa in the diet in Oklahoma and South Dakota mixed prairies were, respectively: orthopterans, 36% and 30%; caterpillars, 20% and 16%; beetles, 18% and 10%; true bugs, 9% and 1%; spiders, 4% and 3%; soft-winged bugs, 0% and 6%; hymenopterans, 0% and 2%; and seeds, 14% and 31%. Seeds in order of abundance included foxtails, sheep sorrel, oats, and smartweeds. The western and Californian subspecies eat seeds of foxtails, ragweed, panic grass, wood-sorrel, sunflowers, sedges, knotweeds, campions, oats, and amaranths. In Oklahoma, South Dakota, and Texas, seeds constituted less than 20% of the diet and frequently less than 10%. Orthopterans dominated the diet at 1 location but were less important at another site. Beetles never comprised more than 8% of the diet; weevils were the most consistently ingested beetles. Caterpillars comprised more than 25% of the diet biomass except at 1 site in 1 year. In several cases, more than 50% of the diet consisted of caterpillars. Other animal prey (hymenopterans, bugs, flies, neuropterans, spiders, and snails) made minor contributions to the diet, although cicadas and other soft-winged bugs constituted more than 10% of the diet at 1 location. The seeds consumed were mostly those of grasses with very small amounts of goosefoots, wood-sorrel, smartweeds, and borages. Variation in the diet was the least for the Grasshopper Sparrow of the studied species. Its dietary stability was also most stable among the species studied, with 87% stability over the years. The diet had limited variety; at 1 site, only 11 prey items were selected by the entire population and individual specimens contained 57% of those taxa on average. There was no significant difference in the diet of the sexes and the diet varied little among locations. It consumed prey 1-32 mm in length, mostly in the 1-4 mm range except at 1 site where it ate many items in the 4-8 mm range. Mean prey sizes in different locations ranged from 3.39 to 9.86 mm (Wiens and Rotenberry 1979). Kaspari and Joern (1993) determined that 67% of the diet of Nebraska Grasshopper Sparrows consisted of arthropods and that grasshoppers were the preferred prey. Bugs were numerically dominant in the environment, but were not preferred. The percentage of seeds in the diet over 2 years was 36% and 18% in June, 22% and 41% in July, and 24% and 40% in August. The diet consisted

of 40% short-horned grasshoppers, 16% beetles, and 14% bugs. The dominant trend was an increase in the proportion of grasshoppers in the diet over the breeding season. It was the only species studied that consumed beetle larvae smaller than 5 mm or 15-25 mm in length. Preferred prey was 15-35 mm in length and it avoided prey outside this range.

Some studies evaluated whether there is competition among grassland birds for food. In Oklahoma, South Dakota, and Texas, the Grasshopper Sparrow had a high niche overlap with the Western Meadowlark at 1 site in all years. Relations to the Eastern Meadowlark at another site were close some years and distant in others, and at 1 site it consistently overlapped highly with the Dickcissel. Larger species (Upland Sandpiper and the 2 meadowlarks) consumed larger prey than the Grasshopper Sparrow and Dickcissel. Wiens and Rotenberry (1979) concluded that food was not normally limiting and that populations were exploiting food resources in an opportunistic fashion. This led to considerable individual, between-year, and between-location variation in diet compositions and interspecific overlaps. Kaspari and Joern (1993) reached a different conclusion in Nebraska. Diets of the Grasshopper Sparrow, Lark Sparrow, and Western Meadowlark strongly varied over time and they preferred most of the same prey. Competition for prey between the Grasshopper Sparrow and Western Meadowlark was partially avoided through prey-size selection, with some large prey avoided by the sparrow and preferred by the meadowlark. This suggested that there was some competition for food and that these species were not dietary opportunists. In Wisconsin, Wiens (1969) concluded that the food supply for grassland birds was abundant and not a limiting factor that would lead to competition.

The Grasshopper Sparrow is an infrequent host of the Brown-headed Cowbird and is capable of fledging some of its own from parasitized nests. In Kansas, parasitism resulted in an average loss of 2 eggs per nest and fledging success was only 7%. In another Kansas area, unparasitized nests had clutches of 4.5 eggs compared with 3.1 eggs in parasitized nests. In Minnesota, parasitism rates decreased with distance from woody edges. There were no differences in predation rates within 100 m of a forest or agricultural edge or more distant from edge. In Illinois, real and artificial cowbird eggs used to artificially parasitize nests were all accepted, as were all eggs that were laid naturally by cowbirds. Many undersized artificial eggs were ejected. Cowbird eggs may be too large for the Grasshopper Sparrow to eject and the eggs of the 2 species are similar, so the sparrow is at risk of ejecting its own eggs. In Ontario, 7 of 83 nests (8.4%) were parasitized. Other parasitism rates include 29% in Manitoba, 2% in Montana, 0 of 51 nests in West Virginia, 0 of 34 nests in Wisconsin, 2 of 21 nests (9.5%) in North Dakota, 0 of 131 nests in Kentucky and Tennessee, 1 of 41 nests (2.4%) in Indiana, 13 of 318 nests (4.1%) in Illinois, 22 of 46 nests (47.8%) in Kansas, 0 of 153 nests in Pennsylvania, 8% of 119 nests at 2 sites in North Dakota and 1 in Saskatchewan combined, 2% in Ohio, 4 of 18 nests (22.2%) in Kansas, 9 of 121 nests (7.4%) in Oklahoma, 7 of 14 nests (50.0%) in Kansas, and 1 of 6 nests (16.7%) in British Columbia. Kansas, where the highest parasitism rates have been reported, has a very high density of cowbirds (Ahlering et al. 2009; Campbell et al. 2001; Dechant et al. 2002b; Galligan et al. 2006; Giocomo et al. 2008; Gransfors et al. 2001; Hill and Diefenbach 2013; S.L. Jones et al. 2010; Peck and James 1998b; Peer et al. 2000; Renfrew et al. 2005; Rivers et al. 2010; Sroor et al. 2025; Verheijen et al. 2022; Vickery 2020; Wray et al. 1982).

Habitat loss is the most significant limiting factor for the Grasshopper Sparrow in Ontario and throughout its range. Habitat loss occurred as a result of converting pastures and grasslands to row crops or urban development, converting grassy hayfields to alfalfa crops, planting marginal farmlands to coniferous plantations, and natural succession. A high proportion of Ontario's pastures have been converted to cropland dominated by row crops. Except in the Norfolk Sand Plain, row crops are rarely, if ever, used for breeding. Traditional hay crops in Ontario consisted of red and white clover, timothy, and limited amounts of alfalfa. This provided heterogeneous and fairly sparse cover that was somewhat suitable for breeding. Most hayfields are now monotypic stands of alfalfa that grow taller and denser and are very uniform. These hayfields have no bare ground and are rarely, if ever, used for breeding. In a Pennsylvania field dominated by poor growth of timothy, alfalfa, and clovers, the Grasshopper Sparrow abandoned it after it was fertilized and planted to a lusher growth of alfalfa. Beginning in the 1930s and still continuing to some extent, marginal farmland has been planted to coniferous plantations. Areas that were particularly targeted for this management were areas of steep slopes, especially on the Oak Ridges Moraine, but also on other moraines, drumlins, and eskers in the southern portion of the province. Many of these areas were probably prime habitat for the Grasshopper Sparrow because they had dry sandy or gravelly soil with low sparse grass cover and areas of bare soil. Introduction of grasses, such as smooth brome and reed canary grass that form tall, dense monotypic stands has been detrimental. These grasses do not provide any suitable habitat for the Grasshopper Sparrow and may eliminate other grass species that are more beneficial. Unmanaged meadows may be invaded by shrubs, reducing habitat suitability; once shrubs become too dense, it disappears. The Grasshopper Sparrow responds well and quickly to appropriate habitat management. Planting of CRP lands in the west slowed its rate of decline and it may become quite common in managed grasslands at airports. Changing agricultural practices in Pennsylvania with an emphasis on grasslands appears to be resulting in an increase. Reclaimed surface mines provide excellent habitat and it may be locally abundant on them. Habitat at most of these areas is temporary due to rapid succession of woody vegetation; some areas may only be occupied for about 3 years. Significant management for the Grasshopper Sparrow is unlikely to occur in southern Ontario due to the intensity of current land uses and the high price of land (Askins et al. 2007; Galligan et al. 2006; Herkert 1988; Savignac 2013; Smith 1963; Smith in Austin 1968; Swanson 1996; Vickery 2020; Whitmore 1979; Wray et al. 1982).

The effects of grazing on the Grasshopper Sparrow vary depending upon the type of grassland and the intensity and timing of grazing. Grazing in arid grasslands is detrimental because these areas tend to be sparsely vegetated even without grazing. Further reductions in vegetation height and density in these grasslands may convert them to unsuitable habitat. Grazing in lusher grasslands may be beneficial because it reduces vegetation height and density and may create areas of bare soil, all of which are beneficial. Light grazing that results in 20-40% vegetative cover 25 cm in height or taller is beneficial but more intensive grazing may be detrimental. In tallgrass prairies and eastern hayfields, light grazing tends to be beneficial. In Ontario, some of the highest densities occur on lightly grazed moraines and limestone plains such as the Mulmer Hills west of Lake Simcoe, the Dummer Moraine east of Peterborough, the Oak Ridges Moraine, the Carden Plain, the Napanee Plain, and Dufferin County. In most other areas south of the Canadian Shield, grazing tends to be intense so that habitat is unsuitable. In Kentucky, clutch size was smaller in grazed areas, and nest

success was significantly higher in ungrazed (70%) than grazed (25%) fields. Invertebrate biomass was significantly greater in ungrazed fields and this may have been the cause of smaller clutch sizes in grazed areas. Grazed areas had less litter, more shrubs, and shorter, less dense vegetation. Late-season grazing after birds had completed nesting resulted in an increase in density of the Grasshopper Sparrow in Illinois. Except for arid grasslands, light grazing has the potential to improve habitat but moderate to heavy grazing is typically detrimental. Not grazing homogeneous stands of mid-height grasses for an entire growing season during wet years could increase its abundance. One adverse effect of grazing is that cattle often trample nests or lay on them. In Wisconsin, trampling by cattle was the second-most common cause of nest failure after predation (Askins et al. 2007; Campbell et al. 2001; Davis et al. 2021; Delany and Linda 1998a; Powell 2008; Renfrew et al. 2005; Rolek et al. 2016; Savignac 2013; Smith and Smith 1992; Sutter and Ritchison 2005; Swanson 1996; Vickery 2020).

Mowing may be beneficial or detrimental to the Grasshopper Sparrow, depending upon the initial characteristics of the grassland and the timing of cutting. Mowing of hayfields during the breeding season may have a variety of effects. Existing nests may be destroyed by farm equipment and undamaged nests are left exposed to predators. After mowing in alfalfa fields, birds that were present tended to remain and renest. Densities of sparrows may increase for 2-3 weeks after alfalfa fields are cut and fields that previously supported no sparrows may be colonized. In Iowa, cut alfalfa fields were attractive to Grasshopper Sparrows until vegetation reached about 30 cm tall then densities began to decline. Hayfields are now cut earlier and more frequently than previously. In many areas, early hay cutting is considered a major contributor to its decline. Mowing prior to or after the breeding season may be beneficial where the grass cover is dense. In Illinois, densities were twice as high in areas cut 1-4 months prior to 1 May than in uncut areas. In Iowa row crops, it nested only on grassed waterways that had been mowed the previous year. When sections of fields were mowed for weed control, it quickly colonized areas with shorter grass cover. Densities were 5 times greater along Illinois roads that were not mowed until after 1 August than those mowed repeatedly during the summer. At a military base in Massachusetts, populations more than doubled as a result of deferred mowing. At a Massachusetts airport, populations declined when grass was mowed in the spring. In grass hayfields in New Jersey, 0.25-ha refugia were left unmowed. Grasshopper Sparrow use of refugia increased following hay harvest and may have reduced field abandonment. It decreased sharply following harvest in fields without refugia but less steeply or not at all in fields with refugia. In grasslands that are already good habitat, mowing may decrease habitat suitability (Allen et al. 2019; Askins et al. 2007; Dechant et al. 2002b; Frawley and Best 1991; Johnston and Odum 1956; Patterson and Best 1996; Smith 1963; Smith in Austin 1968; Swanson 1996; Vickery 2020). In Iowa, disking monocultures of reed canary grass resulted in a change in the vegetation and an increase in insect biomass, but there was no noticeable response by the Grasshopper Sparrow. Overall densities in these habitats were quite low (Benson et al. 2013). Wolcott et al. (2023) recommended that grassland management be delayed until August to protect both nests and fledglings.

The effects of fire on the Grasshopper Sparrow are variable. In Ontario, prescribed burns in arid grasslands often stimulate mass germination of white sweet clover, making the habitat unsuitable. In Washington shrubsteppe habitat, an intense wildfire increased its abundance because most of

the shrub cover was killed. In western areas of the tallgrass prairie, it tends to be more abundant in areas that have not been burned. Fire removes accumulated litter and standing vegetation. This is beneficial in grasslands that are initially too dense for this sparrow but may be detrimental if current conditions are suitable. Spring burning makes habitat unsuitable for that breeding season, so it is preferable to conduct burns in autumn or winter. In Arizona, where shrubs are an important habitat component, densities were similar in native and exotic grasslands prior to fire and 3-4 years after fire. It was absent on burned plots in both types of grasslands for 2 years following fire. In Florida, there was no difference in its abundance before or after fire, but reproductive success was higher 0.5 years postburn than 1.5-2.5 years postburn. Another Florida study determined that its probability of persistence was greatest when areas were burned in early April within 1 year and least when areas had not been burned for 35 years in dry prairie habitat. In Kansas, abundance was higher 1-3 years postfire than during the year of the fire. Numbers were higher in areas that were on annual or 2-year frequencies of burns than areas burned every 4 years, which tended to become invaded with shrubs. In Texas, there was no significant difference in its abundance in burned and unburned areas. It was concluded that fire was important in preventing grasslands from becoming too homogenous. In Maine, density declined for 1 year immediately following fire but was quite high for the subsequent 5-7 years. In Illinois, it preferred recently burned tracts less than 1 year after burning. In North Dakota, it responded positively to fire and was most abundant 2-7 years postfire and absent in grasslands that had not been burned for more than 80 years. In South Dakota, it decreased immediately after fire due to loss of litter but increased 2-3 years postburn. The same was true in Wisconsin, but density decreased when the area was burned a second time. In Kansas, fire had no effect in moist years but resulted in a decline during drought years. In 1 Kansas study, both grazing and fire were beneficial (Askins et al. 2007; Bock and Bock 1992; Dechant et al. 2002b; Delany et al. 2002; Earnst et al. 2009; Larned et al. 2003; Madden et al. 1999; Powell 2008; Roberts et al. 2012; Savignac 2013; Swanson 1996; Verheijen et al. 2022; Vickery 2020; Williams and Boyle 2018; Zimmerman 1989).

The Grasshopper Sparrow may be adversely affected by drought. In Maryland, production of fledglings was particularly low in 2 summers of record-breaking drought. Grassland vegetation was brown and wilted by mid-July, insect density was low, and mortality of fledglings was presumably high (Anthony et al. 2013). In western North Dakota and Saskatchewan, densities were higher during wet springs preceded by warmer winters. Spring precipitation increased primary productivity and invertebrate density. Weather conditions such as precipitation and temperature may be important factors that influence settlement decisions (Ahlering et al. 2009). In eastern North Dakota, it was negatively correlated with the number of ponds present in May and was therefore negatively affected by moisture. Its abundance was correlated to a drought severity index. Niemuth et al. (2008) concluded that it might respond differently to moisture in different locations. In areas where it is sensitive to drought, climate change has the potential to affect population densities and reproductive success. In the northern Great Plains, Gorzo et al. (2016) used BBS data to demonstrate that it was more abundant in wet years, particularly in wet years that followed another wet year. In desert grasslands in Arizona, nest survival decreased with a wetter previous season and with large rain events on previous days. The increased frequency of extreme weather events predicted for the area as a result of climate change may result in reduced nest survival, but lower seasonal precipitation prior to nesting may positively influence nest survival (Ruth and Skagen 2018).

Zuckerberg et al. (2018) summarized data from the United States regarding the effects of temperature and precipitation on the Grasshopper Sparrow. Nesting success was higher following a year with higher precipitation and lower when May temperatures were below or above average in the previous year. Nesting success was lower with increased rain in May and June to August of the year in which nesting occurred.

Cold and wet summers may be detrimental in some areas. In Maryland, many nests were flooded in such a summer and fledgling production was poor (Anthony et al. 2013). In Nebraska, Grasshopper Sparrow abundance was lower in springs with more precipitation, but productivity was not affected. Increased temperatures had no effect on abundance. It is vulnerable to climate change in this area because more frequent droughts and extreme precipitation events are predicted (Glass et al. 2020).

Shaffer and Buhl (2015) studied the effects of wind farms in North and South Dakota. At 1 of 3 sites, there was immediate displacement of the Grasshopper Sparrow, with lower density at the wind farm than at reference sites. At all 3 sites, there was displacement within 200 m of turbines and at 1 site, displacement extended out to 300 m. Wind farms were detrimental. Sparrows did not completely abandon them, but relocated away from them, establishing territories 200-300 m distant from them.

Robertson et al. (2012) examined the potential effects of cultivating grasses for biofuels on the Grasshopper Sparrow. Planting of switch grass for biofuel production has the potential to be beneficial. Production that maximizes biomass and homogenizes vegetation structure is unlikely to support it. If occupied habitat is converted to biofuel production areas in Ontario, it is most likely to be detrimental.

Declines of the Grasshopper Sparrow have been linked to large-scale applications of granular pesticides on agricultural land. These are designed to eliminate insect pests, including grasshoppers that make up a large portion of its diet (Savignac 2013).

In Illinois, Andrews et al. (2015) broadcast vocalizations at some newly created grasslands but not at others to determine if social cues were used as part of the settling decision process. The Grasshopper Sparrow was not more likely to settle at treatment sites than control sites. Densities on treatment sites were twice that of controls. Densities at treatment sites increased sharply at the beginning of the season and remained high. Densities increased slowly at control sites, reaching a peak at the end of July. Social cues are not used upon arrival but are used to select breeding locations within the breeding season. It appeared to disperse in mid-season and use social cues to locate new breeding sites; song may be an indication that successful breeding has taken place.

In Wisconsin, abandonment rates were significantly higher at nests equipped with video cameras than at nests without cameras (Renfrew and Ribic 2003).

Dechant et al. (2002b) recommended management strategies for the Grasshopper Sparrow: create habitat patches a minimum size of 10-15 ha with minimal perimeter-to-area ratio; treat portions of large areas on a rotational schedule to provide a mosaic of successional stages; discourage woody vegetation in eastern and Great Plains grasslands; maintain open grassland by burning every 2-4 years; and lightly graze areas of tall dense vegetation except in arid western areas.

Price (2004) predicted that the population of the Grasshopper Sparrow might increase in southern Ontario if the average summer temperature increased by 2°C. Nixon et al. (2016) predicted the effects of climate change on the Grasshopper Sparrow in Alberta. They concluded that it would benefit from climate change due to a northward expansion of suitable climate with no or limited change in the southern portion of the province.

Status

McIlwraith (1894) was aware of only 2 records of the Grasshopper Sparrow for Ontario, from London and Hamilton. The southern border of the province appeared to be the extreme northern limit of its distribution at that time. He concluded that it might be a rare summer resident but that it was mostly a casual visitor. By 1891, it had not been reported in Elgin County; by 1954, it was a regular breeder in moderate numbers; it was a local and declining breeder in 2000 (Lancaster et al. 2004). Peak populations in Hamilton and Ontario occurred in the 1930s and 1940s, but it has been declining for about the past 50 years (Curry 2006). Between 1900 and the 1950s, it was estimated that it had extended its range northward by about 300 km. The first Kingston record was a spring migrant in 1949, but it has been recorded there every year since except for one (Weir 2008). Baillie and Harrington (1937) reported that it nested north to Grey, Simcoe, and Victoria counties and east to Ottawa. At that time, it was fairly common along Lake Erie. The first atlas demonstrated that the Grasshopper Sparrow bred locally south of the Canadian Shield. There were scattered records in the southern portion of the Shield, near Sudbury, and in the Lake of the Woods area. There were concentrations of records along the Niagara Escarpment, in the Guelph area, and north of Lake Ontario, particularly near Kingston and on the Oak Ridges Moraine (Rising in Cadman et al. 1987). James (1991) considered the Grasshopper Sparrow an uncommon local breeder south of the Shield and rare north to Sudbury and in western Rainy River District.

The second atlas demonstrated that there had been no significant change in the distribution of the Grasshopper Sparrow since the first atlas. There was no significant change in its probability of observation throughout the province, but it declined significantly in the Carolinian Forest Region. These declines were likely due to agricultural intensification. It was fairly common along the Lake Erie shoreline in the 1930s, but there were only scattered breeding records from Rondeau and Long Point, a few records in Niagara, and a larger concentration of records in the Norfolk Sand Plain. The highest concentrations of records were on the Oak Ridges Moraine, Frontenac Axis, Niagara Escarpment, and northern Bruce County. Highest densities occurred in a band from the southern Bruce Peninsula to the Kingston area. This included the Mono and Mulmur Hills in Dufferin County, the Carden Plain, the Oak Ridges Moraine, the Napanee Limestone Plain, and Prince Edward County (Earley in Cadman et al. 2007).

Prior to European settlement, the Grasshopper Sparrow was probably confined to prairies, limestone plains, arid tops of moraines and drumlins, and forest openings created by fire and First Nations. It is uncertain if it even inhabited Ontario during this period because there were few records prior to the beginning of the 20th century. It responded favourably to the creation of abundant suitable habitat by increasing in numbers and extending its range further northward to include Ontario. Numbers in Ontario appear to have peaked in the 1930s and 1940s, and this is true in many other locations. Even where it is common, it tends to be local in occurrence, with many areas of

apparently suitable habitat unoccupied. Populations at a given location may fluctuate considerably annually. Although this may be a response to annual differences in moisture as suggested by some studies, the reasons for this are not clear (Badzinski 2001; Curry 2006; Herkert 1994a; McCracken 2005; Savignac 2013; Smith 1963; Smith in Austin 1968; Vickery 2020; Wiens 1969).

The BBS has limitations for surveying for the Grasshopper Sparrow because it sings infrequently and mostly early in the morning, its density is low, and it is detected on few routes. BBS results for 1970-2021 indicate annual decreases of 2.38% in Canada and 2.99% in Ontario. Results for 2011-21 were annual decreases of 6.58% in Canada and 5.92% in Ontario. The long-term trends were highly reliable. The Canadian short-term trend was of low reliability; the Ontario short-term trend was of medium reliability (A.C. Smith et al. 2023).

The Grasshopper Sparrow is designated special concern in Canada and Ontario.

POSTFLEDGING PERIOD

Usually only 1 or 2 fledglings are seen with an adult, but it is uncertain if brood division occurs. On average, fledglings are capable of flying 4 days after they leave the nest (range 1-7 days). Initial flights average 7 m; fledglings are capable of flights longer than 10 m at an average of 9 days (range 4-12 days). They run mouse-like under the grass and rarely appear at the tops of grasses (Hovick et al. 2011; Smith in Austin 1968; Vickery 2020).

In Maryland, Small et al. (2015) compared the habitat preferences of dependent and independent fledglings and compared these to random sites. Dependent birds selected sites averaging 16% less bare ground, 11% more coverage by warm-season grasses, 17% more total vegetation cover, and 7% more forb cover than independent birds; all differences were significant. Because dependent birds do not forage on their own and are less able to escape predators than older birds, they benefit from remaining in areas with greater vegetation cover. Habitat selected by independent juveniles was similar to that used by adults. Juveniles transitioning to independence must successfully forage on their own, possibly explaining increased use of more open areas where foraging may be easier. Vegetation parameters that were significantly different for dependent fledglings compared with random sites respectively, included 11.5% and 7.6% bare ground, 27.0% and 23.5% litter cover, 31.8% and 38.9% warm-season grass coverage, 61.6% and 68.7% total vegetation coverage, and vertical density 32.5 cm and 37.2 cm. Vegetation parameters that were significantly different for independent fledglings compared with random sites respectively, included 27.5% and 9.5% bare ground, 17.3% and 34.3% warm-season grass coverage, 43.8% and 60.0% total vegetation coverage, and vertical density 30.7 cm and 41.3 cm. Microhabitats where dependent birds were found had significantly more bare ground, litter, and plant species richness than random plots. Random plots had greater cover by warm-season grasses, total vegetation cover, and vertical density. Plots where independent fledglings occurred had significantly more bare ground than random plots. Random plots had greater cover by warm-season grasses, total vegetation cover, and vertical density. Results demonstrated the importance of diverse grassland ecosystems and that homogenous monotypic stands may not provide all the required habitat features.

In Iowa, daily movements from the nest by fledglings increased the first 4 days after fledging and then became stable for the remainder of the 14-day study period. Extreme distances moved by fledglings over the entire study period ranged from less than 1 m to 135 m. Average daily movement

from the nest site was 37.5 m (Hovick et al. 2011). At 1 Maryland site, the distance fledglings dispersed from the nest increased with time. The mean distance travelled from the nest was 346 m. The youngest bird was recaptured 5 days after fledging and had travelled 510 m. The longest distance travelled was 1,615 m and this was accomplished in no more than 20 days. The shortest net distance travelled was 9 m after 18 days. The fledgling that stayed the longest remained at least 97 days and travelled 753 m from the nest. Young travelled a mean of 90 m in 10 days and 1,000 m in 100 days. Most fledglings were encountered within 200 m of their nest throughout the summer (Anthony et al. 2013). Small et al. (2015) compared movement patterns of dependent and independent fledglings in Maryland. Daily movement of recently fledged young increased with age with an average daily distance from the nest of 88.8 m (range 3.4-1,042 m). The average distance travelled from the previous day's location by dependent fledglings was 46.3 m (range 6.1-401.5 m) and was fairly consistent with an overall increase in distance moved daily as the birds aged. The average distance travelled from the previous day's location for independent fledglings was 146.1 m (range 5.2-966 m) and it varied daily. Daily movements by independent birds were greater than for dependent birds. Mean daily distance from the nest for dependent juveniles was 25-50 m at ages 9-24 days, increasing to 350 m by day 31. Mean daily distance moved was 25 m or less at age 9-26 days with a maximum of about 120 m on day 30. Dependent fledglings remained within their natal territories for the first 2.5-3.5 weeks after fledging. Mean distance from the nest for independent juveniles was 0-50 m at age 34-44 days, then varied from 50 to 325 m at age 45-60 days with no apparent pattern. Independent juveniles travelled greater distances than dependent juveniles and crossed neighbouring territories on a daily basis. Territorial males are tolerant of unrelated juveniles. Young of the first brood have usually dispersed from the natal territory by the time adults are feeding young of the second brood. Independent fledglings congregate in loose flocks 3-4 weeks postfledging and both adults and juveniles remain in breeding habitat until they commence autumn migration (Perkins and Vickery 2001; Smith 1963; Vickery 2020).

Hovick et al. (2011) examined survival rates of fledglings in Iowa. The average survival period was 6.8 days (range 0-27 days) and the overall survival rate was 21%. Seventy-four percent of fledgling deaths occurred in the first 3 days. As fledglings aged, their survival rates increased. Survival rates increased rapidly over the first 4 days after fledging, became stable at 5-11 days, then increased for the remainder of the first 2 weeks. Young were most vulnerable shortly after leaving the nest because they were unable to make long flights, relied on their parents for food, and had high energy demands that could result in high thermal stress. Forb abundance and vegetation height had a negative but nonsignificant effect on daily survival rates, possibly because the Grasshopper Sparrow forages preferentially on bare ground and avoids tall dense vegetation. Survival rates were similar in burned and grazed grasslands. Predation accounted for 49% of deaths and an additional 31% died of exposure, usually within 3 days of fledging. In Montana and North Dakota, fledgling survival declined with increasing cover by dead vegetation which may have impeded movement or provided fewer food resources (Bernath-Plaisted et al. 2021).

MIGRATION

The subspecies of Grasshopper Sparrow that breeds in Ontario migrates to Florida and Jamaica in winter. It migrates at night but sometimes continues movement in the morning. It appears to migrate individually or possibly in small numbers. It does not form large conspecific flocks, but

during autumn migration it may join mixed-species flocks of other sparrows (Smith in Austin 1968; Vickery 2020).

In Maine and Massachusetts, males arrive 5-10 days before females and this is likely the case throughout its range. In Pennsylvania, males usually do not arrive in spring until the grass is tall enough to conceal them (Smith in Austin 1968; Vickery 2020). In southern Ontario, the Grasshopper Sparrow arrives in late April and early May, with the earliest records in mid-April (Black and Roy 2010; Curry 2006; Lancaster et al. 2004; Tozer 2012; Weir 2008). Autumn migration is more protracted but the Grasshopper Sparrow is seldom common during this period (Vickery 2020). Because it does not form flocks, does not sing at this time, and prefers grassy habitats, many move through undetected and there are few autumn records. In southern Ontario, it has been observed from early August until early November, but most migrants leave by late September (LaForest 1993; Lancaster et al. 2004; Weir 2008). There is a record for 1 January from Port Credit and 2 isolated records of vagrants overwintering at Port Credit and Brantford (Curry 2006).

Migration habitat is essentially identical to breeding habitat. The Grasshopper Sparrow is seldom seen outside of grasslands. In Ontario, it has also been observed at a sewage lagoon. In British Columbia, all nonbreeding-season records were from the breeding range, but it may occur in grass-dominated habitats near wetlands. Occasionally it may occur in shrubby fencerows and one was caught in a trap set in an elderberry thicket (Black and Roy 2010; Campbell et al. 2001; Smith in Austin 1968; Vickery 2020).

The Grasshopper Sparrow uncommonly strikes television towers during migration. At a Florida tower, 382 were killed during autumn migration compared with 19 in spring (Vickery 2020). It probably strikes other tall structures during migration.

James (1991) considered the Grasshopper Sparrow a rare migrant in Ontario.

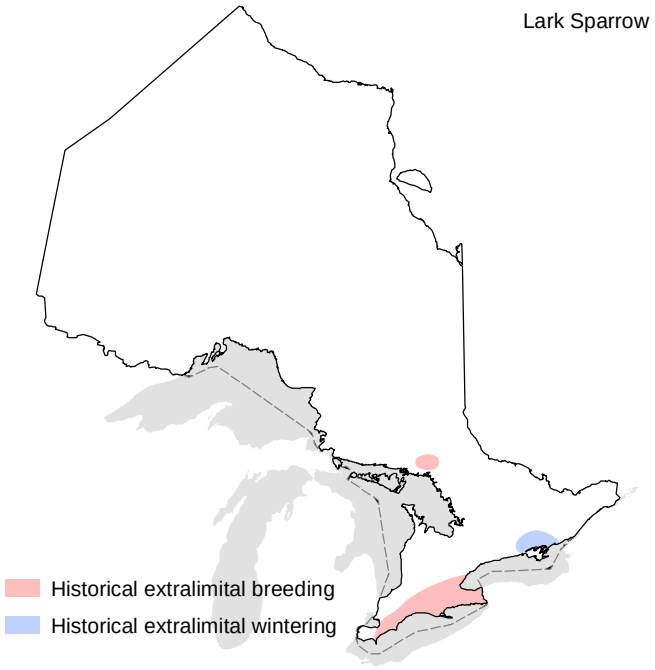
Lark Sparrow

Chondestes grammacus

BREEDING SEASON

Habitat Requirements

In Ontario, the Lark Sparrow has nested in coniferous plantations with scattered trees, in open deciduous woods in a city park, on a roadside bank, and in a garden hedge. At least half of nests were in areas with sandy soils (Peck and James 1987). Curry (2006) was of the opinion that it probably nested on the beach at Hamilton in 1885. At that time, the beach was ideal habitat consisting of mixed shrubs with open sand patches. Austen et al. (1994) concluded that suitable habitats probably included dry savannahs and prairies prior to extensive deforestation, assuming that it was actually present at that time. Later, roadsides, overgrazed pastures, and abandoned and cultivated fields provided suitable habitat. Most records for Norfolk County were from the St. Williams Forest where the Norfolk Sand Plain provided the dry sandy open scrubby grasslands that it prefers.



The Lark Sparrow is an open-country bird, with habitat requirements similar to those of the Vesper Sparrow. The Lark Sparrow is considerably less likely to nest in active agricultural land than the Vesper Sparrow. The Lark Sparrow is more of a shrub or woodland edge species than a true grassland species. In the core of its range, it commonly nests in grazed pastures and grasslands, particularly those with scattered shrubs or trees; shortgrass and mixed-grass prairies and, to a lesser extent, tallgrass prairies; shrubsteppe habitat; savannahs; open or park-like woodlands; brushy edges of woodlands, roads, and cultivated fields; desert scrub; grasslands with juniper or sagebrush cover; sand hills, dunes, and barrens; shelterbelts; and cultivated fields. It occasionally nests in gardens and near farm homesteads (especially those that are abandoned), in cemeteries, in orchards, in wet meadows, in abandoned pits and quarries; in city parks, on edges of towns; and in bare spots in lawns (Baepler in Austin 1968; Campbell et al. 2001; Crowell et al. 1982; Dechant et al. 2002f; Fitch 1958; Gier 1949; Graber and Graber 1963; Houston and Houston 2001; Jacobson et al. 2011; Leighton et al. 2002; Lusk et al. 2003; Martin and Parrish 2020; Mossman et al. 1991; Newman 1970; Rivers et al. 2010; Swanson 1996; Walcheck 1970; Wood et al. 2013).

At the macro level, the Lark Sparrow prefers areas with sandy or other nutrient-poor soils. These result in its preferred conditions of sparse low vegetation with scattered woody plants and patches of bare soil. In Illinois, it demonstrated no habitat preferences and its distribution appeared to be governed by the distribution of sandy and other poor soils. It exhibits a preference for ecotones between grasslands and forested habitat or between shrubby areas and forested habitat. These are often disturbed sites with exposed soils due to grazing, erosion, or recent fires; fallow fields may provide suitable habitat. It has an affinity for shrubsteppe with shrubs 1-2 m tall adjoining woodlands or grasslands. Upland grasslands are significantly preferred over lowland grasslands. Within areas of contiguous suitable habitat, it prefers sites that are slightly elevated. In Saskatchewan, it preferred drier northern valley slopes. In Colorado, it was typical of disturbed areas with more heterogeneous vegetation structure than areas inhabited by the Vesper Sparrow. In this area, it appears to avoid urban edges; it nests close to urban areas in other regions (Baepler in Austin 1968; Dechant et al. 2002f; Fitch 1958; Graber and Graber 1963; Houston and Houston 2001; Jones and Bock 2002; Lowther 1997; Martin and Parrish 2020; Swanson 1996).

In North Dakota, the Lark Sparrow decreased with increasing tree cover within 100 m in 400-m landscapes with both more and less than 30% tree cover. In open landscapes, its probability of observation initially increased, from 3% at 20% tree cover to 9% at 40% tree cover, but decreased to

7% at 70% tree cover. In wooded landscapes, its probability of occurrence was 10% at 10% tree cover, 14% at 40% tree cover, 1% at 70% tree cover, and 0% at 80-100% tree cover. It preferred landscapes that were 25-52% forested (Cunningham and Johnson 2016, 2019).

Some grassy cover is almost essential in territories, with grass coverage greatly preferred to herbaceous cover. Occasionally the Lark Sparrow nests in row-crop agricultural fields. Crop species such as peanuts provide the required nesting cover. Short sparse grasses with no or minimal litter cover are preferred to dense or tall grasses and areas with deep litter. Grazed grasslands are highly preferred over ungrazed areas. Grazing reduces grass height and density and provides more suitable habitat structure than undisturbed areas. Grazing also reduces litter coverage and may create areas of bare soils. Conservation Reserve Program (CRP) lands, where dense grass cover is provided for waterfowl and grassland species, seldom support the Lark Sparrow. In Arizona, it exhibited a significant preference for grazed areas. It was observed 50% of its time in grass shorter than 15 cm, 30-50% of its time in bare ground, and less than 3% of time in shrub canopy, although it usually occurred near shrubs. In Colorado, it preferred shortgrass and mixed-grass prairies to tallgrass prairies and hayfields (Dechant et al. 2002f; Lusk et al. 2003; Martin and Parrish 2020).

Scattered shrubs and trees are an important habitat feature. They provide singing perches for males and are occasionally used to conceal and shelter nests. Where woody vegetation is lacking in territories, boulders, elevated rock outcrops, or fence posts may be used as singing perches. In Montana, density on rock outcrops was 19 times higher than in sagebrush-grassland habitat. Outcrops supported patchy shrub communities and had large sumacs and other shrubs associated with them. These were used for perching, singing, and nesting. It exhibited a positive association with sumac and rock outcrops taller than 0.5 m. It was probably responding to the sumac which was closely associated with the average height of outcrops (Rumble 1987). Also in Montana, presence of creosote bush and sagebrush appeared to be essential in territories, but there were more specific habitat requirements associated with sagebrush. The Lark Sparrow forms a depression in the ground for nesting. The soil under sagebrush was more granular; soil under greasewood was more hardpan because its leaves fail to intercept rainfall. It preferred to nest under sagebrush. Total canopy coverage by shrubs was 64% (Walcheck 1970). Dechant et al. (2002f) reported that it avoided an area of shrubsteppe that was devoid of woody vegetation. In Nevada, it preferred areas of crested wheat grass that were invaded by sagebrush over areas dominated solely by wheat grass. Nonetheless, its abundance was negatively correlated with sagebrush density because it avoids pure stands of shrubs. In Oklahoma, it was correlated with the presence of red cedar and tolerated intermediate levels of canopy cover by this species. There were no relationships between its abundance and visual obstruction or percent grass cover (Chapman et al. 2004). In Washington, it preferred savannahs where shrubs were present but scarce and grasses dominated, particularly downy brome.

Some studies examined microhabitat preferences of the Lark Sparrow. Vegetation in the immediate vicinity of 1 Ohio nest was very sparse and consisted of very short crabgrass and scattered horseweed (Gier 1949). In Oklahoma, percent structural cover (any plant that provided nesting cover similar to woody plants), amount of bare ground, and percent litter cover were important parameters in determining nest location. When the distance to structural elements

exceeded 270 cm, locations became unsuitable for nests. Points with more than 87% bare ground, with more than 74% litter cover, or with less than 9% structural cover were unsuitable. Average nest-site variables included 5.0 m to a visual obstruction (6.0 m overall including nest and random sites), 2.8 mm litter depth (2.8 mm overall), 37.4 cm height of the tallest plant (34.2 cm overall), 3.0 screening cover class (2.9 overall), 8.0 cm to nearest structural element (31.7 cm overall), 16.0% bare ground (30.6% overall), 9.6% grass cover (10.0% overall), 9.1% forb cover (10.3% overall), and 41.6% structural cover (22.5% overall). Nests were shaded from sunlight 60% of the day and 40% at midday. Nesting near structural elements may reduce predation risk and lower temperature at the nest, with thermoregulation probably being the most important function (Lusk et al. 2003). Along the Platte River in Colorado, it spent the early part of the breeding season outside the floodplain in overgrazed weedy annual grasses and forbs with widely spaced cottonwoods. During the peak of the breeding season, it occurred at the fringe of the floodplain in sedges, rushes, willows, and cottonwoods in addition to overgrazed prairie habitat. In the western portion of its range, it may inhabit a variety of seral stages such as woodlands with less than 24% canopy closure, preferring deciduous trees to conifers, and grasslands with moderate to dense coverage of 40-100% (Martin and Parrish 2020). In North and South Dakota, it nests in wooded draws and small wooded areas dominated by green ash. It is an edge species in these woodlots where it is more common in early seral stages, but not significantly. Younger wooded areas had less canopy cover, a patchier canopy, less chokecherry in the understorey, lower basal area, and smaller trees than older stands (Faanes 1987; Rumble and Gobeille 1998). In California, it used oak savannahs significantly more than oak woodlands and montane hardwoods. Occupancy rates were 93% in savannahs with a grass understorey, 94% in savannahs with a shrub understorey, 46% in montane hardwoods, and 35% in oak woodlands. Its abundance was negatively correlated with hardwood and shrub coverage and positively correlated with herbaceous cover and large trees. Coverage by hardwoods was the habitat characteristic that most strongly influenced its occupancy. Wood et al. (2013) considered it an oak affiliate. Augustine and Baker (2013) compared Lark Sparrow usage of sites with and without black-tailed prairie dogs in South Dakota, Montana, and Wyoming. In eastern plots, there was no difference in its abundance off and on prairie dog colonies but in western plots it was significantly more abundant in areas without prairie dogs. Off-colony sites had significantly greater visual obstruction, more grass cover, more shrub cover, a higher percentage of bare ground, and more grass cover than on-colony sites. In Arizona, inhabited areas averaged 38% bare ground, 54% grass cover, and 7% forb cover with less than 2% canopy cover, an average grass height of 13 cm, and 0.068 shrubs per m^2. In Missouri, it was found on only 1 of 53 sites which was characterized by sparse litter and few (24-50 stems per ha) woody stems 2.5 cm diameter at breast height or less (Dechant et al. 2002f).

In Colorado, the Lark Sparrow occurred more frequently on plots 200 m from suburban edge than in plots closer to suburban areas (Dechant et al. 2002f). Suburban edges may support higher densities of predators than areas distant from edge.

It is unknown if the Lark Sparrow is area sensitive. It has been estimated that 10-100 ha of contiguous grassland is required to maintain a viable population (Swanson 1996), but there appears to be no documentation to verify these estimates.

Seven Ontario nests (87.5%) were on the ground and the other was elevated at a height of 1.1 m in a honeysuckle vine in a garden hedge. One nest each was below an overhanging bank, under a small pine, and under a fallen oak branch (Dale 1931; Peck and James 1987).

The Lark Sparrow may nest either on the ground or a short distance above it in a shrub or sapling. In California, Texas, and Oklahoma, more than 50% of nests were on the ground; ground-nesting is more frequent in the east. Ground nests are prepared by scraping a depression in the ground. Several scrapes may be made before one is chosen for the nest site. Ground nests are often in a bare or eroded site but under or very close to a shrub or tall herbaceous plant that provides some shade to the nest and aids in concealing it from predators. Some ground nests are completely exposed. In North Carolina, nests were orientated southeastward on areas with 3° or less slope. Mean heights of elevated nests in 2 areas were 1.46 and 1.39 m with maximum heights of 2-7.6 m; most nests are within 2.1 m of the ground. Favoured nest trees and shrubs include red cedar, pine, juniper, prairie rose, white cedar, black willow, hawthorn, oak, elm, raspberries, osage orange, and other species not found in Ontario. In Oklahoma, some nests were in green milkweed, red clover, greenbrier, and little bluestem. In California, 28 nests were in crevices in caves 1.5-3 m from the ground. In Oklahoma, nests were often in ornamental conifers near buildings, often only about 20 m apart. One nest was in a cavity in a dead black willow and another was under a cow chip that had been raised by grass. The chip completely surrounded the nest except for an opening to the southeast. It may reuse its own nest or another Lark Sparrow nest, with nest reuse most prevalent in Oklahoma and Texas. It may also use old nests of Scissor-tailed Flycatcher, Western Kingbird, Curve-billed Thrasher, Pyrrhuloxia, and Northern Mockingbird. Nests of the mockingbird and thrasher are used more often than those of other species (Baepler in Austin 1968; Campbell et al. 2001; Crowell et al. 1982; Dechant et al. 2002f; Gier 1949; Leighton et al. 2002; Martin and Parrish 2020; McNair 1984; Newman 1970; Swanson 1996; Walcheck 1970).

The Lark Sparrow is territorial, but typically only in the vicinity of the nest early in the breeding season. Most authors state that only the immediate area of the nest is defended but 1 Kansas pair had a territory that was 200 m wide. The male defended both boundaries against his neighbours. Even at the height of the breeding season, it may be gregarious, feeding in flocks distant from the nest site. It appears as though foraging areas are not defended. A Kansas pair had a home range larger than 6 ha but foraging was concentrated in small parts of it, usually within 30 m of a woodland edge or isolated trees. Individuals sometimes range over 10-100 ha to meet all their habitat requirements. During nest building and early incubation, both sexes drive away other Lark Sparrows. Once incubation is well underway, there is no response to other birds (Baepler in Austin 1968; Fitch 1958; Martin and Parrish 2020).

No information is available on natal philopatry and almost nothing is known about adult site fidelity. Five adults banded during the breeding season were recaptured in subsequent years in the same 10-minute block, indicating some degree of site fidelity. One bird was recaptured 8 years later where it was banded (Dechant et al. 2002f; Martin and Parrish 2020).

Limiting Factors

Nests with eggs have been found in Ontario from mid-May to early July, with most present from the last week of May until mid-June (Peck and James 1987). First nests take 3-4 days to build but later or

reused nests may take only 2 days. Usually a full day elapses between nest completion and laying of the first egg. At 1 nest, egg laying began after only 2 days of construction when the nest was still incomplete; the lining was added later. It is probable that 1 egg is laid per day. In first nests, incubation does not begin until the clutch is complete but it may start with the first or second egg in replacement clutches; incubation seldom starts before the penultimate egg is laid. The incubation period at 1 Ontario nest was no more than 11 days. Elsewhere, incubation periods of 11-12 days have been reported. The nestling period is 9-12 days but young may leave the nest as early as age 6 days if disturbed (Baepler in Austin 1968; Martin and Parrish 2020; Peck and James 1987).

It is probable that only a single brood is raised in Ontario. Double broods have been suspected or confirmed in other areas, but the Lark Sparrow typically raises a single brood. Many birds that successfully fledge young early in the season do not attempt to raise a second brood. Renesting is common if the first nest fails. In Ontario, clutches of 4 and 5 eggs have been reported (mean 4.50 eggs). Throughout its range, clutches of 3-6 eggs have been reported. Nests typically contain 4 or 5 eggs, with 3-egg clutches occurring occasionally and 6-egg clutches rare. In Oklahoma, the average size of unparasitized clutches was 3.63 eggs. Mean overall clutch size has been reported as 4.09 eggs (mode 4 eggs; Baepler in Austin 1968; Campbell et al. 2001; Martin and Parrish 2020; Newman 1970; Peck and James 1987).

The age at first breeding has not been confirmed but is probably 1 year. The mating system is typically monogamous. One instance of polygyny was reported in Saskatchewan where the females of a single male nested approximately 100 m apart (Baepler in Austin 1968; Martin and Parrish 2020).

The Lark Sparrow forages mostly on the ground for insects and seeds, but also gleans arthropods from low annuals and the lower stems and leaves of shrubs. It searches the litter for seeds, and insects on bare ground or among grasses, forbs, and shrubs. It tends to walk from 1 foraging location to another. Even during the breeding season, birds gather together in small flocks when foraging. Members of a pair tend to keep within a few metres of each other when foraging. At 1 Oklahoma site, the adults gathered food for their young from an unmowed lawn where the grass was 38 cm tall (Baepler in Austin 1968; Fitch 1958; Martin and Parrish 2020).

Prey fed to nestlings averaged 25 mm (range 24-26 mm) compared with an average of 13-14 mm for adults (range 5-23 mm). Caterpillars, short-horned grasshoppers, and crickets dominate nestlings' diets, with lesser numbers of adult beetles and brome grass seeds. Caterpillars may be the most important nestling food item; grasshoppers may be the most important food item for fledglings (Baepler in Austin 1968; Martin and Parrish 2020; Swanson 1996). Judd (1901) analyzed the contents of 167 stomachs. The food consisted of 73% vegetable matter, which was all seeds, and 27% animal matter, which consisted entirely of insects. Over half the vegetable food was seeds of grain and grasses, especially foxtails and panic grasses; it also ate Johnson grass. Grass seeds comprised 21% of the annual diet. It eats more grain than most other sparrows, with corn, wheat, and oats constituting 13% of the total diet; most was consumed in winter and was waste grain. Eight percent of the diet consisted of legumes such as clover and alfalfa. Fifteen percent of the food consisted of seeds of ragweeds and smartweeds that were about equal in abundance in the diet. The remainder of the plant food was made up of a variety of seeds, with wild sunflowers and purslane most prevalent; wood-sorrel, lamb's-quarters, and amaranths were a minor component of

the diet. More than half the animal food consisted of grasshoppers and they comprised 43% of the June diet. In the prairies and plains, it helped check invasions by the Rocky Mountain locust, which is now extinct. It ate fair quantities of weevils, but the amounts of other beetles and caterpillars consumed were far less than average for sparrows. Throughout its range during the breeding season, the Lark Sparrow eats more insects than seeds by biomass. Seeds are the predominant food when the weather is colder and insects are less available. It opportunistically exploits temporary or seasonally abundant prey such as irruptions of locusts or beetles. During outbreaks by the Rocky Mountain locust, this insect formerly constituted 91% of the diet; large quantities of alfalfa weevils are also consumed. An adult female in Kansas had eaten terrestrial snails in addition to insects and seeds. In shortgrass prairie in Nebraska where froghoppers and leafhoppers were numerically dominant, the diet consisted of 61% seeds and 39% insects. The insects were comprised of 60% short-horned grasshoppers, 13% adult beetles, 12% caterpillars, 5% locusts, 5% hymenopterans, and a few bugs, flies, and froghoppers. There was an increase in consumption of short-horned grasshoppers as the season progressed from June to August. Prey less than 15 mm in length was avoided and intermediate-sized prey (15-35 mm) was selected (Baepler in Austin 1968; Kaspari and Joern 1993; Martin and Parrish 2020).

The Lark Sparrow is commonly parasitized by the Brown-headed Cowbird. When a parasitic egg is added to an incomplete clutch, the nest may be abandoned. Once incubation has started, eggs are more likely to be accepted. Cowbird eggs may be too large for sparrows to eject them. The effects of parasitism on the Lark Sparrow are unknown. It is capable of fledging both its own young and cowbirds, but it is likely that reproductive success is reduced as a result of cowbirds ejecting sparrow eggs. Parasitism rates are variable, even within the same general area. In Ontario, 1 of 8 nests (12.5%) was parasitized. In Oklahoma, 7 of 11 ground nests (63.6%) were parasitized compared with 8 of 22 elevated nests (36.4%). Ground nests were in pastures where they were probably more accessible to cowbirds, and cowbirds were more abundant in this habitat. In 2 Oklahoma studies, 15 of 33 nests (45.5%) and 4 of 21 nests (19.0%) were parasitized. Other parasitism rates include 12 of 17 nests (70.6%) in Kansas, 7 of 30 nests (23.3%) in Illinois grasslands, 1 of 17 nests (5.9%) and 9 of 11 nests (81.8%) in unspecified areas, and 1 of 25 nests (4.0%) in British Columbia. Second broods or replacement clutches are seldom parasitized (Baepler in Austin 1968; Campbell et al. 2001; Dechant et al. 2002f; Martin and Parrish 2020; Newman 1970; Peck and James 1987; Peer et al. 2000; Rivers et al. 2010).

In South Dakota, habitat loss due to increasing agricultural use over a 6-year period was considered the major factor in the Lark Sparrow becoming rare or absent in parts of the state (Swanson 1996). Agricultural intensification, urbanization, and succession to forest are probably largely responsible for its withdrawal from much of eastern North America (Martin and Parrish 2020).

Nest success can be affected by a number of factors. In Oklahoma, nests above ground were significantly more successful (44.5%) than those on the ground (23.7%). Above-ground nests were better protected from the elements and less likely to be depredated. Snakes were the main predators and they may be more likely to find ground nests. Successful nests were associated with less bare ground and had one third of the coverage by bare soil of unsuccessful nests. Successful nests had 2 times the litter coverage as unsuccessful nests. There was more variation in structural

coverage at successful nests (18.1-57.1%) than at unsuccessful nests (35.1-55.2%; Lusk et al. 2003; Newman 1970). A high rate of nest failure occurs when reusing nests built by other species due mostly to aggressive behaviour of the other species (Martin and Parrish 2020).

Grazing is usually beneficial to the Lark Sparrow because it reduces grass height and density and may create areas of bare soils. In Oklahoma, Lusk et al. (2003) studied plots on a pasture where no grazing had occurred for more than 50 years, on pastures moderately grazed with 0.2 animals per ha, and on heavily grazed pastures with 0.4 animals per ha. Of 40 nests, 2 (5%) were in the control pastures, 22 (55%) were in moderately grazed pasture, and 16 (40%) were in heavily grazed pasture. Among successful nests, 0% were in the control pasture, 60% were in moderately grazed pasture, and 40% were in heavily grazed pasture. In Kansas, Fitch (1958) reported that it was formerly more abundant when livestock grazing kept the herbaceous vegetation cropped short. In Arizona, higher nesting densities occurred on grazed than ungrazed semi-desert grasslands (Swanson 1996).

Fire may be either beneficial or detrimental depending upon the intensity of the fire and whether it occurs in native or nonnative grasslands. Long-term fire suppression allows communities to develop dense stands of grasses and shrubs, reducing the amount of edge habitat and bare soils that the Lark Sparrow prefers. In stands of nonnative grasses and weeds, fires are more intense and frequent, further promoting growth of nonnative species. A Utah fire removed dense living and dead annuals, exposed bare soils, and left standing snags. Numbers of adults and juveniles remained high in the 2 years following fire. In the third year, annual weeds had increased enough that the Lark Sparrow abandoned nesting attempts except in areas that were burned again. In Texas, burns that completely eliminated woody vegetation negatively affected it and its nesting success. In Montana, only minor reductions occurred where shrubs were partially killed but areas where all sagebrush was killed were avoided. In Texas, nest survival rate was negatively correlated with the frequency of burning. In Utah, it increased at an artillery training area where contiguous juniper and shrubsteppe vegetation was fragmented by fires and roads. On Kansas CRP lands, abundance was significantly higher on lands that were burned in the spring than in unburned fields. In Arizona desert grasslands, it increased 2 years postburn and its abundance was positively correlated with herbaceous cover. In a Washington fire in shrubsteppe habitat, it increased shortly after fire but the increase was short-lived. The increase immediately after fire may have been a result of an increase in the amount of bare ground. In summary, fire that retards natural succession and lowers the amount of litter and dead and alive vegetation and creates patches of bare ground is beneficial; intense fires that kill all woody cover are detrimental (Dechant et al. 2002f; Earnst et al. 2009; Jacobson et al. 2011; Martin and Parrish 2020; Roberts et al. 2012).

A number of miscellaneous factors may affect the Lark Sparrow. Precipitation may adversely affect it; some Oklahoma nests were washed away by heavy rains and in Washington fewer individuals were recorded in wetter years (Earnst et al. 2009; Newman 1970). There are large annual variations in its breeding density. These are likely related to overwintering survival. Grasshoppers are a major food item and it has declined in response to intensive grasshopper control measures using pesticides (Martin and Parrish 2020). In British Columbia, it may be adversely affected by recreational vehicles (Campbell et al. 2001).

In Alberta, Nixon et al. (2016) predicted the effects of climate change on the Lark Sparrow. They projected that the area of suitable habitat would increase by 250% by the 2050s and 400% by the 2080s. Suitable climate was expected to expand to the north with little change in the south, resulting in an expansion in occupied range.

Several management recommendations have been proposed for the Lark Sparrow. For Oklahoma, Lusk et al. (2003) recommended that management should attempt to provide moderate levels of litter accumulation and bare ground. Maintaining bare-ground coverage below 12% should increase nest success. Increased structural cover should also increase the attractiveness of habitat and decrease the distance between nests. Dechant et al. (2002f) concluded that the keys to management included providing open grassland with sparse to moderate herbaceous and litter cover and allowing moderate grazing or occasional burning. They recommended conducting burns before it arrives in spring at intervals of 5-8 years and retaining approximately 10% shrub coverage.

Status

During a brief eastward expansion of its range, the Lark Sparrow was a rare and irregular breeder in Ontario. The first report of it in Ontario occurred near Hamilton in 1862. In June 1885 a male and 2 females were seen on the Hamilton beach and these may have nested. Some birds were observed as far north as Sault Ste. Marie in 1880 and as far east as Toronto in 1891. It was a rare and very local summer resident in Toronto by 1907 where nesting was confirmed in the oak plains in High Park in 1898 and 1899. From 1878-89, 1 or 2 pairs nested regularly near London. It was rare at Point Pelee in the 1900s although it was believed to have been common there previously; nests were found there in 1884, 1905, and 1913. A pair was seen near Komoka in 1900. There were no further breeding season records until a nest was found near Walsingham in 1930. Prior to the first atlas, breeding had been confirmed only from Toronto, Sudbury District, Chatham-Kent, and Essex, Middlesex, and Norfolk counties. At that time, the last confirmed breeding record was a nest on the Norfolk Sand Plain in 1976. The nest found at Sudbury in 1973 is the northernmost confirmed record. During the first atlas, the only record was of a pair east of Thunder Bay seen in 1982. No other records were obtained during the subsequent Ontario Rare Breeding Bird Program (Austen et al. 1994; Baillie 1967; Baillie and Harrington 1937; Curry 2006; Dale 1931; Fleming 1907; Hussell in Cadman et al. 1987; McIlwraith 1894). James (1991) considered the Lark Sparrow an occasional rare summer resident in the south north to Bruce County and Durham Region and in Sudbury. There are summer records from Atikokan, Thunder Bay, and Moosonee.

During the second atlas, no breeding records for the Lark Sparrow were obtained. Documentation was received for 7 records, all involving apparent vagrants (Sutherland in Cadman et al. 2007).

Prior to European settlement, the Lark Sparrow nested eastward only to the prairies and Great Plains. With deforestation, it spread its breeding range as far east as the northern and central states. This range expansion was short-lived, with it withdrawing from the east to its original range as a result of more intensive agriculture, urbanization, and natural succession of marginal farmlands to forest. Its status in Ohio was very similar to what occurred in Ontario. It expanded into Ohio in the late 1880s and was common in several areas by 1900. It began declining there during the 1930s and disappeared from much of its former range by 1965. The Breeding Bird Survey indicates that the Lark

Sparrow decreased significantly at a rate of 2.5% per year from 1966 to 2004. This was attributed to the withdrawal from the east with populations in the western United States remaining stable or increasing slightly (Graber and Graber 1963; Houston and Houston 2001; Leighton et al. 2002; Lusk et al. 2003; Martin and Parrish 2020; McCracken 2005; Swanson 1996).

The greatest limiting factor to the Ontario breeding population of Lark Sparrows is the general contraction of its range from the east. Even when it was more widespread, Ontario was on the extreme outer limits of its range. Due to its current almost complete absence in the states south of Ontario (New York, Pennsylvania, Ohio, and Indiana), it is unlikely that it will re-establish itself as a breeding species in southern Ontario. If breeding occurs in future in Ontario, it will most likely be in the northwest. There are currently populations in southern Manitoba and northern Wisconsin that are potential sources of breeding birds.

POSTFLEDGING PERIOD

If undisturbed, young are capable of flight when they leave the nest. They are led to more shrubby areas by adults after fledging. In Ohio where a pair nested in a garden, the adults and young remained in or near the garden for at least 3 days. Almost immediately after fledging, some adults leave the breeding grounds; this may occur as early as mid-July or August. Mixing of migratory adults with adults that are still breeding is common in late summer. In Oklahoma after fledging, most pairs joined other families in flocks in nearby fields. Flock sizes increase as the summer wanes and flocks may be joined by other species such as the Field Sparrow. In British Columbia and probably elsewhere, similar open habitats were used during the postfledging period and migration. These included beaches, trails, brushy edges of fields and hedgerows, urban lawns, weedy fields, and feeders (Baepler in Austin 1968; Campbell et al. 2001; Gier 1949; Leighton et al. 2002; Martin and Parrish 2020).

MIGRATION

During migration, and particularly in autumn, the Lark Sparrow occurs in conspecific or mixed-species flocks that may contain 40-50 individuals in September and October (Griscom 1948; Martin and Parrish 2020).

In the southern portion of the Lark Sparrow's range, males arrive 30 or more days before females. Timing of arrival of the sexes has not been documented in Ontario but it is unlikely that males would arrive here much more than a week before females. There are few spring records, so the timing of spring migration is somewhat unclear. Throughout the province, spring records span the period 3 April to 29 May (Black and Roy 2010; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Martin and Parrish 2020; Speirs 1985; Tozer 2012; Weir 2008). In Algonquin Park, autumn migrants have been observed from 3 September to 13 October (Tozer 2012). In the Kingston area, average departure is 6 October and the extreme dates are 2 September to 22 December, excluding an overwintering bird (Weir 2008). The only recent autumn record in Hamilton was on 15 August (Curry 2006). In Elgin County, autumn migrants have been reported from 19 September to 1 November (Lancaster et al. 2004).

Migration habitat is very similar to breeding and postfledging habitat. A spring migrant at Presqu'ile foraged on mowed grass along the park road and perched on roadside wires (LaForest 1993). In Algonquin Park, a spring migrant fed on seeds below a feeder. Autumn migrants were seen

on the grassy tile bed of the museum, along a roadway on the abandoned airfield, and along the weedy edge of a large field (Tozer 2012). In British Columbia, migrants inhabit beaches, trails, shrubby edges of fields and fencerows, urban lawns, weedy fields, and feeders. Habitat similar to that inhabited during the breeding season may also be used including shrubsteppe grasslands and grazed pastures (Campbell et al. 2001). In Kansas, spring migrants foraged where bluestem prairie had been burned the previous month and new growth of grass was beginning to appear (Fitch 1958). In the heart of its range, autumn migrants may be found in open cottonwood stands, floodplains with dense vegetation comprised predominantly of small cottonwoods and weedy annuals, and overgrazed prairies. At this time, migrants and residents mix together (Martin and Parrish 2020).

Baillie (1967) stated that the Lark Sparrow was still rarely observed during migration, mostly along the Lake Erie shoreline. James (1991) considered it a rare migrant. Because it no longer occurs anywhere within the province regularly during migration and may be completely absent for many successive years, it might better be described as a vagrant during migration.

WINTER

James (1991) considered the Lark Sparrow a vagrant in Ontario during winter. One remained in the Kingston area from 30 November to 22 March (Weir 2008), the only known overwintering attempt.

Chipping Sparrow

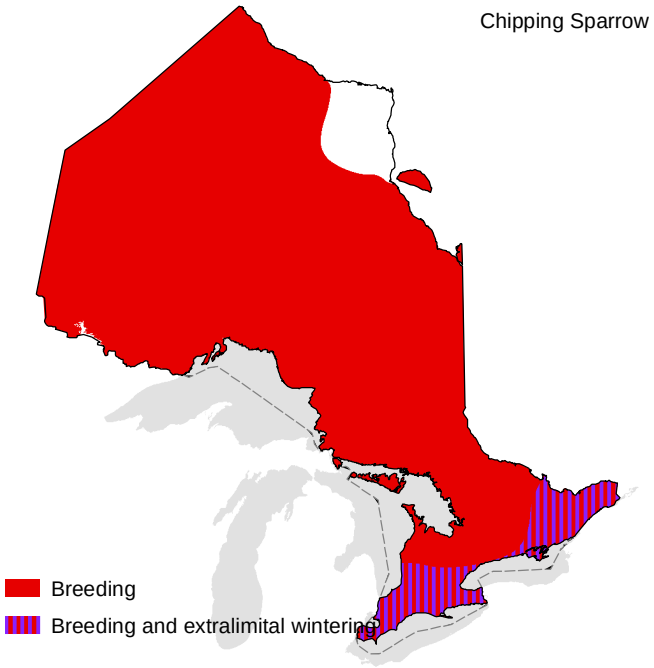
Spizella passerina

BREEDING SEASON

Habitat Requirements

Ontario Chipping Sparrow nests were in residential gardens and farmyards (55.6% of nests); in wooded areas, including natural coniferous stands and plantations (12.8%), mixed stands (4.3%), and deciduous stands (2.1%); in overgrown fields and pastures, orchards, vineyards, and nurseries (10.4%); in parks, campgrounds, and cottage lots (7.2%); in other rural and urban habitats including schoolyards, cemeteries, golf courses, tennis courts, parking lots, and gravel yards (2.9%); on road and railway rights-of-way (2.7%); in treed sand dunes (1.6%); and in treed bogs (0.5%). Most nesting habitats were dry and almost invariably contained trees and shrubs. Nests in wooded areas were usually in areas of open canopy or at edges (Peck and James 1987).

In the Hudson Bay Lowland, the Chipping Sparrow was a common breeder in the Moosonee area, particularly around the town site (Wilson and McRae 1993).



In the Boreal Forest Region from Pickle Lake north to the Manitoba border, the Chipping Sparrow was most abundant in deciduous and coniferous scrub followed by mixed scrub and coniferous forest with a deciduous understorey, coniferous forest without an understorey, and heath. It was absent in deciduous forest and tundra (McLaren and McLaren 1981). It occurred in disturbed or open mixed woods and about towns in the Pickle Lake area (James 1980). Near Hearst, it occurred in low density in a 9-year-old clear-cut in coniferous lowland forest (Welsh and Fillman 1980). Near White River, it was much more abundant in stands cut 8-10 years previously than in stands 3-5, 13-15, 18-20, 23-25, and 4-10 years old. It was an indicator species of 8-10-year-old stands (Venier and Pearce 2005). Near Manitouwadge, highest densities occurred in stands 1-21 years old; it was uncommon in stands 24-36 years old and absent in stands 60-223 years old (Venier et al. 2009). It occurred both in forests and around settlements in the Clay Belt (Smith 1957). In the same physiographic region, it was most abundant in stands dominated by jack pine followed by those dominated by white spruce, trembling aspen–white birch (often mixed with spruce), black spruce, and balsam poplar. It occurred in both nutrient-poor and nutrient-rich sites, mostly in wetter areas (Welsh 1993; Welsh and Lougheed 1996).

In the Canadian Shield in the Great Lakes–St. Lawrence Forest Region, the Chipping Sparrow occurred in both old-growth and mature white pine stands (Kirk et al. 2012). In Quetico Park, it was equally abundant in 1-23-year-old jack pine stands with scattered black spruce and trembling aspen regeneration and 67-73-year-old jack pine–poplar stands; half as abundant in 112-176-year-old stands of jack pine, poplar, spruce, and balsam fir, and absent in 367-370-year-old stands of white pine, red pine, spruce, balsam fir, and white cedar (Apfelbaum and Haney 1985). Near Gogama, it was characteristic of jack pine stands where it preferred openings and edges and avoided closed-canopy areas. It first appeared when trees attained an age of about 10 years. Although it occurred in all older stands, it reached its maximum abundance when trees were about 20 years old when there were still numerous openings in the canopy that allowed shrub growth (James and Peck 1995a). In jack pine stands near Parry Sound, it was one of the most abundant species. These were very open stands mixed with deciduous tree species and contained numerous bedrock outcrops (James 1979a). The Chipping Sparrow was one of the most common breeding birds in Parry Sound and Muskoka districts where it nested in residential and rural areas, along road sides, and at forest edges (Mills 1981). In largely forested areas near Restoule Park, it appears to prefer to nest in areas of open bedrock outcrops with scattered white spruce (personal observation). Middleton (2020) reported that it nested in habitats dominated by white spruce, white pine, and balsam fir in

Algonquin Park. MacLulich (1935) observed that it was common in more open areas in the park but absent in unbroken forest. It frequented trees in clearings, edges of woods, and burns. Tozer (2012) noted that it was less abundant in the western portion of the park that is dominated by hardwoods than in the conifer-dominated east side. Nesting habitat included clearings, forest edges, road margins, gravel pits, clear-cuts, logging landings, open coniferous forests, open areas around buildings, campgrounds, and open shorelines of rivers, lakes, and ponds. Kingsley and Nol (1999) determined that it was associated with coniferous non-white pine habitat in the park. There was no difference in its abundance in stands with no recent history of cutting and those that had been cut 2-9 or 10-16 years previously. Martin (1960) documented the Chipping Sparrow breeding in hemlock stands in the park. Also in Algonquin Park, the dominant plants and trees within 1 m of nests were typically early successional species that occurred in well-drained areas. The frequency of tree species nearest nests was 45% white spruce, 11% trembling aspen, 8% balsam fir, 8% white pine, 8% black cherry, 5% red pine, 2% red maple, and 2% sugar maple. The frequency of plant species within 1 m of nests was 91% white spruce, 82% grasses (mostly poverty oat grass), 45% haircup moss, 45% lowbush blueberry, 14% balsam fir, and 6% red pine (Reynolds and Knapton 1984).

At Presqu'ile in the off-Shield portion of the Great Lakes–St. Lawrence Forest Region, the Chipping Sparrow favoured coniferous plantations for nesting and commonly nested around residences. It also nests in open woodlands, open areas near forests, or open areas with scattered trees (LaForest 1993). In Durham Region, highest densities were in a mature pine plantation dominated by red pine but that contained some white pine. It also occurred in a black spruce bog fringed with white spruce and tamarack; low densities occurred in mature beech–sugar maple forest. Speirs and Orenstein (1975) considered it associated with conifers, particularly pines. On the University of Guelph campus, it nested in open grassy areas surrounded by extensive plantings of species such as maples, crabapples, cherries, plum, junipers, pines, spruces, yews, and white cedar (Middleton and Prescott 1989).

In the Carolinian Forest Region, it was common on the University of Western Ontario campus at London (Scott and Lemon 1996). In Hamilton, it was the most common bird around buildings until the arrival of the House Sparrow. Although it declined with increased populations of House Sparrows, it continued to nest in gardens, shade trees in cities, and weedy corners and thorn bushes in pastures (McIlwraith 1894). In Elgin County, it frequently occurs around rural and urban homes (Lancaster et al. 2004).

The tree species it uses vary geographically but the Chipping Sparrow nests in similar habitat throughout its range. It is more abundant in suburban areas and around rural residences, orchards, and farms than in undisturbed areas. Park-like streetscapes and landscaped urban and rural residential areas often provide ideal habitat. In the north, it may be more common around isolated human habitation than in natural habitat, and may occur around cottages, hunting and trapping camps, and along roads through boreal forests. In more natural habitats, it prefers open woodlands, edges of natural forest openings, margins of rivers and lakes, and shrubby weedy fields. It prefers groves and open glades of coniferous forests for nesting and shrubby open areas for foraging and is well adapted to human-altered habitats. It may be the most abundant species in areas with ornamental plantings and in coniferous plantations, including Christmas tree plantations. In the

southern portion of its range, it inhabits a variety of deciduous forest types but retains its affinity for nesting in shrubby habitats with conifers. Mixed pine and oak stands provide suitable habitat in the south (Middleton 2020).

In Quebec, the Chipping Sparrow is most common where urbanization and agriculture have created open habitat. It breeds in urban residential areas, city parks, cemeteries, golf courses, farm fields, coniferous and Christmas tree plantations, and road and hydro rights-of-way. It occurs mostly in openings, woodland edges, and clumps of trees bordering open grassy areas. A few conifers appear to be required because it frequently nests in them. It needs a certain minimum amount of open space in its territory. The small yards typical of new subdivisions may not be large enough to support it (Perreault and Barrette in Gauthier and Aubry 1996). Mousley (1916a) reported that it could be found nesting around every farm home in Quebec as well as throughout the agricultural south. It is one of the typical species in the Boreal Forest Region. It is frequent in jack pine stands and among the species most commonly detected in tamarack stands and bogs. It is characteristic of human-altered habitat including settlements, alpine ecotones with boreal forest, prairie-forest ecotones, and open bogs with scattered trees. In poplar-birch stands, it is associated with openings or young growths of deciduous species. In addition to open pine stands, it also occurs in those dominated by spruce and balsam fir and occasionally is present in hemlock stands (Erskine 1977). In the Prairie Provinces, the Chipping Sparrow was most abundant in black spruce or jack pine stands. It occupied sites that tended to be drier and nutrient-poor. Kirk et al. (1996) considered it an early successional species, being most abundant in stands 15-20 years old. In trembling aspen forests in Alberta, it was equally abundant in young and mature stands. It was more abundant in old stands, but not significantly. Old stands had more conifers in the understorey, possibly making them slightly more attractive (Schieck et al. 1995). In British Columbia, it breeds in a variety of shrubby habitats where it usually occurs in open spaces and is often associated with edges of both coniferous and deciduous forests, wetlands, clear-cuts, and agricultural areas. Seventy-two percent of nests along the coast were in areas modified by humans, including 27% in suburban areas and 15% on farms. Other breeding habitats include open fir and oak stands, open coniferous forests, deciduous woodlands dominated by birch, subalpine grasslands and meadows, rangeland, grass or sedge meadows, trembling aspen stands, and wetlands surrounded by patches of willow, alder, and birch (Campbell et al. 2001). In the Yukon, it inhabits open forests that are mostly in lowland areas. These include mixed forests with some spruce, shrubby woodlands with openings, areas above the treeline, and mature trembling aspen forests where it is the most abundant songbird (Sinclair et al. 2003). In the United States, the Chipping Sparrow is abundant in urban and suburban areas. In Illinois, almost every yard that has a blue spruce supports a pair. In that state and others in the Midwest, it is common in savannah-like habitats and may also occur in a variety of woody and old-field habitats. It may be one of the most abundant species in coniferous plantations and in Scotch pine plantations managed for Christmas tree production. These short but dense trees within open habitat provide ideal conditions. Other habitats used for breeding include open pine stands, shrubby fields with scattered trees (particularly if red cedar or other conifers are present), clear-cuts, open deciduous and mixed stands including riparian vegetation, small woodland openings, mixed tallgrass prairie, savannahs with either grass or shrub understorey, montane meadows, aspen stands in the west, hydro rights-of-way, black spruce bogs, and pine and pine-oak barrens (Allaire and Fisher

1975; Beals 1960; Bielefeldt and Rosenfield 1994; Brush 1987; Buech 1982; Capen 1979; Dawson 1979; Flack 1976; Graber and Graber 1963; Hebrard 1978; Hoffman 1989a; Hughes and Hudson 1997; Mossman et al. 1991; Niemi and Hanowski 1984a; Noon et al. 1979; Ortega and Ortega 2001; Rotenberry and Wiens 1980; Rumble and Gobeille 1998; Samson 1979; Simmons and Sloan 1974; Stull in Austin 1968; Swanson et al. 2004; Taylor and Taylor 1979; Temple et al. 1979; Walk et al. 2011; Walkinshaw 1944; Wood et al. 2013; Yahner et al. 2002).

At the landscape level, abundance of the Chipping Sparrow in southern Ontario was positively correlated with the amount of forest cover within 2 km and the amount of regional forest cover, but not significantly (Austen et al. 2001). In Saskatchewan, it occurred both in fragmented and forested landscapes. It was more common in large forest fragments where there were low amounts of forest cover within 5 km (Hobson and Bayne 2000). It preferred landscapes that were 33-59% forested in North Dakota and 44-58% forested in New York (Cunningham and Johnson 2019).

Several studies examined microhabitats of the Chipping Sparrow. In the northeast, it was in a guild that was common in mature coniferous upland forests, uncommon in mature coniferous lowland forests, and rare in alder thickets, mature deciduous upland forests, disturbed shrub habitat, young plantations, aspen regeneration, and recent clear-cuts (Niemi and Pfannmuller 1979). In North Carolina, its abundance was negatively correlated with canopy closure (Lumpkin and Pearson 2013). In Saskatchewan, it was significantly more abundant in spruce and mixed forests than in trembling aspen forests (Hobson and Bayne 2000). In Pennsylvania, it occurred in 90.9% of old-growth mixed forests, 97.1% of forests statewide, and 93.1% of forests in the Appalachian Plateau. Haney (1999) considered it to have neutral affinities with old-growth forest. In Massachusetts suburban habitat, coniferous shrub volume 3.4-4.6 m from the ground was the most important variable in determining its abundance. It was associated with conifers as tall as 4.6 m with little overstorey, and open grassland or lawn (Thomas et al. 1977). In British Columbia, it strongly selected for nest patches with more vegetation, particularly deciduous shrubs. It nested in habitats with open canopies, choosing patches with greater percent coverage by shrubs, high numbers of stems of deciduous trees that preferred dry sites, and areas with high numbers of pine and fir stems. It consistently selected nest patches with more deciduous vegetation than was available. It chose patches with conifers for nesting but also areas with deciduous vegetation that provided sources of seeds and ground-dwelling invertebrates (Easton and Martin 2002).

Freemark and Collins (1992) classified the Chipping Sparrow as a forest edge species. In Arizona, Battin and Sisk (2011) restored thinned pine forest and conducted prescribed burns, reducing the basal area by 45% and the density of pines by 80%. It was significantly more abundant in the treated area, with detectability 91% greater in the treated area. In the treated area, it occurred throughout the habitat and demonstrated no preference for edge. In the untreated forest plot, it was significantly more abundant near edge.

The Chipping Sparrow is not an area-sensitive species. In southern Ontario, its abundance was negatively correlated with woodlot size and the amount of forest habitat 100 m or more from edge, but not significantly (Austen et al. 2001). In Saskatchewan, its abundance was not correlated with forest size, although it was more common than expected in mature white spruce stands that were large but isolated (Hobson and Bayne 2000). In Maryland and Delaware, it was equally abundant in

riparian forests 50, 100, 200, 300, and 800 m wide (Keller et al. 1993). In Minnesota, Howe (1979) found it nesting on islands as small as 0.4, 0.9, and 1.1 ha.

In Michigan suburban habitat, 1 female roosted overnight in a dense white cedar 1.2 m from the nest and another roosted in a dense clump of lilacs 13.7 m from the nest. Males often roosted in white cedars (Walkinshaw 1944).

Most Ontario nests (98.2%) were elevated in living trees, shrubs, and vines. Eight species of coniferous trees and shrubs supported 88.0% of elevated nests. Twenty-nine species of deciduous trees, shrubs, and vines were used, but supported only 12.0% of nests. The most frequently selected species used for nesting were spruces (90 nests), pines (80 nests), junipers (48 nests), white cedar (37 nests), hawthorns (30 nests), balsam fir (15 nests), and elms (12 nests). Many nests in gardens were in hedges. Nests in vines or roses were often on trellises or against a wall. Single nests were found among the branches of a fallen pine, on a willow stub, on an apple tree stump, on the ground in a clump of red clover, in a clump of goldenrod, in an implement shed, in a notch in the side of an upright timber, and in the corner of a barnyard rail fence. Tree and shrub nests were on lateral branches or in crotches and were more often away from the trunk than near it. Distances from trunks were 0.5-4.6 m, with most nests 0.9-2.4 m from the trunk. Heights of elevated nests were 0.2-15 m with most 0.9-2.2 m from the ground (Peck and James 1987). Reynolds and Knapton (1984) described 22 nests from Algonquin Park: 19 were in white spruce and 1 each were in hemlock, balsam fir, and red pine. Usage of spruce (86.4% of nests) was greater than its availability (42.5% of trees). The median height of nest trees was 2.5 m (range 1.1-13.7 m) and this did not differ significantly from nearby trees. The median height of nests was 1.1 m (range 0.4-2.5 m). Successful nests averaged 1.51 m in height (range 0.64-2.46 m); unsuccessful nests averaged 0.69 m in height (range 0.38-1.30 m). Orientation of successful nests averaged 158.1°, significantly different from unsuccessful nests (28.7°). Successful nests averaged 4.8° from the mean whereas unsuccessful nests averaged 124.6° from the mean; mean orientation was 153.3°. Most nests were positioned so that they were exposed to the early morning sun. Prevailing winds were from the northwest and the southeastern orientation may have offered some protection. In Muskoka and Parry Sound districts, the Chipping Sparrow nested mainly in conifers at heights of 0.3-12 m. Average nest height was 1.5 m but those in white pine were higher. Nests were also in white elm, juneberry, and a deciduous shrub in a gravel pit (Mills 1981). Middleton (2020) summarized the characteristics of 224 nests on the University of Guelph campus. Conifers supported 87.9% of nests and 12.1% were in deciduous trees and shrubs. Spruce was the preferred nesting substrate, supporting 32.7% of nests, followed by pine (23.0%), juniper (20.6%), white cedar (5.5%), yew (4.3%), and larch (1.7%). The most preferred deciduous tree was crabapple (3.9% of nests), followed by maple (2.0%), and a variety of ornamental trees, shrubs, and vines (3.6%), including hawthorn, beauty bush, currant, and English ivy. Mean nest height was 2.6 m (range 0.5-10 m). There was a tendency for nest height to increase with the season, but this trend was not significant. No preference for orientation was exhibited at Guelph where trees were often sheltered by buildings. Overhead cover was not essential for nests. Those in pine and spruce were often uncovered; those in cedar, juniper, and deciduous species were covered. In 15 years at Guelph, there were no records of the same nest being used more than once in a season (Middleton and Prescott 1989). In Michigan, there were 2 cases of the same nest sites being used in the same season after the first nests were intentionally removed, and the same nest site may be

used in subsequent years. Many nests are abandoned during the nest-building and egg-laying stages and materials from them may be used to construct a new nest.

Where available, conifers are highly preferred for nesting; in deciduous stands in Colorado, 77% of nests were in oaks. Spruces, pines, cedars, firs, junipers, and yews are most frequently selected for nesting. In addition to the nest-species reported in Ontario, the Chipping Sparrow has nested in spiraea bushes, rose bushes, horse chestnut, pear, apple, grape, cottonwood, birch, willow, and red-osier dogwood. Nests in ornamental trees and shrubs are often very close to human dwellings. Nests are usually 1-2 m from the ground. In Michigan, mean nest height in suburban areas was 1.09 m in May, 1.53 m in June, and 2.29 m in July. In a Michigan Christmas tree plantation, mean nest height was 1.43 m, significantly higher than for Clay-colored and Field sparrows. In Colorado, the Chipping Sparrow tended to nest at one third of the pine height two thirds of the way out the branch. Mean nest height was 2.55 m. Nests were in clusters of pine needles on outer branches an average of 1.36 m from the trunk and 0.58 m from the tip of the branch. Average orientation of nests was 155.7°, almost identical to what was reported for Algonquin Park, and nests were significantly clumped around the mean. In a Vermont Christmas tree plantation, nests in trees 1.5-2.0 m tall averaged 0.8 m from the ground (range 0.3-1.1 m). All these nests were next to the tree trunk, which probably provided shelter from the wind. In British Columbia, nests were 0-9 m from the ground, but mostly 0.8-2.2 m up. In Minnesota, 61.5% of nests were less than 1.8 m from the ground and 13.3% were higher than 3.4 m. In a Minnesota bog, it nested in tops of black spruce at heights of 16.6 m and 17.2 m. The highest nest reported was 19.1 m up in the top of a maple overgrown with vines in Pennsylvania. Most Yukon nests were about 0.5 m from the ground (range 0.1-4.5 m). The Chipping Sparrow rarely nests on the ground. In green ash woodlands in South Dakota, all nests were on the ground, and many Alberta nests were on the ground. Unusual nest locations include on a mowing machine in a semiopen tool shed, on the sides of old stacks of straw, in a moss-filled hanging basket, in pepper plants hung to dry, and 10 cm down from the opening of a Hairy Woodpecker winter roost hole. Some British Columbia nests were in fallen trees, against a rock, or on the ground sheltered beneath a clump of vegetation (Allen 1939; Buech 1982; Campbell et al. 2001; Fillmore and Titman 1977; Harrison et al. 2005; Hughes and Hudson 1997; Leighton et al. 2002; Middleton 2020; Ortega and Ortega 2001; Rumble and Gobeille 1998; Sinclair et al. 2003; Stull in Austin 1968; Swanson et al. 2004; Walkinshaw 1944, 1952, 1959).

Males commence territorial defence as soon as they arrive in spring. In Algonquin Park, males sang from conspicuous perches, usually in white spruce or balsam fir. The female may defend an area around the nest tree and occasionally assists in territorial defence. Territorial disputes were frequent in mid-May in Algonquin Park but declined progressively thereafter. No territorial behaviour was observed after mid-August in a Michigan suburb. Even during the height of territoriality, 2 males may sit on opposite sides of a tree. Pairs may share feeding areas outside territories and feed close to each other, yet each male defends a discrete territory. In natural areas, territories tend to be compact and contiguous. In settled areas, territories tend to be discontiguous with boundaries imposed by urban landscaping. In suburban Michigan, territories were 0.4-0.6 ha. Most territories are 0.2-1.0 ha but 1 Georgia male had a territory of 3.1 ha during nest building and incubation that declined to 1.1 ha during the nestling stage. Home ranges are larger but there is no information on their size. In addition to wandering off territories to forage, males frequently make

extra-territorial forays early in the breeding season when females are receptive (Middleton 2020; Middleton and Prescott 1989; Odum and Kuenzler 1955; Reynolds and Knapton 1984; Stull in Austin 1968; Walkinshaw 1944).

Natal philopatry rates are low. At Guelph, 1 of 229 nestlings (0.4%) returned as a breeding female 2 years later. A juvenile banded in Pickering in September was recovered in July at the same location almost 4 years later. In Michigan, 0 of 28 nestlings returned (Middleton 2020; Speirs 1985; Walkinshaw 1952).

Adult females tend to return to their previous breeding areas but males vary in their fidelity. Return rates at Guelph were 25.6% for females and 15.6% for males. In Minnesota, 21.0% of females and 10.5% of males returned. In Michigan, 50% of both sexes returned, but only 6 females and 4 males were banded. At Guelph, there was 1 record of a male on the same territory in 2 consecutive years and 4 females were documented in 3 successive years. One Michigan female was present in 5 years and her 12 nests were within an area of 0.08 ha (Middleton 2020; Middleton and Prescott 1989; Walkinshaw 1952).

Limiting Factors

Peck and James (1987) reported eggs in Ontario nests from the beginning of May until mid-August, with most present in the first 3 weeks of June. In Algonquin Park, nests are under construction from late May to late June, eggs are present from late May to mid-July, nestlings are present from early June to mid-July, and dependent fledglings have been observed from late June to mid-August (Tozer 2012). The modal date for nest initiation in Algonquin Park was 31 May. Reynolds and Knapton (1984) concluded that the few nests started through early July were probably replacement nests. At the University of Guelph, the earliest egg date was 7 May, the mean was 12.8 May, and the latest egg was laid on 15 July (Middleton 2020).

Pairing occurs 1 or 2 days after the females arrive. Most birds are paired by late May in Algonquin Park. In Algonquin Park, nests took 4 days to build. The mean time to construct nests at the University of Guelph was 4.1 days (range 2-8 days). Later nests were built significantly quicker: mean times to build nests were 4.4 days in May, 3.6 days in June, and 2-3 days in July. In Colorado, nests took an average of 4.1 days to build. In Michigan, nests took an average of 3.4 days to complete (range 2-5 days); July nests took only 2 days to build. One Michigan nest took 15 days to build, but no work was done on it for an 8-day period. In most cases, the first egg is laid the day after the nest is complete. As many as 7 days have elapsed between nest completion and laying of the first egg, with longest intervals occurring early in the season. One egg is usually laid per day, but laying may be interrupted by cold and wet weather. Laying may resume 2-3 days later with no apparent effects on the original eggs. Incubation may start with the laying of the penultimate egg, the night before the last egg is laid, or after the final egg is laid. Incubation periods of 7-14 days have been reported in Ontario, with most eggs hatching in 10-11 days. In Algonquin Park, the incubation period was 11-12 days; the mean incubation period at both the University of Guelph and University of Western Ontario was 11.9 days. Elsewhere, the typical range for the incubation period is 10-15 days. The mean incubation period in Michigan was identical to that at Guelph and London (11.9 days, range 10-14 days). The mean incubation period in Colorado was 10.4 days. Nests have no insulative properties and cool temperatures result in longer incubation periods. Hatching may be synchronous or spread over 24

hours, depending upon when incubation started. Most young in Algonquin Park fledged when they were 9 days old. The nestling period is 7-12 days, mean nestling period was 9.85 days at 52 nests, and the mean nestling period at Fort Simpson, Northwest Territories was 9.6 days. In Colorado, the mean nestling period was 8.5 days. Nestlings that leave the nest before they are 9 days old have greatly reduced chances of survival (Allen 1939; Ball and Bayne 2012; Middleton 2020; Ortega and Ortega 2001; Peck and James 1987, 1998b; Reynolds and Knapton 1984; Scott and Lemon 1996; Stull in Austin 1968; Swanson et al. 2004; Walkinshaw 1944, 1952).

As many as 3 broods have been raised by the Chipping Sparrow in Ontario and other locations, but 2 broods is usually the maximum. In Algonquin Park, there was no evidence of second broods being attempted. The same was true at the University of Guelph where the maximum number of nests in a season was the original nest and 2 replacement nests. At the University of Western Ontario, 8 of 27 pairs (29.6%) raised 2 broods with an average of 1.26 broods per pair. Only a single case of 3 broods has been reported in the province, with all raised in different nests. Some second broods were raised in the same nest, but nest reuse appears to be rare. In Michigan, 1 female attempted 5 nests in a year; 2 failed and 3 broods of 1, 2, and 3 young were raised. This female had 12 nests in 5 years. Despite the occasional pair raising 2 or even 3 broods, most pairs are successful in raising only a single brood a year. Twelve to 24% of pairs raise a second brood. The time between fledging of the first brood and building the next nest averages 11 days (range 3-24 days). When more than 1 brood is raised, the male cares for earlier broods while the female is incubating the next clutch. It regularly initiates replacement clutches if the first one is lost or abandoned, usually the day after the loss. Clutches of 2-5 eggs have been reported in Ontario; 1 nest contained 7 eggs. Two-egg clutches were uncommon, but some were incubated and produced young. The average clutch size of 396 Ontario nests was 3.36 eggs; the most frequent clutch size was 4 eggs. In Algonquin Park, clutches of 3-5 eggs were reported. The mean clutch size 1 year was 3.8 eggs and the mean was 4.3 the following year for an overall average of 4.0 eggs. At the University of Guelph, 377 unparasitized nests had a mean clutch size of 3.7 eggs (range 2-5 eggs). The normal range of clutch size is 2-5 eggs, but there are rare records of 6- and 7-egg clutches. Most clutches contain either 3 or 4 eggs and clutch size declines with the season; second and replacement clutches are smaller than first clutches. Average clutch sizes were 3.62 in Michigan, 3.00 for unparasitized nests in Minnesota, 3.08 in Colorado, and 3.79 in Pennsylvania (Allen 1939; Buech 1982; Campbell et al. 2001; Middleton 2020; Mousley 1916a; Peck and James 1987; Reynolds and Knapton 1984; Scott and Lemon 1996; Stull in Austin 1968; Swanson et al. 2004; Walkinshaw 1944, 1952).

Yearlings are probably capable of breeding and older birds breed every year. Originally considered strictly monogamous, recent research demonstrated that the Chipping Sparrow employs a variety of reproductive strategies, including polygyny, intraspecific parasitism, and extra-pair copulations. Of 9 pairs nesting on the University of Guelph campus, polygyny was presumed in 1 case and strongly suspected in another. In North Dakota, 1 of 32 pairings (3.1%) was polygynous. Low rates of polygyny have been documented in New York, North Dakota, and Michigan. In Michigan, 2 cases occurred where 2 females contributed eggs to a single nest, with resulting clutches of 8 eggs and 7 sparrow eggs and a cowbird egg. In the first case, both females were mated with the same male and 3 adults attended the nestlings. At Guelph, there were 6 instances of 493 nests (1.2%) where more than 1 female contributed eggs to the same nest. Extra-pair copulations

appear to be common and are sought by both sexes. During nest building and egg laying, the male maintains close contact with the female and is probably guarding her from other males. Once incubation begins, males frequently wander off their territories, apparently to seek extra-pair copulations. Most territories at the University of Guelph contained dense stands of conifers where males could trespass on other territories without being detected. Pair bonds may persist for the entire breeding season or change as the season progresses. If a mate is lost, new pair bonds are formed quickly (Middleton 2020; Middleton and Prescott 1989; Walkinshaw 1959).

During the breeding season, the Chipping Sparrow forages either individually or in pairs. In Algonquin Park, foraging occurred on the ground along edges of wooded areas, gravel roads, and parking lots. Most foraging occurs on the ground or in low vegetation, predominantly in open areas such as lawns, fallow fields, along hedgerows, and in forest litter. In Michigan, most food for nestlings was obtained in a woodland adjacent to the nesting field. It may scratch through accumulated plant litter in search of fallen seeds, invertebrates, and grit. It feeds directly on ripened seed heads of low grasses and herbaceous species. It sometimes feeds by reaching out from a perch in brush piles, fallen trees, low shrubs, or fences and by eating seeds directly from tips of stems within 1 m of the ground. It hunts insects by searching from a perch 30-40 cm from the ground and peering into the vegetation, never spending more than 10 seconds on a single perch. When it detects prey, it descends from the perch and attempts to capture it in the bill. It occasionally takes insects on the wing. It may follow flying moths and cabbage white butterflies for several metres, making several attempts to capture them, but is seldom successful (Evans 1964; Middleton 2020; Reynolds and Knapton 1984; Stull in Austin 1968; Walkinshaw 1944). In the Clay Belt of Ontario, 68.0% of foraging was in conifers, 69.0% was in foliage, 26.1% was by aerial attacks, 1.4% by hanging, 3.5% by hovering, 12.1% by reaching, at an average height of 7.2 m which was 54.0% of tree height. In the Mackenzie District, 94.0% of foraging was in conifers, 91.0% was in foliage, 11.6% was by aerial attacks, 1.0% by hanging, 3.3% by hovering, 32.0% by reaching, at an average height of 10.2 m which was 69.3% of tree height (Greenberg et al. 1999). Hebrard (1978) compared the foraging tactics of Chipping and Field sparrows in South Carolina. Both fed mostly in old-field habitat and almost always on the ground regardless of habitat type. Both species frequently flycatched during warmer months and they increased the amount of foraging in treed habitat in April. The Chipping Sparrow occasionally foraged briefly along pine branches. During nonfeeding periods, the Chipping Sparrow perched more frequently in treed habitat; the Field Sparrow remained in the old field. In Texas, Allaire and Fisher (1975) compared the foraging strategies of the Chipping and Field sparrows. Both species foraged mostly within 1 m of the ground and took seeds that had not yet fallen to the ground, as well as those that were on the ground. Both hunted from a perch 30-40 cm from the ground. The Field Sparrow made more frequent use of perches in brush piles, fallen trees, low shrubs, and fences than the Chipping Sparrow. Chipping Sparrows were most common in a grazed pine stand. They typically perched in the upper half of a pine and slowly, one by one, flew down to the ground among the grasses. After a while, they flew up into the trees, moved to another area, and repeated the process. Chipping and Field sparrows were very similar in the types of seeds and arthropods that they ate, but were very flexible in their diet. Flexibility enhances chances for survival if a particular type of food becomes scarce. They may not compete for food because it is so abundant. Benkman and Pulliam (1988) observed that the Chipping Sparrow ate seeds that were about an order of

magnitude smaller than finches of approximately the same size. Consequently, it must spend much more time foraging than finches and is not able to spend as much time searching for food. As a result, it is much more sedentary and restricted to areas of dense seed concentrations.

Younger nestlngs appear to be fed mostly seeds with the amount of invertebrates fed them increasing as they mature. They have been fed grit, small caterpillars, grasshoppers, aphids, and beetles. In Michigan, the percent occurrence of food items in nestlings' feces and gizzards consisted of 24% odonates, 92% orthopterans, 20% true bugs, 96% soft-winged bugs, 60% beetles, 96% lepidopterans, 52% flies, 44% hymenopterans, 92% spiders, 4% snail shells, and 52% plant material. Larvae or nymphs of lepidopterans, beetles, orthopterans, and bugs were preferred to adults. Adults feed on seeds most of the year but add invertebrates to their diet during the nesting period. Seeds of grasses and annual plants are most important in the diet, with fruits infrequently consumed. The summer and autumn foods of birds collected throughout the range consisted of 62% plant matter and 38% invertebrates, which were mostly insects. The Chipping Sparrow prefers seeds of hairy crabgrass and yellow foxtail, but eats seeds of many other grass species including those of timothy and orchard grass. Dandelion is an important food early in the breeding season. It eats many other seeds including those of black bindweed, sweet clovers, knotweeds, lamb's-quarters, oats, chickweeds, amaranths, purslane, ragweeds, wood-sorrels, and wild and cultivated cherries. All life stages of insects are eaten, with lepidopterans, beetles, and orthopterans most important. In June, 93% of the diet consists of insects, including 36% grasshoppers, 25% caterpillars, and 6% leaf beetles. Other beetles consumed include weevils, ground beetles, dung beetles, click beetles, and June beetles. Less frequently, the Chipping Sparrow feeds on bugs, flies, hymenopterans, termites, and spiders. One was observed pecking at a block of salt (Allen 1939; Beal and McAtee 1912; Evans 1964; Judd 1901; Middleton 2020; Stull in Austin 1968; Walkinshaw 1944). In summer in Texas, 68 seeds eaten by 5 birds consisted of 77.5% crabgrass, 8.9% foxtails, 5.3% spinifex grass, 6.5% marshelder, and 1.8% spurges. They had consumed 8 invertebrates including 5 orthopterans and 3 beetles. Chipping and Field sparrows ate similar species of seeds and the same orders of insects. The Chipping Sparrow tended to eat seeds that were slightly larger than those consumed by the Field Sparrow (Allaire and Fisher 1975). The diet of 8 Chipping Sparrows in spring in Michigan by percent occurrence in gizzards consisted of 37.5% orthopterans, 62.5% true bugs, 62.5% soft-winged bugs, 75.0% beetles, 75.0% lepidopterans, 25.0% flies, 37.5% hymenopterans, 62.5% spiders, 62.5% plant material, 25.0% wiregrass seeds, 25.0% Indian grass seeds, 25.0% unidentified grass seeds, and 12.5% smartweed seeds. The percent occurrence of food items in 41 gizzards of adults and fledglings in summer consisted of 51.2% orthopterans, 82.9% true bugs, 82.9% soft-winged bugs, 85.4% beetles, 36.6% lepidopterans, 2.4% flies, 36.6% hymenopterans, 39.0% spiders, 46.3% plant material, 2.4% quack grass seeds, 12.1% poverty oat grass seeds, 9.8% wiregrass seeds, 4.9% panic grass seeds, 7.3% bluegrass seeds, 2.4% foxtail seeds, 2.4% Indian grass seeds, 2.4% wood-sorrel seeds, 2.4% smartweed seeds, 2.4% dock seeds, and 43.9% seeds of all kinds. Beetles were represented in the diet mostly by ground beetles and weevils in spring. Leaf beetles and click beetles were common in the summer diet. The lepidopterans consisted mostly of hairless owlet moth and brush-footed butterfly caterpillars. Adult grasshoppers became frequent in the diet in summer. Ants were the primary hymenopterans consumed, but small ichneumonid wasps and other parasitic wasps were also eaten (Evans 1964). In Michigan, some did not feed on jack pine budworms; others readily ate

larvae, pupae, and adults. It concentrated feeding on the most abundant life form of the budworm, but did not start eating them until they reached the fifth instar. All budworms consumed contained hymenopteran parasites. It was estimated that the Chipping Sparrow ate only 0.92% of the available budworms even through it was the most abundant of 60 species of birds present and represented 37.7% of the avifauna (Simmons and Sloan 1974; Sloan and Simmons 1973). In Maine, 3 stomachs collected during a spruce budworm outbreak contained 71% and 67% budworm larvae and pupae by volume in 2 years (Mitchell 1952).

Evans (1964) compared the diets of the Chipping, Field, and Vesper sparrows in Michigan, and the diets of nestlings and adults of individual species. Nestlings of Chipping and Field sparrows consumed significantly higher frequencies of odonates, orthopterans, lepidopterans, flies, and spiders than adults, and significantly lower frequencies of true bugs. Nestling Chipping Sparrows consumed significantly fewer beetles than adults. The frequency of rapidly flying insects and sluggish larvae was much greater in food provided to nestlings than was eaten by adults. Insects that spend most of their time on the surface of the ground or on low-growing vegetation appeared with equally high frequency in the diet of both age classes. The results suggested that, while searching for food for nestlings, adults spent less time on open ground and more time in active flight or in taller vegetation. The Vesper Sparrow consumed orthopterans more frequently than Field and Chipping sparrows (but the difference was significant only for the Field Sparrow) and fewer true and soft-winged bugs (difference significant only for the Chipping Sparrow). The Chipping Sparrow ate significantly more lepidopterans than the other 2 sparrows. Chipping and Field sparrows ate seeds much less frequently in summer than the Vesper Sparrow. The only difference in the diet of nestlings among the species was that Chipping Sparrow nestlings were fed true bugs significantly less than Vesper Sparrow nestlings. There was no shortage of food within the study area and no apparent competition for it; food did not appear to be a limiting factor.

The Chipping Sparrow is a common host of the Brown-headed Cowbird. At the University of Guelph, 35.3% of 381 nests were deserted, with many desertions coinciding with the appearance of a cowbird egg, particularly during nest building or early egg laying. Desertion was likely if there were 2 or fewer sparrow eggs in the nest and unlikely if there were 3 or more sparrow eggs. Data from the Ontario Nest Records Scheme (ONRS) south of the French and Mattawa rivers and Lake Nipissing indicated that parasitized nests were significantly more likely to be deserted (52%) than unparasitized nests (7%). Acceptance rates of cowbird eggs did not differ before (53%) or after (44%) the peak of nest initiation, or in singly parasitized (52%) or multiply parasitized (45%) nests. Desertion may be triggered if the female encounters a cowbird near the nest. Cowbird eggs deposited before the nest is complete may be buried in the nest. At Guelph, 37.5% of cowbird eggs were laid before the first sparrow egg, 37.5% with the first egg, 15% with the second egg, 7.5% with the third egg, and 2.5% with the fourth egg. At the University of Western Ontario, most nests were parasitized when 2 sparrow eggs were present followed by when 3 sparrow eggs were present; more than 50% of nests were parasitized in those 2 days. In Colorado, significantly more parasitized nests were abandoned (29.4%) than unparasitized nests (5.1%). The female cowbird may remove sparrow eggs with the result that parasitized nests have smaller clutch sizes. At Guelph, mean clutch sizes were 3.7 eggs for unparasitized nests and 2.5 eggs for parasitized nests. In unparasitized nests, 81.3% of sparrow eggs produced fledglings compared with 28.0% of eggs in parasitized nests (3.0 fledglings

produced per unparasitized nests and 2.0 in parasitized nests). In only 3 cases did no sparrows fledge. Similarly in Colorado, clutch size of unparasitized nests was significantly higher (3.7 eggs compared with 2.9 eggs) and parasitized nests produced significantly fewer sparrow fledglings. In Minnesota, the clutch size of unparasitized nests was 3.00 eggs compared with 2.33 eggs for parasitized nests. Despite the lower fledging success rate, all parasitized nests produced some sparrow fledglings. The abandonment rate due to parasitism was 30%, but it is likely that many of these birds renested. At Guelph, nests in deciduous trees were more commonly parasitized than those in conifers and nests 1.5-2.5 m from the ground tended to be less heavily parasitized than others. Similar studies in Michigan showed no such differences. In Colorado, there were no significant differences in parasitism rates related to nest height or concealment (Buech 1982; Earley 1991; Graham 1988; Middleton 2020; Ortega and Ortega 2001; Rothstein 1975; Scott and Lemon 1996; Strausberger and Hauber 2017). Parasitism rates vary dramatically geographically, even within Ontario. Peck and James (1998b) reported that 484 of 1,600 nests (30.3%) reported to the ONRS were parasitized. In Algonquin Park, 0 of 22 nests were parasitized (Reynolds and Knapton 1984). At the University of Guelph, 40.6% of 374 nests were parasitized (Middleton 2020); 23 of 25 nests (92.0%) were parasitized at the University of Western Ontario (Scott and Lemon 1996). In Quebec, Perreault and Barrette (in Gauthier and Aubry 1996) reported that 12% of nests were parasitized. In British Columbia, 10% of 508 nests were parasitized (Campbell et al. 2001). In 2 studies in Michigan, 3 of 66 nests (4.5%) and 1 of 18 nests (2.6%) were parasitized (Stull in Austin 1968; Walkinshaw 1944). In Minnesota, 3 of 12 nests (25.0%) were parasitized (Buech 1982). In 2 Colorado studies, 6 of 83 nests (7.2%) and 17 of 77 nests (22.1%) were parasitized (Ortega and Ortega 2001; Swanson et al. 2004). In the first study area, the parasitism rate was low despite the fact that the Chipping Sparrow was the most abundant species, suggesting that it may not have been a preferred host. The Plumbeous Vireo was scarce yet experienced a 49.6% parasitism rate. In Illinois, 33 of 49 nests (67.3%) were parasitized (Strausberger and Hauber 2017).

McLaren et al. (2006) examined the ONRS to analyze Ontario parasitism rates from the 1870s to the 1990s. They reported that 509 of 1,749 nests (29.1%) were parasitized and 139 of 509 nests (27.3%) were multiply parasitized with more than 1 cowbird egg. There was a significant increase in multiple parasitism in the century prior to 1970 but a nonsignificant decline in multiple parasitism after 1970. Results supported the hypothesis that intensity of parasitism is related to cowbird density and that multiple parasitism is a recent phenomenon associated with increases in cowbird density. The cowbird has been declining in Ontario and this may explain why the rate of multiple parasitism decreased after 1970. Peck and James (1998b) observed that only 33 of 188 nests (17.6%) were parasitized in the decade prior to their publication compared with an overall rate of 30.3%.

There appear to be no major limitations to the Chipping Sparrow, which benefits from most human activities. Development of subdivisions was previously beneficial but modern high-density housing may not provide adequate habitat. In many cases, the roofs of the houses are almost touching and it would probably need several adjacent lots with suitable landscaping in order to set up a territory. Because it is often abundant around human settlements, it and its nests are highly vulnerable to being preyed upon by cats (Middleton 2020).

The Chipping Sparrow responds positively to forestry activities that open up the forest canopy yet retain some tree cover. In the Boreal Forest Region of Ontario, it increased by 50% when 30% of trees were removed (Vanderwel et al. 2007). In the Canadian Shield of Ontario, there were no differences in its abundance in early successional and mid-successional clear-cuts and burns of the same ages. It was significantly more abundant in early successional than mature stands and equally abundant in mid-successional and mature stands (Zimmerling et al. 2017). In partial cuts in Alberta, it increased significantly when 80% of trees were removed in deciduous forests with a coniferous understorey and when 50% of trees were removed in mixed stands (Harrison et al. 2005). In Idaho, it exhibited a significant increase due to single-tree selection logging in coniferous forests (Medin and Booth 1989). Tittler et al. (2001) compared the abundance of the Chipping Sparrow in Alberta mature mixed forests and clear-cuts with varying amounts of residual tree cover. In 1 of 3 years, it was significantly more abundant in clear-cuts than controls, but there were no significant differences in other years. It exhibited no significant response to clear-cutting and was unaffected by the amount of residual tree cover. In New York northern hardwoods, it was absent in uncut forest and occurred in low abundance where 25%, 50%, 75%, or 100% of merchantable timber was removed (Webb et al. 1977). In British Columbia, density of deciduous vegetation in coniferous plantations was manipulated by cutting in some treatments and by cutting and spraying stumps with herbicide in other treatments. Because of its reliance on deciduous vegetation for nest patches in this area, it was negatively affected by the management. It compensated by finding patches of untreated or recovered vegetation to nest in (Easton and Martin 2002). In Pennsylvania, it was significantly more abundant in woodlots where snags were retained as part of timber stand improvement. Where snags were retained, there was significantly more woody plant material 0-1.5 m from the ground that probably provided nest sites (Stribling et al. 1990).

In Alberta and West Virginia, the Chipping Sparrow was significantly more abundant at seismic lines, pipelines, access roads, and well pads than in forest interior adjacent to these features (Bayne et al. 2016; Farwell et al. 2019).

Forest fires are either beneficial for the Chipping Sparrow or have no discernible effect; fires in savannahs may be detrimental. In a mature California coniferous forest, it nested in areas that had been burned 6-8 years previously, but was absent in unburned forest (Bock and Lynch 1970). In a mixed forest in Oregon, its density 1 year before fire and in each of 9 years postfire showed no clear response to the fire (Stephens et al. 2015). In Indiana savannahs, it occurred at maximum density when the fire frequency was 0 per 15 years. Density dropped from 35 per km^2 with a fire frequency of 0 in 15 years to 20 with 1 fire in 15 years and to 10 with 2 fires in 15 years (Grundel and Pavlovic 2007a).

The Chipping Sparrow declined significantly shortly before the turn of the 20th century. Competition with the House Sparrow and parasitism by the Brown-headed Cowbird were considered responsible. These relationships were never confirmed and by the 1950s the Chipping Sparrow was common in many areas where the other 2 species were abundant. It declined from the 1900s to the point where it was very rare in Illinois in the 1950s. The explanation for this was unclear but was possibly related to pesticide use (McIlwraith 1894; Middleton 2020; Stull in Austin 1968; Walk et al. 2011). Nichols (1946) suggested that its decline in the 3 decades prior to his publication was

because of decreasing availability of horsehair that was used to line essentially all nests. This seems implausible as the Chipping Sparrow readily uses hair from other mammals and occasionally does not use hair in the lining.

Organophosphates used in orchards and other agricultural uses have been demonstrated to be harmful to the Chipping Sparrow (Middleton 2020; Perreault and Barrette in Gauthier and Aubry 1996).

Nests in exposed trees and shrubs facing prevailing winds are often worked loose and tipped by wind action. Wind caused 1.6% of nest failures at the University of Guelph (Middleton 2020).

In Minnesota, the Chipping Sparrow spent more time on or near the ground where the Song Sparrow was not regularly present than where both species were present. Interference competition was likely responsible because the Song Sparrow frequently chased the Chipping Sparrow from mutually occupied areas (Howe 1979).

In Alberta, there was no significant difference in the abundance of the Chipping Sparrow at noisy compressor stations and quiet well pads. It did not appear to be affected by chronic noise (Bayne et al. 2008), but negative responses to noise have been detected during autumn migration.

In Minnesota, extremely low-frequency electromagnetic fields produced by a hydro transmission facility had no apparent effect on the Chipping Sparrow (Hanowski et al. 1996).

Status

Prior to European settlement, the Chipping Sparrow probably inhabited open woodlands, prairie-forest ecotones, and clearings created by fires, watercourses, water bodies, and First Nations. Forest clearing created considerably more habitat for it and it is more abundant now than prior to deforestation by Europeans. Much new habitat was created by the initial expansion of agriculture and forestry followed by naturalization of associated weeds and insects. Its population probably peaked around the mid-1850s and then declined due to reversion back to forest, more intensive farming, cowbird parasitism, competition with the House Finch and House Sparrow, and predation by cats (Middleton 2020; Stull in Austin 1968).

McIlwraith (1894) stated that the Chipping Sparrow occurred throughout the province. Prior to the arrival of the House Sparrow, it was the most familiar bird around dwellings. He noted that it was then in a minority to the House Sparrow. Weir (2008) stated that the Chipping Sparrow was common in the mid-19th century in the Kingston area and that habitat changes over the past 150 years had helped increase its numbers. Baillie and Harrington (1937) considered it one of the most common breeding birds south of the Albany River and the southern end of James Bay. They concluded that it probably ranged westward to Lake of the Woods. The first atlas demonstrated that it ranged almost throughout the entire province except in the northeast portion of the Hudson Bay Lowland. In that physiographic region, it was found mostly along the James Bay coast. It was among the most abundant species in the province (Middleton in Cadman et al. 1987). James (1991) considered the Chipping Sparrow a common summer resident throughout the province, north to Big Trout Lake and Moosonee and rare north to Fort Severn and Attawapiskat.

The second atlas demonstrated that there had been no change in the range of the Chipping Sparrow since the first atlas. There was no significant change in its probability of observation province-wide. A significant decline occurred in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, although the number of squares it was documented in was essentially the same. The decline in this region may have been due to forest maturation and in-filling. The decline was most apparent in Algonquin Park, consistent with this hypothesis. It increased significantly in the Boreal Forest Region where it was seen in more than twice as many squares during the second atlas. It increased at a nonsignificant rate in the Hudson Bay Lowland where it is predominantly confined to settlements and riparian habitat along major rivers. It was most abundant south of the Canadian Shield and in the northwestern portion of the Great Lakes–St. Lawrence Forest Region in the Shield. It was one of the most abundant species in the province; over 50% of the population was in the Boreal Forest Region (Cadman in Cadman et al. 2007).

The Breeding Bird Survey (BBS) may not adequately sample the Chipping Sparrow because there are no routes in the northern portion of its range or within urban habitats. BBS data indicate that the Chipping Sparrow decreased at annual rates of 1.42% in Canada and 1.26% in Ontario 1970-2021. The annual rates of decrease 2011-21 were 3.43% in Canada and 5.27% in Ontario. All results were of medium reliability except for the short-term trend in Ontario, which was highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

When leaving the nest, young may move gradually out into the branches of the nest tree. If nestlings fall to the ground, they are led by an adult into a shrubby area. By age 10 days, they can hop onto the lower branches of shrubs where they sometimes remain for long periods on 1 perch. By age 12 days, they can fly short distances and are capable of sustained flight. Young may cross territorial boundaries and, at first, the adults lead them back. As soon as the young of the final brood are independent, both the young and adults leave the territory. Young are usually independent when they are approximately 3 weeks old but adults occasionally feed young as old as 35-40 days (Middleton 2020; Walkinshaw 1944, 1952).

Initially family groups remain discrete. In a Michigan suburb, 3 pairs and their young roamed over the same area but remained separate from each other. Eventually, young gather into small flocks of 5-15. These flocks grow as summer progresses and they are joined by postbreeding adults. Both adults and juveniles remain in flocks until autumn migration; these flocks may be joined by Field and Song sparrows (Middleton 2020; Stull in Austin 1968; Walkinshaw 1944).

Premigratory flocks usually inhabit weedy areas where there is an abundance of seeds for foraging (Middleton 2020; Stull in Austin 1968). In Pennsylvania, Stoleson (2013) netted birds in 3-6-year-old clear-cuts and adjacent mature forests during the postfledging period. He caught 15 adults and 8 juveniles in clear-cuts and 1 adult and no young in forests. In the same state, postbreeding adults were rare on transmission line corridors and absent in the adjacent forest; no family groups were observed (Yahner et al. 2002).

In Algonquin Park, adults and juveniles may forage in flocks of 200 or more where grass and weed seeds are abundant (Tozer 2012).

MIGRATION

There is evidence for the Chipping Sparrow migrating both during the day and at night. It is possible that it makes short-distance movements diurnally and long-distance movements nocturnally. It migrates in stages with many feeding stopovers along the route, particularly in autumn. It migrates in small to large flocks that often contain other species such as Field and Song sparrows. In spring, many birds moving through Long Point travel northwest. In autumn, Ontario birds move south or southeast and at least some birds that breed in Ontario winter in Florida (Allen 1939; Brewer et al. 2018; Campbell et al. 2001; Middleton 2020; Stull in Austin 1968). Gesicki et al. (2016) monitored nocturnal calls of Chipping Sparrows during spring migration on the Ohio coast of Lake Erie and at sites within the lake. Sparrows migrating in the western basin of the lake were more likely to engage in a lake crossing than those in the central basin. The central basin of Lake Erie may inhibit water crossing by the Chipping Sparrow.

Males usually arrive on the breeding grounds 1 week before females but in Michigan the first female arrived 14 days after the first male. The earliest birds arrive about 2 weeks before the peak of migration (Middleton 2020; Perreault and Barrette in Gauthier and Aubry 1996; Walkinshaw 1944). In Ontario, the Chipping Sparrow usually arrives in mid-April and migration continues until mid-May; early migrants may arrive in the last 1-2 days of March (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). Wilson and McRae (1993) concluded that single birds at Ekwan on 13 and 16 June and one at Longridge on 14 June were either late migrants or unmated birds following the coast.

In the Yukon, adults departed south ahead of juveniles. The latest an adult was observed was 1 August but groups of juveniles were encountered until the end of August (Sinclair et al. 2003). Overall, birds may depart from the breeding grounds from July to November, but peak migration in Ontario occurs in September until mid-October (Middleton 2020) with stragglers into early November or even later.

In Massachusetts, Ellwood et al. (2010) examined spring arrival dates of the Chipping Sparrow from 1851 to 2007. It arrived earlier in warmer springs.

During migration, the Chipping Sparrow may inhabit a variety of open habitats, particularly grassy and weedy areas that provide ample food. It may occur in roadsides, hedgerows, open grassy areas, old weedy fields, suburban and rural yards, forest edges, upland thickets, urban parks, shoreline thickets, field borders, hydro transmission line corridors, grain fields, gardens, villages, open forests, and edges along rivers, lakes, and wetlands. In spring, it appears to prefer upland well-drained areas. During spring in Wisconsin and Minnesota, about 2.5 times more were observed in upland oak and elm stands than in floodplain forests dominated by silver maple and green ash (Campbell et al. 2001; Kirsch et al. 2013; Middleton 2020; Sinclair et al. 2003; Stull in Austin 1968; Walkinshaw 1944).

In spring, the Chipping Sparrow forages singly or in small flocks but tends to occur in larger flocks in autumn. Foraging strategies in the nonbreeding season are similar to those used during the breeding season except that large rolling flocks may occur in autumn. Birds fly to the front of the flock, scratch for seeds where they land, then fly again to the front of the flock which bypasses them as they forage. Autumn flocks often contain 25 to more than 200 birds, or even as many as

1,000 (Allaire and Fisher 1975; Middleton 2020). In Texas, 695 seeds eaten by 15 birds included 42.9% crabgrass, 9.2% foxtails, 8.2% panic grasses, 13.9% unidentified grasses, 22.9% spurges, and 2.9% marshelder. They also ate 9 lepidopterans and 6 termites (Allaire and Fisher 1975).

The Chipping Sparrow collides with television towers and other tall structures during both migration periods (Middleton 2020).

During autumn migration in Idaho, McClure et al. (2013b) created a phantom road through a forest by playing recordings of traffic noise. The Chipping Sparrow was significantly negatively affected by noise with an average of 0.8 birds present under quiet conditions and 0.25 at noise levels of 55 dB(A). Although it does not appear to be adversely affected by noise during the breeding season, it may choose to avoid noisy areas during migration. Noise has the potential to reduce the quality of stopover areas.

James (1991) considered the Chipping Sparrow a common migrant in Ontario.

Hussell et al. (1992) reported that captures of the Chipping Sparrow at Long Point Bird Observatory increased significantly at a rate of 3.3% per year 1961-88. Trends by period included: 1961-70, +2.2% per year; 1970-79, –8.4% per year; and 1979-88, +15.3% per year.

WINTER

Root (1988) concluded that the Chipping Sparrow appeared to winter where the American Tree Sparrow is absent, where the average minimum January temperature rarely drops below –7°C to –1°C, and where pines, scrub oaks, or both are present. It is uncertain if the American Tree and Chipping sparrows restrict each other's range. The Chipping Sparrow does not normally winter in large numbers north of the North Carolina coast (Stull in Austin 1968). There are many records of stragglers lingering beyond normal autumn departure dates, often well into winter. There is evidence of an increasing tendency to overwinter in northern breeding areas (Middleton 2020). Ontario continues to be well north of the normal wintering range.

Winter habitat is similar to breeding habitat, but the Chipping Sparrow may be more common in riparian forests than coniferous forests in winter. In the Hamilton area, it may occur in sheltered valleys. It commonly shares its habitat with other sparrows in winter where their differing behaviours and microhabitat use may allow them to coexist, often in flocks (Curry 2006; Middleton 2020).

The Chipping Sparrow is readily attracted to feeders. A high proportion of Ontario winter birds are seen at feeders. Under harsh weather conditions, it may depend upon feeders for survival. Presence of other species may inhibit its usage of feeders. Favourite feeder foods include mixed seeds, millet, hulled sunflowers, and canary seeds. Infrequently consumed foods include black oil and striped sunflowers, cracked corn, niger, suet, bird puddings, milo, popped corn, and water (Dunn and Tessaglia-Hymes 1999; Middleton 2020). A total of 13,312 Chipping Sparrow foraging bout observations indicated that it preferred white proso millet in tube or hopper feeders (Horn et al. 2014).

Arizona is at the northern extent of the winter distribution of the Chipping Sparrow. Pulliam and Dunning (1987) added grass seeds to experimental plots in oak woodlands. Its abundance was lower when seed production was very low but there was no further increase in its abundance once seed

production exceeded 10 or 15 kg per ha. The authors concluded that food density limited local abundance of Chipping Sparrows when food was scarce but competition limited density when food was abundant. In winter in Texas, 9 birds ate 583 seeds and no arthropods. Seeds consisted of 35.2% crabgrass, 6.5% foxtails, 5.2% windmill grass, 1.7% panic grass, 48.1% unidentified grasses, and 3.3% spurges (Allaire and Fisher 1975).

James (1991) considered the Chipping Sparrow a rare winter resident in the south, north to Ottawa. It is rarely seen in winter in Elgin County (Lancaster et al. 2004). In the Hamilton area, it is observed in winter about every other year (Curry 2006). In the Kingston area, single birds were seen during 14 of 35 winters (40%) since 1972 (Weir 2008).

Clay-colored Sparrow

Spizella pallida

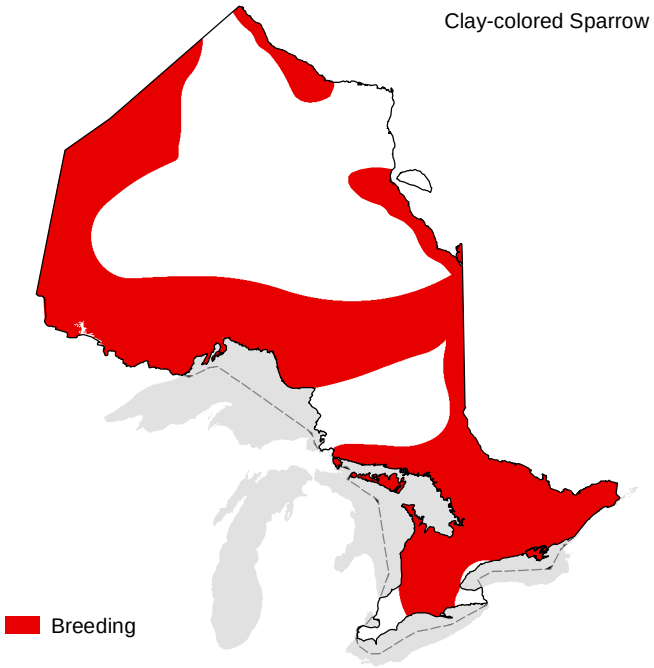
BREEDING SEASON

Habitat Requirements

In Ontario, the Clay-colored Sparrow has nested in Christmas trees and other coniferous plantations in grassy fields (65.5% of nests), in shrubby overgrown fields and pastures (24.1%), in a cottage area (3.4%), in a dried-up muskeg burn with some tree regeneration (3.4%), and in a graminoid opening in willow scrub near a salt marsh (3.4%; Peck and James 1987).

In the Hudson Bay Lowland, the Clay-colored Sparrow nests along the Hudson Bay coast, in the southern James Bay area, and often around settlements (Wilson and McRae 1993). Within this region, it nests predominantly in open willow and birch thickets (Rising in Cadman et al. 2007). It is rare in the Boreal Forest Region where it probably nests in forest clearings and openings, burns, clear-cuts, and shrubby areas near wetlands, watercourses, and water bodies.

In the Canadian Shield in the Great Lakes–St. Lawrence Forest Region, the Clay-colored Sparrow is most abundant in Rainy River District and southern Kenora District near Lake of the Woods. It is



rare in the eastern portion of this forest region. In this area, it nests in abandoned rough pastures with low willows (Rising in Cadman et al. 2007). James and Peck (1995a) observed one in jack pine stands near Gogama. It was most likely associated with very open areas where pines were less than 10 years old. Breeding habitat near Sault Ste. Marie consisted of grassy fields with clusters of willows 3 m tall interspersed with 6-m tall aspens. The fields were flooded to a depth of 30 cm early in spring due to melting snow. When birds first appeared, the water was still ankle deep but the area was completely dry by mid-June (Warburton 1952). In Algonquin Park, breeding habitat included young pine plantations and a hydro corridor (Tozer 2012). In Muskoka District, it nested in an abandoned pasture and in areas of open bedrock outcrops with young trees and shrubs and scattered mature pines, hemlock, and oaks (Mills 1981).

In the Great Lakes–St. Lawrence Forest Region south of the Shield, the Clay-colored Sparrow is commonly associated with alvars such as the Flamborough Plain, Carden Plain, and the Frontenac Axis. It nests in open, shrubby fields with scattered trees in these habitats. Red cedar and junipers on limestone pavement is favoured habitat near Kingston on the Frontenac Axis. Christmas tree and other coniferous plantations are favoured on the Flamborough Plain (Curry 2006; Knapton in Cadman et al. 1987; Rising in Cadman et al. 2007; Weir 2008). It is widespread on the Oak Ridges Moraine where it nests in young plantations and old-field habitat (personal observation). Near Ottawa, it nested in open bogs and willow thickets and at the airport (Godfrey 1966; Knapton in Cadman et al. 1987). Near Craigleith and Merrickville, it nested in old shrubby pastures overgrown with hawthorns, roses, apples, raspberries, gooseberries, cedars, and snowberries with herbaceous species such as ragworts, St. John's-worts, and cinquefoils (Mitchener 1956; Terrill 1952).

In the Carolinian Forest Region near London, the Clay-colored Sparrow nested in an old field on sandy soils grown up with hazel and young scrubby oaks (Dale 1927).

The core of the Clay-colored Sparrow's range is in the prairies of southern Canada and the northern United States. It may be the most abundant passerine of low shrub communities in the southern portions of the Prairie Provinces. It is associated predominantly with shrubs there, especially snowberry and silverberry. In addition to shrubby prairies, it commonly nests in old fields with shrubby growth, pastures, wet meadows, forest edges, burns, and planted grasslands. Less frequently, it nests in hayfields, particularly those planted to alfalfa and sweet clover. These clovers are taller than other species in this family and may function as singing perches in the absence of shrubs. Another habitat used on the prairies is young aspen stands with an open canopy; it may

occur in a variety of open deciduous woods. This habitat is avoided in the east. It rarely nests in croplands other than hay and in urban areas such as parks, vacant lots, and yards. Away from the prairies, it is associated predominantly with areas that have a mixture of shrubs in open grassy and herbaceous areas. These may include old fields and meadows, ungrazed or lightly grazed pastures, shrubby areas bordering these habitats or agricultural fields, overgrown utility corridors, clear-cuts, regenerating burns, dense herbaceous and grassy cover around margins of wetlands where there is some shrub coverage, pine and oak barrens, and open parkland habitat with scattered copses of aspens, willows, or shrubs. It also nests in Christmas tree farms and young coniferous plantations (Askins et al. 2007; Buech 1982; Campbell et al. 2001; Davis 2003; Dechant et al. 2002c; Faanes and Andrew 1983; Flack 1976; Fox 1961; Grant and Knapton 2020; Hill and Sealy 1994; Knapton 1979a, 1980; Mossman et al. 1991; Paquin and Letourneau in Gauthier and Aubry 1996; Root in Austin 1968; Salt 1966; Tews et al. 2013; Tittler et al. 2001; Walkinshaw 1939a; Watts and Albin 1996; Winter et al. 2004).

Some information is available on landscape preferences of the Clay-colored Sparrow. In Saskatchewan woodlots, it was more common in small forest fragments in landscapes with low forest cover (Hobson and Bayne 2000). In the same province, it was the only species that Johns (1993) studied that increased significantly with increasing isolation of woodlots. It occurred in all sizes of woodlot studied (range 0.04-36.7 ha). In 1 Saskatchewan study, its abundance was unaffected by the amount of cropland or wetland within 1.6 km. In another study, its presence was negatively correlated with the number of wetlands 2.8 km^2 around point counts, but it was observed in wetlands and wetland margins within all farmland types. It was more frequent along roadside routes passing through cultivated land than through areas of more native grassland (Dechant et al. 2002c). Grant and Knapton (2020) concluded that population densities were highest in grass-dominated landscapes and lower where the proportion of cropland was greater. Fedy et al. (2018) used Breeding Bird Survey (BBS) data for the Prairie Pothole Region of Canada to determine that it was associated with native and nonnative grasslands and shrubland areas at the 3,200-m scale. Erskine (1977) stated that it was a species of open shrubby areas rather than forest and considered it characteristic of prairie-forest ecotone and poor fields or areas of old-field succession. In North Dakota, it preferred landscapes that were 6-32% forested (Cunningham and Johnson 2019).

Although the Clay-colored Sparrow nests in woodlots and open grasslands devoid of woody cover, highest densities are associated with shrubs near grassy or herbaceous areas. In the Prairie Provinces, snowberry is highly preferred and silverberry is another preferred shrub. In North Dakota, these 2 shrubs and sumac are preferred. In 1 North Dakota study, it was abundant in shrubby fields and absent in grassy and herbaceous plots without shrubs. In Alberta, it is most abundant in habitats with more than 50% shrub coverage. It prefers a mix of vegetation types and is negatively associated with plant communities dominated solely by shrubs, native grasses, or wet-meadow vegetation. In Manitoba, grassy areas, treed bluffs, areas of standing water, marshes, and pure stands of silverberry were not defended. Large territories had proportionately less dense ground cover by snowberry than smaller territories suggesting that snowberry represented higher quality habitat. In Wisconsin, there was significantly more willows and meadowsweet within territories than in unoccupied areas. Near Edmonton, areas of pure grasses were not included in territories, and each territory contained at least 1 clump of poplar and willow; cultivated wheat fields were also not included in territories.

Territories contained grassy areas, patches of roses and snowberries, and shrubs bordering a woodlot. In Minnesota, its density was predicted to increase as woody cover increased (Arnold and Higgins 1986; Campbell et al. 2001; Dechant et al. 2002c; Knapton 1979a, 1979b; Munson 1992; Root in Austin 1968; Salt 1966; Thompson et al. 2014). Leston and Koper (2017) studied Clay-colored Sparrow usage of hydro transmission rights-of-way (ROWs) in the Winnipeg area. It was less abundant along ROWs with more wooded or urban habitat within 100 m. It declined as woody plant cover increased and increased as litter cover increased, including within hayed ROWs.

In western aspen stands, the Clay-colored Sparrow is a forest-edge species. It is significantly more likely to occur in groves with open canopies than those with closed canopies. Open canopies allow development of understorey species such as snowberry, grasses, bedstraws, and wild sarsaparilla. It is associated with very young aspen stands on moderately moist sites that are mid-range between nutrient-poor and nutrient-rich. In Saskatchewan, it demonstrated no preference for forest size. It was significantly negatively related to forest size in North Dakota. It is possible that presence of an open canopy and understorey is more important than forest size (Faanes 1987; Grant and Berkey 1999; Hobson and Bayne 2000; Johns 1993; Kirk et al. 1996).

Some studies compared the habitat quality of native grasslands and planted grasses. In Manitoba, nonnative vegetation included spurges, Kentucky bluegrass, and smooth brome; these were absent in native grasslands. The Clay-colored Sparrow was negatively correlated with native vegetation and positively correlated with nonnative vegetation, but not significantly (Wilson and Belcher 1985). In Saskatchewan grasslands, it preferred pasture in native habitat to planted pastures, possibly because native pastures supported more shrubs, predominantly snowberry and silverberry. Its abundance was associated with native grassland characterized by increased cover by shrubs, standing dead vegetation, and narrow-leaved rhizomatous grasses (Davis et al. 2016). In Alberta, its frequency was similar in native and tame pastures. In native pastures, it used areas of high cover diversity. In tame pastures, it used areas of high herbaceous biomass, moderate height variability, and a high forb to grass ratio. Highest densities occur in grasslands that have been ungrazed for more than 11 years and not burned for more than 80 years. Its use of idle grasslands decreases after mowing and as snowberry cover decreases. In Alberta, it was absent from tame grasslands less than 2 years old; abundance increased until the grassland was 5 years old then decreased (Dechant et al. 2002c). In Saskatchewan waterfowl management areas, percent occurrence of the Clay-colored Sparrow was 93.7% in planted dense nesting cover, 88.9% in native grasslands, and 10.5% in wheat fields (Hartley 1994). In Minnesota, Thompson et al. (2014) concluded that improving the quality of grass cover by increasing litter depth, grass height, and grass extent would lead to only a marginal increase in its density. Increasing the extent of grasses by 11.6 ha within a 500-m radius would lead to a 10-20% increase in this sparrow. Removal of woody vegetation within 100 m would result in a 5% decrease. In Saskatchewan, it was more abundant in brome-dominated plots than those dominated by Kentucky bluegrass (Dale et al. 2000).

Considerable information is available on microhabitat preferences of the Clay-colored Sparrow. In Wisconsin, the five most important plant species by frequency in territories were goldenrod, meadowsweet, Canada bluegrass, reed canary grass, and butter-and-eggs. The respective coverage by these species was 35%, 20%, 29%, 20%, and 12%; coverage was greater than 100% because leaves

overlapped. Some plants of lesser dominance may have been critical elements of territories based on high preference for them. Plant species significantly more abundant within than outside territories included sandbar willow, meadowsweet, reed canary grass, and sedges. Species more abundant outside territories included Canada bluegrass and timothy. Woody species richness, vegetation height (186.3 cm within and 88.9 cm outside), plant species diversity, and vertical density were all higher within territories. Habitat features of high value included sandbar willow and meadowsweet occurrence and stem density, woody species richness, vegetation height, plant species richness, and vertical density. None of the habitat features that were more abundant outside territories had high value as nest cover. The percent coverage of 44 additional plant species, stem density of 7 additional woody species, and frequency of occurrence of 53 additional plant species were similar within and outside territories. It selected territories containing dense stands of woody vegetation and avoided open grasslands. Only 22 of 118 habitat features (18.6%) available to sparrows had high value as nest cover, yet 8 of 11 habitat features (72.7%) that were more abundant within territories were of high value. Because it forages outside the territory, nest cover may be the dominant influence on territory selection (Munson 1992). In Minnesota and North Dakota, the substrate at nests consisted of 0.2% bare ground, 8.9% grasses, 10.4% forbs, 33.2% litter, and 42.9% shrubs (Winter et al. 2004). It increased with increasing amounts of tree and shrub coverage within 200 m. Nest success was unaffected by the amount of woody vegetation (Winter et al. 2006). In North Dakota, maximum vegetation height, amount of shrubs, amount of aspen within 100 and 500 m, and amount of Kentucky bluegrass were significantly greater where it was present than where it was absent. There was significantly less native herbaceous vegetation within 100 m of sites where it occurred than where it was absent (Grant et al. 2004). In Manitoba, nests were more often in a 5-m wide band around the edge of the territory than in the centre of the territory. Many territories encompassed a complete patch of snowberry. Nests were at edges of these patches rather than in the interior (Knapton 1979b). In Minnesota and North Dakota, its density increased with density of trees and shrubs in the landscape. In North Dakota, vegetation was taller and denser at nest sites than within a 30-m radius around nests or within the nest fields, which were 41-69 ha. Nest sites were closer to shrubs, had greater shrub coverage, and greater vegetation heterogeneity than areas within 30 m or the fields. Nests in snowberry had smooth brome as the least-preferred understorey species; native grasses or Kentucky bluegrass were preferred. In recently burned fields, litter depth and amount of residual vegetation were greater at nests than within 30 m or the fields (Grant and Knapton 2020). Dechant et al. (2002c) summarized the results of several studies. In Saskatchewan, its occurrence was negatively correlated with distance from the nest to a shrub and positively associated with narrow-leaved (less than 5 mm) grasses 10-30 cm tall. In North Dakota, its abundance was positively correlated with the density of low-growing shrubs (snowberry and silverberry) and introduced grasses (smooth brome, Kentucky bluegrass, and quack grass). It was negatively associated with plant communities dominated solely by shrubs, native grasses, or wet-meadow plants. The strongest predictor of its abundance was increasing coverage by low-growing shrubs. In Conservation Reserve Program (CRP) lands in North Dakota, it was positively correlated with alfalfa and sweet clover which may substitute for shrubs. In Alberta, hayfields mowed after 15 July were preferred to fields mowed earlier, but use of idle land was greater than hayfields. Lightly to moderately grazed grasslands are often used for nesting, but shrub cover is probably a more

important factor in determining habitat suitability than grazing intensity. Cropland is rarely used for nesting but may provide sparser shorter vegetation that is suitable for foraging.

In grasslands and shrubby areas, the Clay-colored Sparrow tends to nest near edges of patches. In Alberta, it decreased in abundance as the distance to a crop edge increased. It demonstrated no clear attraction or avoidance of gravel roads but decreased with distance from wetlands and selected for wetland-edge habitats. It prefers denser vegetation, which occurred at wetland margins, and croplands may provide foraging habitat. Although it was more abundant near edge, it did not avoid the interior of habitat patches. Edges of grasslands are more likely to be invaded by shrubs and therefore be superior habitat. In some cases, density of small-mammal predators is high in the interior of grasslands (Sliwinski and Koper 2012). In Saskatchewan, it was more abundant in irregularly shaped patches with greater density of shrubs (Davis 2004; Davis et al. 2006; Johnson and Igl 2001).

The Clay-colored Sparrow does not appear to be an area-sensitive species. In Ohio, Watts and Albin (1996) reported a territory in a 2-ha field with an adjacent 8-ha grassland. Near Edmonton, Salt (1966) reported 15 pairs nesting within a 2.6-ha patch of habitat, of which only 2.0 ha were used. In Saskatchewan, Davis (2004) did not record it nesting in the smallest patch he studied, which was 8 ha. It tended to occur more often in smaller patches, but this relationship was not significant. Davis et al. (2006) found that patch size and shape had no effect on its density or nest survival rate. In Minnesota, its probability of observation was highest in small patches near a forest edge but nest productivity was greatest distant from an edge (Dechant et al. 2002c). In Wisconsin, its abundance was not related to patch size. In Minnesota and North Dakota, nest density was influenced by patch size but the magnitude and direction of the relationship varied by year and location; patch size did not influence nest success. The patches studied were fairly large, with a mean size of 226.1 ha (range 2.4-1,245.6 ha; Grant and Knapton 2020; Winter et al. 2006). Johnson and Igl (2001) studied fields 2.2-270.5 ha in Montana, North Dakota, South Dakota, and Minnesota. The fields had been recently planted with grasses and legumes so minimal shrub invasion had occurred. They concluded that the Clay-colored Sparrow tended to favour larger grasslands even though it was negatively correlated with patch size at 2 of 9 of their study areas.

Eighty percent of Ontario nests were in living trees and shrubs and the remainder were on or near the ground. Small conifers supported 70.0% of nests in trees and shrubs and 30.0% were in deciduous saplings and shrubs. The most common nest-species included pines (8 nests), spruces (2 nests), and raspberries (2 nests). Nests were well concealed and usually near or against the trunk in a crotch. Some were low enough that they were partially supported by grasses growing through the lower tree branches. Elevated nests were 0.1-1.8 m from the ground with most 0.2-1.0 m up. Ground nests were in grass and forb clumps, often near the base of a tree. One was concealed by an overhanging clump of dead grass and vetch (Peck and James 1987). Warburton (1952) reported 3 nests near Sault Ste. Marie that were 10-36 cm from the ground. They were in willows, anchored to almost vertical stems.

A high proportion of nests in the prairies are in snowberry so the height of nests is generally lower. In Manitoba, 110 of 125 nests (88.0%) were entirely or mainly in snowberry and only 6 nests (4.8%) did not have snowberry as support of the nest. Snowberry represented 58.0% of the

vegetation in the study area but 89.0% of the vegetation in territories was snowberry and 83.7% of nests were in snowberry. Grass stems were incorporated into the nest substrate slightly more than expected, possibly due to the tendency to nest at edges of snowberry patches where grass was more prevalent. Approximately 85% of nests were within 30 cm of the ground or lower. Individual pairs tended to construct their nest at a constant height throughout the season (Knapton 1979a). Near Edmonton, first nests tended to be on the ground in tussocks where snow and wind had matted dead grasses into clumps. Some were as high as 25 cm from the ground (average 12.7 cm). Later in the season, the Clay-colored Sparrow nested in roses or snowberry and the average nest height increased to 33 cm. In other areas near Edmonton, it nested in willow, caragana, spruce, and pine. In 3 of 5 cases, replacement nests were in similar cover to the first nest, but at greater height (Salt 1966). A Saskatchewan replacement nest was 45 cm closer to the ground than the original nest; the first nest was in snowberry and the second was in a tussock of grass. Average nest height from the ground was 8.0 cm (Fox 1961). In Minnesota and North Dakota, the average height of 793 nests was 13.5 cm. Nests averaged 11.0 m to the nearest shrub and 9.2 m to the nearest tree. Litter depth at nests was 4-9 cm and vegetation height averaged 48.7 cm. Clay-colored Sparrow nest sites differed significantly from those of the Savannah Sparrow and Bobolink. Clay-colored Sparrows placed their nests more frequently in shrubs and less frequently in litter, and were higher above ground. Vegetation surrounding its nests had less grass and litter cover and more shrub cover, vegetation was taller, visual obstruction readings were higher, and nests were closer to shrubs and trees (Winter et al. 2004). In North Dakota, the average height of 602 nests was 24 cm (range 0-66 cm). Thirty-three percent of nests were oriented east-southeast and 25% faced south-southwest counter to the prevailing northwest wind (Grant and Knapton 2020). In British Columbia, 64% of nests were in shrubs or low vegetation, 23% were on the ground, and 6% were in low deciduous shrubs. Ground nests were often in a clump of grass at the base of a tree or shrub. Nest height ranged from 0 to 1.8 m, with most nests 0.1-0.5 m from the ground (Campbell et al. 2001). Nests near the ground may be completely covered with grasses, and nest species may include hawthorn, juneberry, and conifers (Root in Austin 1968). In Michigan, nests averaged 50 cm from the ground (range 27-75 cm) in shrubs 1.5-1.8 m tall. Nests were usually in the densest part of the shrub in a crotch or in a natural cupping of the vegetation. Nest shrubs were typically on the slope of a hill and not at the top or in the valley. Six nests were in maples, 2 were in oaks, and 1 each were in juneberry and hawthorn (Walkinshaw 1939a). One Ohio nest was 19.1 cm from the ground in a multiflora rose 112 cm tall (Watts and Albin 1996). Old nests are not reused and they do not survive the winter (Grant and Knapton 2020).

In Manitoba, males started to establish territories the day they arrived. In Alberta, males arrived in the first week of May but did not establish territories until about mid-May. Once boundaries were established, neighbours rarely trespassed and aggressive interactions declined significantly by mid-May in Manitoba. Males returning from previous years had few aggressive encounters among themselves. Most aggression was between old and new birds and among new birds. Once established, territorial boundaries did not change and returning birds used exactly the same territories. Even when birds were removed, neighbours did not encroach into the vacant territory. Interspecific territoriality may occur between the Clay-colored Sparrow and Chipping, Brewer's, and Song sparrows. This involves only singing and song-post displacement. The Clay-colored Sparrow

does not forage in its territory. Territories in Manitoba were clumped together in a small patch but this was best explained by the distributional pattern of snowberry, which provided nesting habitat. Clumping was not related to coloniality. Peripheral territories were significantly larger than those in the centre of the patch, probably due to the greater number of neighbours associated with central territories. Peripheral territories might be superior because adults have less distance to travel to reach foraging areas. There was no difference in nest success in peripheral and central territories. Returning males reoccupied 74.2% of central territories and 72.2% of peripheral territories and new birds claimed whatever territories remained unoccupied. There was no preference for either peripheral or central territories. Nests close together were significantly less successful than those further apart. Internest distances were greater than random distances, so nest placement was affected by the locations of neighbours' nests. Each year at 2 Winnipeg sites, there was a size of territory that was more frequent than others. Overall mean territory sizes were 971 m^2 and 1,053 m^2 on 1 study area over 2 years and 739 m^2 and 676 m^2 on the other. At the first study area, the most frequently defended territories were 800-1,000 m^2 in both years and 400-800 m^2 and 400-600 m^2 on the other site. More young were fledged in the size range of territories that was most abundant. Lower reproductive success occurred in territories smaller than optimal, probably due to predation. Elsewhere, territory size has been estimated at 0.1-0.5 ha. Territory size and arrangement may depend on shrub coverage. It is possible that some of the estimated territory sizes included foraging areas and may be more representative of home range sizes than territory sizes (Dechant et al. 2002c; Grant and Knapton 2020; Knapton 1979a, 1979b; Root in Austin 1968; Salt 1966; Watts and Albin 1996).

Natal philopatry rates are very low, although there are limited data. In Manitoba, 0 of 146 nestlings returned and 4 of 305 juveniles (1.3%) returned (Knapton 1979a).

Males have high site fidelity rates; females do not. Male return rates at 2 Manitoba study areas were 35 of 66 (53.0%) and 85 of 120 (70.8%). Of those that returned, 76% occupied the same territory and often used the same song perches. Occasionally 2 adjacent males exchanged territories. Seven of 10 males involved in these exchanges had not raised any young the previous year; the other 3 had been successful. Female return rates at the same study areas were 12 of 66 (18.2%) and 20 of 120 (16.7%). Returning females usually did not return to the same territory and had a different mate. Three males were translocated. None returned in the same year but 1 returned the following year and reoccupied his original territory (Knapton 1979a, 1979b). In Minnesota, 3 of 52 adults (5.8%) returned. One North Dakota bird was recaptured in the same location 5 years later (Dechant et al. 2002c).

Limiting Factors

Eggs have been reported in Ontario nests from mid-May until the third week of July, but most are present 10-26 June (Peck and James 1998b). Nest construction takes 2-4 days. It appears as though egg laying begins the day after the nest is complete. Normally 1 egg is laid per day but the fourth egg was laid at least 3 days after the third in 1 nest. Incubation begins with laying of either the penultimate or final egg and often when the third egg is laid regardless of clutch size. The incubation period near Sault Ste. Marie was 10-11 days and the incubation period was estimated to be at least 11 days at 3 other Ontario nests. Elsewhere, the incubation period has been reported as 10-14 days.

Because incubation may start before the clutch is complete, hatching may either occur on the same day or be spread over 2 consecutive days. Young leave the nest when they are 6-11 days old. In North Dakota, the age at fledging averaged 8.7 days (range 6.9-10.3 days) for nests monitored by video and an average of 8.2 days (range 6-11 days) for nests visited by humans. The presence of predators or observers may induce young to leave the nest earlier (Fox 1961; Grant and Knapton 2020; Knapton 1979a; Peck and James 1987; Root in Austin 1968; Salt 1966; Walkinshaw 1939a; Warburton 1952).

Second broods are rare, with most pairs raising a single brood in a season. Second broods have not been documented in Ontario. Second broods have been suspected in Michigan, Minnesota, and North Dakota, but not confirmed. One Minnesota male raised 2 broods in a year, but with different females. Double broods have been confirmed only in Manitoba. In 1 year, pairs that successfully raised a brood did not attempt a second one. The following year, 11 of 20 pairs (55.0%) that fledged young prior to 23 June attempted a second brood, and 5 (45.5%) were successful. No birds that fledged young after 23 June attempted a second brood. If the first nest is lost or deserted, replacement clutches are laid. Building of the new nest usually begins the day after the loss. As many as 4 attempts to raise a clutch may be made. Replacement nests are usually close to the original nest. Two Saskatchewan replacement nests were 16 and 23 m from the original nests, and another replacement nest was 3.7 m from the first nest. In 1 case, a replacement clutch was laid 3 m from the original nest. When the replacement nest was lost, a third nest was initiated between the first 2 nests. Clutches of 2-5 eggs have been reported in Ontario, with 4 eggs most frequent (mean 3.89 eggs). Elsewhere, clutches of 3-5 eggs have been reported, with most containing 4 eggs. A review of North American clutches determined that 7% of clutches contained 3 eggs, 82% contained 4 eggs, and 11% contained 5 eggs. In Manitoba, there was no difference in the clutch sizes of early nests (mean of 3.56 and 3.83 eggs over 2 years) and late clutches (3.75 and 3.60 eggs). Replacement clutches have 4 eggs and occasionally 5 eggs; most 3-egg clutches are laid late in the season. In Saskatchewan, later clutches were as large as early clutches; early clutches were larger in Minnesota and North Dakota. Mean clutch sizes reported elsewhere include 3.3 eggs in unparasitized nests in Minnesota, 3.80 eggs in unparasitized nests and 3.77 eggs overall in Minnesota and North Dakota, 3.8 eggs in Saskatchewan unparasitized nests, and 3.83 eggs in Alberta (Buech 1982; Campbell et al. 2001; Davis 2003; Dechant et al. 2002c; Fox 1961; Grant and Knapton 2020; Hill and Sealy 1994; Knapton 1979a; Peck and James 1987, 1998b; Root in Austin 1968; Salt 1966; Walkinshaw 1939a; Warburton 1952; Winter et al. 2004).

The Clay-colored Sparrow is capable of breeding when it is 1 year old and breeds every year thereafter. In 1 year in Manitoba, new pairs took over territories and attempted to breed midway through the breeding season in late June and early July after territories had been vacated by successful pairs. When territorial males were experimentally removed, all were replaced by an unbanded male within 3 days and each replacement male attracted a female. This suggested that there was a surplus of nonterritorial birds. There is a high probability that these are yearling birds and those that breed later where other pairs have successfully nested may also be inexperienced birds. The mating system is monogamous; no evidence of polygyny or extra-pair copulations has been found. Pair bonds remain stable throughout the breeding season and for replacement nests. Returning females usually do not mate with their previous year's male and typically pair with another

male on a different territory. In Manitoba, 29 of 32 returning females (90.6%) did not mate with the same male. One pair occupied the same territory and remained together 3 consecutive years (Grant and Knapton 2020; Knapton 1979a, 1979b).

Foraging and food gathering for the nestlings occurs away from the territory in arable and pasture land, weedy edges, and around margins of ponds and marshes. Individual males appear to forage in specific locations but there was no evidence that these areas were defended. Pairs with peripheral territories foraged adjacent to their territories; those with central territories probably flew to the nearest foraging area. Within pairs, the male flew significantly further from the nest to the foraging location. When both left the territory together, the female alighted first and closer and the male flew further before landing. This suggests that there is spatial partitioning of foraging areas between the members of a pair. Mean foraging distance for 6 males was 32.5-94.7 m compared with 29.9-78.9 m for 6 females. The Clay-colored Sparrow typically gleans from ground vegetation and rarely forages above ground in shrubs. Males may flycatch insects from their singing posts and feed the female while she is incubating (Fox 1961; Grant and Knapton 2020; Knapton 1980).

The Clay-colored Sparrow eats mostly seeds and other vegetable matter. Nestlings are fed invertebrates and adults may also consume them at this time. In Manitoba, food brought to nestlings consisted of 42.8% caterpillars, 18.1% orthopteran nymphs, and 15.6% odonates. Other prey included 9.7% flies, 3.8% adult lepidopterans, 2.0% beetles, 1.8% neuropterans, 0.7% spiders, 0.1% bugs, and 5.4% unidentified invertebrates. There were large differences in the diet of nestlings in different nests. A pair whose territory was close to a pond fed their young narrow-winged damselflies almost exclusively. Another pair fed their young predominantly short-horned grasshoppers and caterpillars dominated the nestlings' diet at 5 other nests. More caterpillars were taken in June, odonates increased in the diet in July, and there tended to be a general increase in the number of orthopteran nymphs brought to young over the breeding season. Similar-aged nestlings in different nests did not receive the same foods, suggesting that adults were not selectively choosing prey according to the age of nestlings. Both adults and young eat a high proportion of grasshoppers. In an area where grasshoppers had been controlled by a pesticide, adults ate twice as many dead as live grasshoppers. In Manitoba, young were fed grasshoppers exclusively for the last 4 days they were in the nest (Forsyth et al. 1994; Knapton 1980; Root in Austin 1968; Walkinshaw 1939a; Warburton 1952). In early spring, adults often eat willow catkins and buds of snowberry, elms, and other trees; geometer moth caterpillars are consumed in spring. Adults also eat leafhoppers, ants and other hymenopterans, adult lepidopterans, and spiders. In late summer, it eats seeds of lamb's-quarters, amaranths, tall tumble mustard, sweet alyssum, pepperweed, Russian thistle, green foxtail, and other grasses. In banding traps operated in autumn, the Clay-colored Sparrow may be attracted by cracked corn, millet, sunflower seeds, bread crumbs, and occasionally berries. Crabgrass seeds are particularly favoured in autumn (Root in Austin 1968; Warburton 1952).

The Clay-colored Sparrow is a common host of the Brown-headed Cowbird. It may either accept or reject cowbird eggs. The rate of parasitism is highly variable, even in locations quite close to each other, and depends upon factors such as nest placement, tree coverage, abundance of cowbirds, and availability of other host species. None of these factors appear to be constant and relationships with them and the rate of parasitism may be positive in 1 area and negative in another. In 2 nearby

study areas in Manitoba, sparrows accepted cowbird eggs in 1 area and consistently rejected them in the other by deserting the nest. Where eggs were accepted, 54 of 93 nests (58.1%) were parasitized compared with 30 of 139 nests (21.6%) where eggs were rejected. The higher parasitism rate in the first study area was thought to be due to higher numbers of cowbirds and fewer nests of other species to parasitize. The parasitism rate in the first area declined in the last 2 years of study, possibly due to cessation of cattle grazing which may have resulted in better nest concealment. Individual pairs were consistently either acceptors or rejecters of cowbird eggs throughout the season. Of 6 parasitized females that returned in a subsequent year, the same 4 were acceptors and the same 2 were rejecters (Knapton 1979a). In another Manitoba study, 22 of 204 nests (10.8%) were parasitized, mostly prior to 21 June. The Clay-colored Sparrow deserted 59.1% of these nests, accepted cowbird eggs at 36.4% of nests, and the outcome at 1 nest was unknown. Cowbirds removed sparrow eggs in a 24-hour period before or after parasitism. Ten of 15 clutches (66.7%) that had the clutch size reduced were abandoned but 100% of 67 clutches that received a real or artificial egg without clutch reduction were accepted. Clutch reduction and not the act of parasitism may trigger nest desertion (Hill and Sealy 1994). In North Dakota, 27 of 246 nests (11.0%) were parasitized. Pietz et al. (2009) compared parasitism rates in areas with differing tree cover, which ranged from 2-41%. The probability of parasitism was negatively associated with the percent tree cover within 2 km. For every 1% decrease in percent tree cover, the odds of a nest being parasitized increased by 15%. Parasitism rates tend to be lower for grassland species nesting in landscapes with more trees, probably due to the higher bird density in treed habitat and greater availability of alternate hosts. Parasitism decreased further from woody edges in Minnesota tallgrass prairies. In a North Dakota area, no nest further than 52 m from a perch was parasitized. Also in North Dakota, 5.1% of 781 nests were parasitized in aspen parkland and 14% of 694 were parasitized in treeless prairie (Dechant et al. 2002c; Grant and Knapton 2020). Trees may provide perches where female cowbirds can watch sparrows to find their nests. In a Minnesota Christmas tree plantation, parasitized nests were better concealed than unparasitized nests, suggesting that female cowbirds detected host nesting activity and then searched for nests (Buech 1982). In addition to removing eggs from sparrow nests that the cowbird intends to parasitize, it may also remove eggs or nestlings from nests that it has no intention of parasitizing. The cowbird may do this to induce renesting, thereby providing additional opportunities for parasitism (Granfors et al. 2001). Because of egg removal, reproductive success of the Clay-colored Sparrow is reduced. In 1 Manitoba study, parasitism accounted for the loss of 2.16% of sparrow eggs and in only 1 case did both a cowbird and sparrow fledge. In all other cases, all sparrow nestlings died if a cowbird was raised. In another Manitoba study, 32 sparrow eggs were removed from 22 parasitized nests, a loss of about 1.5 eggs per nest. In Saskatchewan, no sparrows fledged from 8 parasitized nests, but an average of 2.0 sparrows fledged from successful parasitized nests in another study in that province. This was not significantly different from unparasitized nests. In Minnesota and North Dakota, the clutch size of parasitized nests was 0.7 eggs less than for unparasitized nests. Successful parasitized nests fledged 1.32 fewer sparrows than unparasitized nests. In 26 North Dakota nests, 13 fledged both cowbirds and sparrows and 13 fledged only cowbirds. In Minnesota, 23% of sparrow eggs produced fledglings in parasitized nests compared with 49% in unparasitized nests. Because few sparrows fledge from parasitized nests, it is maladaptive to accept cowbird eggs. The incidence of parasitism decreases with the season so replacement nests are less likely to be parasitized (Buech 1982; Davis 2003; Fox 1961; Grant and

Knapton 2020; Hill and Sealy 1994; Knapton 1979a; Winter et al. 2004). In Ontario, 11 of 35 nests (31.4%) were parasitized (Peck and James 1998b). Results from different areas demonstrate the high variability of parasitism rates: 13 of 40 nests (32.5%) in a Minnesota Christmas tree plantation (Buech 1982); 8 of 9 nests (88.9%) and 26.8% of 82 nests in Saskatchewan (Davis 2003; Fox 1961); 5.1% of 781 nests in tallgrass prairie in Minnesota and North Dakota (Winter et al. 2004); 68 of 492 nests (13.8%); 38% of 42 nests, and 16.9% of 496 nests in North Dakota (Granfors et al. 2001; Grant and Knapton 2020); 2 of 58 nests (3.4%) in British Columbia (Campbell et al. 2001); and 20 of 31 nests (64.5%) and 26 of 52 nests (50.0%) in Manitoba (Root in Austin 1968).

Habitat loss does not appear to be an issue in Ontario, and much potentially suitable habitat is unoccupied. Coniferous plantations may become unsuitable once they mature and the crown closes, killing the understorey vegetation. In the core of its range in the prairies, conversion of grasslands to croplands results in habitat loss and is one of the contributing factors to its decline in that area. Removal of shrubs is also detrimental because the Clay-colored Sparrow is more of a shrub than grassland species. The quality of remaining grasslands has been diminished by fragmentation, invasive plants, fire suppression, certain livestock grazing practices, roads, and energy extraction (Askins et al. 2007; Curry 2006; Grant and Knapton 2020; Paquin and Letourneau in Gauthier and Aubry 1996; Root in Austin 1968; Winter et al. 2004).

Several factors can influence nest success. In Manitoba, nests within 10 cm of the ground were significantly more successful (60.9%) than higher nests (30.5%). Light penetration was significantly lower at successful than unsuccessful nests suggesting that less-concealed nests were more easily found by predators. Nests closer to the ground would have more overhead cover. Males returning to breed for at least the second year had higher nest success than males breeding for the first time. At 2 study areas, returning males had 65.0% and 82.8% nest-success rates compared with 20.0% and 53.8% for first-time breeders (Knapton 1979a). In North Dakota, nest survival was higher near forest edges because predators were more common in the interior of grasslands. Nests with more cover by Kentucky bluegrass and that were better concealed by vegetation had higher survival rates (Grant and Knapton 2020; Grant et al. 2006).

Niemuth et al. (2008) investigated the effects of drought on the Clay-colored Sparrow in North Dakota. It was positively correlated with the number of ponds present in spring. It was possibly responding to vegetation characteristics influenced in the previous year and conditions in the current year. Drought affects agricultural practices, with changes in crops, intensity of grazing, and timing of harvest. During drought conditions, CRP lands are often released for emergency haying or grazing, which alters the structure of grassland vegetation. This may be detrimental to the Clay-colored Sparrow because these practices reduce the shrub coverage that it prefers. In South and North Dakota, Montana, and Wyoming, there was no relationship between its abundance and weather (Gorzo et al. 2016).

Early haying can destroy Clay-colored Sparrow nests (Winter et al. 2004). Tews et al. (2013) estimated that the incidental take of this sparrow in Canada due to mowing and other agricultural practices was 111,071 annually. These numbers represent eggs and nestlings that are potentially destroyed. All incidental mortality due to agriculture was in western Canada. It does not typically nest in hayfields in Ontario.

In Alberta, the Clay-colored Sparrow nested on undisturbed and grazed grasslands and was absent in mowed, fallow, and seeded fields. Territories were always associated with low shrubs such as wolfberry or willow. It occurred on roadside counts in all landscape types and was most abundant where there was a mix of grazed and cultivated land. Agricultural practices did not appear to have affected its distribution and may have had a positive influence. Its preference for shrubby areas allows it to take advantage of ditches which are common in agricultural areas (Owens and Myers 1973).

Robertson et al. (2012) concluded that the Clay-colored Sparrow could benefit from the production of perennial grasses for biofuels. This type of habitat is unlikely to be used in Ontario and may be marginal habitat elsewhere because of the tall dense grasses and lack of shrubs. Use of corn for biofuels does not provide habitat for it.

The Clay-colored Sparrow tolerates light to moderate grazing because this typically results in short grass with scattered shrubs and tall unpalatable herbaceous species such as thistles. Heavy grazing is detrimental because this usually results in the removal of the shrub coverage that it prefers (Dechant et al. 2002c; Pylypec 1991).

Burning of grassland habitat appears to be detrimental to the Clay-colored Sparrow, particularly if the fire is intense enough to kill shrubs. In Wisconsin, spring burning of residual cover resulted in a 94% decline of this sparrow even though shrub density was not decreased. In South Dakota, it avoided burned areas. In North Dakota, it responded negatively to fires in mixed-grass communities and was most abundant in areas that remained unburned for more than 80 years compared with those burned 0.5-8 years ago. Numbers increased with the number of years since fire suggesting that moderate and long fire-return levels would be most beneficial. Some burned areas were used immediately after burning, but by lower numbers (Madden et al. 1999). In North Dakota, nest survival was not related to fire history but declined with increasing prevalence of woody cover in the landscape. Tall woody cover consisted mostly of chokecherries and 3-6-m-tall green ash. The proximity of nests to the nearest patch of tall woody cover or low shrub cover had no effect on nest survival. Murphy et al. (2017) concluded that the use of prescribed fire to reduce patches of tall woody growth does not adversely affect Clay-colored Sparrow nest survival and may improve it. In Saskatchewan fescue grassland, populations were reduced by prescribed burning. Three years after burning, the breeding population was 66% of what it was prior to burning (Grant and Knapton 2020). The effects of fire are likely to vary at different sites depending on how dense and tall the woody vegetation is prior to fire.

Forsythe et al. (1994) analysed the effects of spraying carbofuran to control outbreaks of grasshoppers. There was no evidence of reduced nestling survival for 3 days following spraying in a pasture and there was no mortality of adults that ate grasshoppers killed by carbofuran. This suggested that adults and nestlings are able to tolerate dietary exposure to carbofuran sprayed at the rate of 134 g per ha.

In North Dakota and South Dakota, Shaffer and Buhl (2015) studied the reaction of the Clay-colored Sparrow to turbines in wind farms. There was no significant change in its abundance before and after the turbines were present, but the trend was negative. The magnitude of differences in density of more than 20 birds per km^2 between turbine sites and reference sites suggested that it

may have experienced immediate displacement. After 1 year, it exhibited significant displacement within 200 m of turbines at 1 site and more than 300 m at the other study area. Delayed displacement may have been due to site fidelity with birds not returning in subsequent years, and new birds may be unwilling to settle near turbines. Removal of woody vegetation during road construction and turbine installation may have reduced breeding habitat. The displacement distance for it from turbines was considered to be 200 m. In Minnesota, higher densities of the Clay-colored Sparrow occurred more than 180 m from turbines than within 80 m of turbines (Grant and Knapton 2020).

In Alberta, there was no significant difference in the abundance of the Clay-colored Sparrow along seismic lines and in forest interior. It was significantly more abundant near pipelines and well pads than in adjacent forest interior (Bayne et al. 2016).

Some nests may be lost due to exposure to wind and rain, but this is usually a minor impact. In Manitoba, 1.3% of nests failed due to exposure and 2.9% of abandoned nests failed due to exposure (Grant and Knapton 2020). In Minnesota, 3 storms that produced more than 18 cm of rain in 2 weeks destroyed 82.4% of 17 nests (Root in Austin 1968).

Dechant et al. (2002c) offered recommendations for managing prairie grasslands for the Clay-colored Sparrow: allow grasslands to remain idle for long intervals to encourage shrubby growth, leave patches of shrubs when using fire or herbicides, maintain grasslands with tall forbs and abundant litter, discourage conversion of shrubland to cropland, maintain shrubby areas around cropland, and avoid heavy grazing that removes ground cover or shrubs. Woodland edges, wooded riparian areas, and other linear woody habitats such as windbreaks and shelterbelts could provide habitat.

Price (2004) predicted that the Clay-colored Sparrow could disappear as a breeding species from southern Ontario if the average summer temperature increased by 2°C. Nixon et al. (2016) predicted the area of suitable climate in Alberta would decrease slightly by the 2050s and by 26% by the 2080s. This was due to a northward shift in suitable climate to outside of the province. They projected that the area of suitable habitat within suitable climate regions would be reduced by approximately 20% by the 2050s and 40% by the 2080s.

Status

The Clay-colored Sparrow is a relatively recent arrival in Ontario. Forest clearing followed by regeneration and planting of coniferous plantations allowed it to expand north and east into Ontario. Prior to deforestation by Europeans, it is likely that it was confined to prairie habitat in the central portion of North America. There is some evidence that its eastward extension into Ontario occurred both north and south of Lake Superior (Baillie 1967; Campbell et al. 2001; de Vos 1964; Grant and Knapton 2020; Root in Austin 1968).

The Clay-colored Sparrow was first recorded in Ontario at London in 1894. The first nest was found at Thunder Bay in 1922 (Baillie 1967; Dale 1927). Baillie and Harrington (1937) stated that it occurred not uncommonly in various locations along Lake Superior westward to the Manitoba border. Breeding had been confirmed by then at Thunder Bay and Kenora and it was thought that it could breed in most suitable locations between Lake Superior and Lake of the Woods. Nesting

rarely occurred in the southern portions of the province at that time, with breeding records from Renfrew, Huron, Simcoe, and York. It was not known to nest east of Lake Superior until 1931 when the first record occurred in Algoma District. It first nested in southern Ontario in 1950. By the 1960s, it had nested in the Sault Ste. Marie, Ottawa, Craigleith, Halton, Waterloo, and Hamilton areas and there were scattered records in the north east to Fort Albany (Baillie 1967; Baillie and Harrington 1937; Curry 2006; de Vos 1964; Godfrey 1966; Mitchener 1956; Peck and James 1987; Warburton 1952). The first atlas demonstrated that it was widespread yet sparingly distributed throughout the province, with the exception of the Boreal Forest Region where it was very rare and sporadic in occurrence. Several breeding records were obtained in the Hudson Bay Lowland where it occurred sparingly along the Hudson Bay coast and more commonly along the southern James Bay coast from Moosonee to Attawapiskat. This represented a northward extension to the known breeding range. It was most abundant in the Thunder Bay and Lake of the Woods areas, with minor concentrations in the Ottawa area and along the southern edge of the Canadian Shield (Knapton in Cadman et al. 1987). James (1991) considered it a common local breeder in western Rainy River District; uncommon at Thunder Bay; and rare and local in the south and the north at Moosonee. There were scattered summer sightings north to Fort Severn and Attawapiskat. Wilson and McRae (1993) reported that there was an established breeding population in the coastal regions of the Hudson Bay Lowland.

The second atlas indicated that there had been no substantial change in the breeding range of the Clay-colored Sparrow, although it was slightly more widespread in the Boreal Forest Region than previously. Considerable infilling occurred within its range. Its probability of observation increased province-wide, but not significantly. In all regions, the trend was positive and was significant in the Carolinian, Great Lakes–St. Lawrence, and Boreal forest regions. Highest densities were in the Rainy River area. In the south, it was most abundant on shrub alvars and in old fields on the Carden Plain and the Napanee Limestone Plain between Belleville and Kingston (Rising in Cadman et al. 2007).

The BBS has some limitations for the Clay-colored Sparrow because only the southern portion of its range is sampled in the Prairie Provinces. In Saskatchewan, there was no significant difference in its abundance along roads and trails, so BBS results were representative of its abundance (Sutter et al. 2000). BBS data for 1970-2021 indicate that the Clay-colored Sparrow decreased at annual rates of 1.22% in Canada and 0.272% in Ontario. The trends for 2011-21 were annual decreases of 2.5% in Canada and 2.78% in Ontario. The long-term trend for Ontario and short-term trend for Canada were highly reliable; the other trends were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young are incapable of flight when they leave the nest. Fledglings disperse radially and hop through the shrubbery or may be lead by the adults to a safer place. In Manitoba, 8 fledglings initially moved an average of 13.6 m (range 6-21 m) from the nest to shrubbery. Once in dense shrubbery, they usually climb up the base of a shrub and remain motionless, waiting to be fed. When they are a bit older, the young become very active within snowberry or the prevailing shrub cover. Young are fed by the adults for at least 8 days after they leave the nest. By the time the young are 14-15 days old (about 5-6 days after leaving the nest) they are capable of flight. They gather together in small loose flocks and disperse onto adjacent territories where they are shown no aggression. Soon they begin

to wander widely and may appear in habitats such as grain fields, around ponds and potholes, in other shrubby habitats, in gardens, and among trees. Dispersal from the nesting area may be rapid. One bird banded as a nestling was recovered 2 km distant 13 days later. Others may congregate in favourite foraging areas, such as pond margins, a short distance from the nesting area. Nesting areas are usually devoid of birds by mid- to late July, although birds may remain in the general area into August. Little is known of their movements from then until the onset of autumn migration (Dechant et al. 2002c; Grant and Knapton 2020; Knapton 1979a; Root in Austin 1968; Salt 1966).

MIGRATION

The Clay-colored Sparrow migrates both nocturnally and diurnally, with diurnal migration most evident in autumn. It travels in flocks either by itself or in the company of other sparrows. Very large flocks may occur in autumn in the core of its range. In Ontario, where it is seldom seen during autumn migration, only solo birds are typically seen. In the Great Lakes region, spring migrants pass through Point Pelee, Sault Ste. Marie, and Manitoulin Island into western Ontario. It also passes through Manitoba and Minnesota in spring, and lesser numbers pass through Point Pelee in autumn (Grant and Knapton 2020; Root in Austin 1968).

In Manitoba, males arrived an average of 5 days before females in spring (range 3-7 days; Grant and Knapton 2020; Knapton 1979a). In southern Ontario, the Clay-colored Sparrow is usually on territory by mid-May, but birds may arrive in late April, mostly near the beginning of May. In the southern Shield, it arrives in the third week of May. There are few autumn records for Ontario, possibly because it migrates further west in autumn or because it may be difficult to distinguish from the Chipping Sparrow. The latest observation at Longridge was 5 September. The 3 autumn records for Algonquin Park span the period of 30 August to 10 October. In the south, migration extends from early September or very late August until mid-October, with stragglers to early November (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Tozer 2012; Weir 2008; Wilson and McRae 1993).

In Algonquin Park, spring migrants are usually seen along hydro corridors, at old sawmill sites, and in open areas with small trees (Tozer 2012). Elsewhere, migrating Clay-colored Sparrows occur in thickets, copses in open parkland or pastures, weed patches, and grassy areas where it shows a preference for borders of fields, woods, roads, and streams. During autumn migration, it may occur in urban parks and gardens, and sometimes comes to lawns, bird baths, and lawn sprinklers. During spring migration in British Columbia, it frequents open landscapes such as open hillsides, clearings, gravel pits, beach edges, dykes, regenerating clear-cuts, and lawns where the plant cover is dominated by grasses, dead forbs, and shrubs. In autumn, most are observed in shrub patches bordering fields, overgrown fields, pastures, hedgerows, and at margins of lakes, ponds, and marshes. Areas where grass and forb seeds are abundant are selected (Campbell et al. 2001; Leighton et al. 2002; Root in Austin 1968).

James (1991) considered the Clay-colored Sparrow a rare migrant in Ontario. Most regional books on Ontario's avifauna classify it as a rare or very rare migrant and it appears to be very rare in autumn throughout the province. Most migration records are of individuals or very small numbers. An exception is the 27 seen on 23 May in the Kingston area (Weir 2008).

Field Sparrow

Spizella pusilla

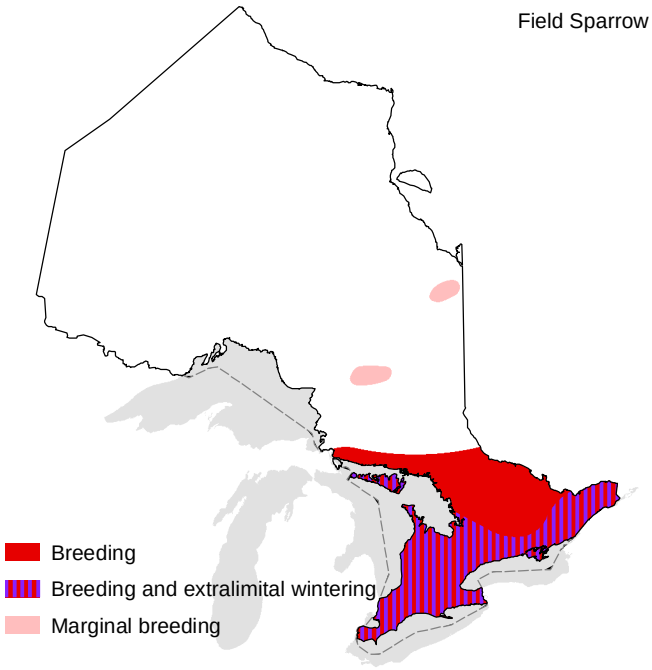
BREEDING SEASON

Habitat Requirements

In Ontario, the Field Sparrow has nested in open and overgrown fields and pastures (33.3% of nests); in Christmas trees and open coniferous plantations with small trees (33.3%); in open woodlands, woodland edges, and clearings (18.3%); in sand dunes with some grass, shrub, and tree growth (10.3%); in old orchards (1.6%); on farm and public lawns (1.6%); on overgrown bedrock outcrops (0.8%); and along railway embankments (0.8%). Most nests were in dry areas, but 4 were in undescribed wet areas, 1 was in a wooded swamp, and 1 was in a shallow marsh (Peck and James 1987).

In the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, the Field Sparrow nested on abandoned farmland, on hydro corridors, and in young plantations in Muskoka and Parry Sound districts (Mills 1981).

In the off-Shield portion of the Great Lakes–St. Lawrence Forest Region, it preferred open habitat such as shrubby fields, thickets, and overgrown pastures in the Kingston area (Weir 2008). In Durham Region, it was common in a very young red pine plantation dominated by shrub willows with an understorey of meadowsweet. The largest pines were 1.8-2.4 m tall but most were less than 0.9 m tall. It also nested in an abandoned apple orchard that contained hawthorns. The woody vegetation was 4.6-6 m tall with an understorey of grasses. Speirs and Orenstein (1975) considered it an early forest succession species.



The Field Sparrow is an open-country species that nests in a variety of early successional habitats. Taylor and Taylor (1979) characterized it as a species of both large and small openings and forest edges. Presence of shrubs is one of the most critical habitat components. It is most common in shrubby areas with an understorey of grasses and herbaceous species, infrequent in forest edges and forests with open canopies, and rare in grasslands with no woody cover. In Quebec, it occurs mostly in lands reverting to scrub, hedgerows bordering pastures, and young pine plantations (Yank and Dauphin in Gauthier and Aubry 1996). In New York, it nested at the edge of a Scotch pine plantation (Brooks 1980) and in 2-6-year-old clear-cuts. It was most abundant 2-3 years after cutting and declined significantly as the shrub-edge openings that it used largely disappeared (Keller et al. 2003). In New Jersey pine barrens, it was a local but fairly common breeder in recently burned pine forests and in pine plains (Brush 1987). In Maine, it nested in grassland barrens dominated by lowbush blueberry with lesser amounts of grasses and sedges, loosestrifes, and shrubs such as chokeberry, alder, and birch (Vickery et al. 1994). In West Virginia, Margenau et al. (2019) compared its abundance on reclaimed surface mines. The first stage of succession was grassland 5-19 years old dominated by nonnative grasses and forbs. Shrublands were 13-27 years old and supported shrubs and trees as large as 8 cm diameter at breast height (DBH). Other plots were in remnant forests and undisturbed intact forests. It was almost 2 times as abundant in shrublands as in grasslands; it was absent in the forested habitats. In Maryland, it was abundant in an unsprayed apple orchard with an unmowed ground cover and in an abandoned field with a new growth of young pines. It was uncommon in damp deciduous scrub with standing dead trees. In Georgia, it inhabits fields and pastures overgrown with raspberry thickets and deciduous underbrush. It avoided older pine woods but readily inhabited them after they were clear-cut or until they were 25-35 years old and still had a grassy understorey (Johnston and Odum 1956; Walkinshaw in Austin 1968). In North Carolina, it was abundant in fields recently planted with pines and common in pastures regenerating with pine (Carey et al. 2020). Planted pine trees less than 1.8 m tall codominated with Virginia broomsedge

supported a much higher density than where the pines were less than 0.9 m tall and codominant with fescue grasses and bush-clovers. Reproductive success was significantly higher in the latter habitat with larger clutches, more fertile eggs, a higher survival rate, and fewer female desertions. Its density may not be an indicator of habitat suitability (Fretwell 1969a). In North Carolina, Moorman et al. (2017) compared Field Sparrow usage of warm-season grass forage fields (hayed or grazed), nonnative cool-season hayed or grazed forage fields, and fields of native warm-season grasses and forbs. It occurred in all field types but its density was more than 3 times greater in native grasses than those that were hayed or grazed. Preferred fields had taller grass and greater forb density than other field types, had dense litter layers, and were often near woody edges. In Arkansas, it nested in fields dominated by grasses and sedges (Luscier and Thompson 2009). In the same state, as fields became invaded by shrubs and small trees, it became characteristic of the habitat and was among the most abundant species. It occurred in a burned field of Virginia broomsedge with scattered dead trees, in Virginia broomsedge and herbaceous species with clumps of trees, in a sassafras stand where the canopy was not quite closed but the grass layer had been killed out, and in forest edge with dense sumac and blackberry (Shugart and James 1973). In Pennsylvania, it was absent in uncut aspen and oak forests but appeared 2-3 years after 1-ha patches were clear-cut within them. The cuts provided temporary early successional habitat that was good nesting habitat (Yahner 1993, 2003). In the same state, densities declined 58% over a 6-year period in an old field, probably due to natural succession. The Field Sparrow begins breeding in old fields 1-2 years after human disturbance ceases, increases for about a decade, then declines, and by about 30 years of field age the area is not used due to natural succession (Carey et al. 2020). In Pennsylvania, it was common on a power-line corridor passing through deciduous forest but absent in the forest. It was 1 of the 6 most abundant species on the right-of-way (Yahner et al. 2002). In another Pennsylvania study area, breeding habitat consisted of old fields of grasses, herbaceous species (mostly goldenrods) and clumps of woody vegetation averaging 1.5 m in height, particularly dogwood, blackberry, viburnum, meadowsweet, ash, and honeysuckle (Carey 1990). Fields 20-35 years old were dense thickets of shrubby vegetation with only small scattered areas of open grassy habitat. It preferred breeding in open habitat with some woody vegetation (Smith et al. 2017). In Kentucky and Tennessee, its abundance was positively correlated with the amount of shrub coverage within 100 m (Lituma and Buehler 2016). In Illinois in 1957-58, it was most abundant in edge shrubs followed in order of decreasing abundance by hedgerows, along drainage ditches, shrub-grown areas, orchards, pastures, fallow fields, ungrazed grasslands, forest, and wheat. Preferred habitats included shrubs of all types, hedgerows, orchards, and pastures (Graber and Graber 1963). This survey was repeated in the 2000s. It was abundant in shrubs, common to uncommon in idle grass and savannah, and rare in row crops, hayfields, upland forests, floodplain forests, grazed grass, and grass mowed for hay (Walk et al. 2011). On reclaimed strip mines in Illinois, it was common in early shrub succession where the largest trees were 10 years old and in old shrubs where the largest trees were 37 years old (Karr 1968). Best (1977a, 1978, 1979) studied an area in Illinois that consisted of 8.5 ha of shrub-woodland, 9.0 ha of shrub-grassland, and 6.1 ha of grassland. The shrub-grassland was dominated by Kentucky bluegrass, Indian grass, big bluestem, panic grasses, and timothy. The dominant forbs included tall goldenrod, wild carrot, early goldenrod, Canada goldenrod, parsnip, yarrow, asters, and ironweed. Trees and shrubs, all less than 8 m tall, were scattered throughout and included smooth sumac, black raspberry, poison ivy, and black cherry. The shrub-grassland was the preferred habitat with all

available space occupied by contiguous territories. Territories extended into the grassland but were never completely in this habitat. Extension of territories into the shrub-woodland was limited, occurring where the forest canopy was more open. The Field Sparrow occupied transitory seral communities where succession is impeded by processes such as fire. In Ontario, more permanent habitat may occur on alvars or soils that are very nutrient-poor, but eventually even these areas regenerate into unsuitable habitat. In Indiana, Grundel and Pavlovic (2007a, 2007b) considered it the strongest indicator of open habitat in areas ranging from savannah to forest. It was significantly more abundant in open habitat with little woody vegetation than in prairie remnants and areas previously disturbed by farming or strip mining; significantly more abundant in savannahs with a moderate canopy of oak and little woody understorey than in the remaining habitats; significantly more abundant in woodlands, which were similar to savannahs but with more canopy closure than in the remaining habitats; and significantly less abundant in scrub with a high density of black oak saplings less than 5 m tall and in forest with multiple woody layers than in other habitats. It exhibited a high sensitivity to tree density, declining as tree density increased, but tree density alone did not strongly predict its distribution. On Indiana reclaimed surface mines, nests were found in shrublands and savannah areas with many scattered young trees 4-8 m tall, in open grasslands, and in open grasslands with a few areas of shrub or savannah habitat (Galligan et al. 2006). Nolan (1963) reported it breeding in abandoned upland fields separated by small timbered tracts or wooded ravines in Indiana. It was the most abundant species but less common in fields where half the ground was shaded during part of the day, either by saplings 7 m or taller or by densely growing hawthorns. In Michigan, the Field Sparrow nested on a hillside covered with blackberries, young trees, and shrubs; grass-grown meadows; pastures; and weed-grown fencerows. The dry hillside sparsely covered with blackberry was the preferred habitat but young oak trees, hazel shrubs, cinquefoil, or any other dense short vegetation in open fields may provide nesting habitat. Its habitat had tall grasses with patches of blackberry, staghorn sumac, shining sumac, New Jersey tea, and bush-clover and supported scattered small oaks, hickories, and hawthorns (Walkinshaw 1936, 1939b, 1945). Evans (1964, 1978) studied the Field Sparrow in 2 fields in Michigan. One was a grassy area dominated by Canada bluegrass and wiregrass with a rich variety of other grasses and forbs and scattered hawthorns, common junipers, and small trees. The other was grassland from 1949 to 1957, but an increase in the size and number of woody plants made the field less open by 1974-75. By 1975 the field was dotted with junipers, red cedars, and hawthorns several metres tall, there were dense patches of blackberries, and black cherry saplings 60 cm or shorter were scattered throughout. The number of junipers increased from 82 in 1950 to 273 in 1975 and they were also taller. The increase in the number of junipers created additional superior nest sites; density of sparrows increased by 73% from 1956 to 1975. The field gradually became more suitable habitat as natural succession progressed. In Missouri, cropland was planted to swamp white oak and pin oak at 9 by 9 m spacing. One of the 2 areas was planted to redtop, producing a low dense ground cover; no ground cover was planted at the other site. It nested predominantly in control areas and areas with a redtop understorey; significantly fewer nested in oaks where no ground cover was planted (Burhans et al. 2010). In Missouri, it nested in regenerating forests, glades, and forest-pasture edge habitats surrounded by forest cover. Regenerating areas had been clear-cut 3-5 years previously. The glades were burned 4-6 years previously and were characterized by dolomite outcrops with grassy areas and scattered trees and shrubs (Woodward et al. 2001). In Kansas, it nested in shrub thickets in

stream headwaters and along rock outcrops and in the border between grassland and woodland, especially in former pastures and cultivated fields growing up into thickets. It occasionally nested in woodlands where the canopy was open and the understorey was sparse. Open areas were occupied only where thickets were available (Fitch 1958; Zimmerman 1989). In Iowa, it was most frequent in upland woodland followed by woodland edge, herbaceous areas, and floodplain woodland (Stauffer and Best 1980). In Wisconsin, it was abundant in pine and oak barrens. It was abundant in oak savannahs, pine-dominated barrens, diverse barrens, river terraces, and coniferous plantations; common in shrub prairies, nearly forest, and clear-cuts; and fairly common in open-aspect barrens. It was one of the most common species in Christmas tree and forestry plantations. Its relative abundance was 12 in shrub habitat compared with 1 in open areas, heaths, and heaths with shrubs (Mossman et al. 1991). Buech (1982) reported it nesting in a Christmas tree plantation in Minnesota. In South Dakota, Gentry et al. (2006) reported it both in small (3.5 ha) tableland woodlots and large contiguous floodplain forests. In green ash woodlands in the same state, it occurred in both early and late seral stages of forest but was more abundant in young forests. Younger stands had less canopy cover and were patchier than older stands (Rumble and Gobeille 1999). In the northeast, the Field Sparrow has nested in upland deciduous forests, sapling and pole-sized poplar-birch stands, seedling-sapling-stage pine forests, and burned pine forests (Back 1979; Capen 1979; Samson 1979). Additional habitats that may be used for nesting include grassed waterways, untilled and idle cropland, shelterbelts, wooded draws, road and railway allowances, and nurseries. It avoids nesting in the vicinity of human habitation (Carey et al. 2020; Dechant et al. 2002g; Judd 1901).

Some studies examined habitat requirements of the Field Sparrow at the landscape level. In North Dakota in 400-m landscapes with less than 30% tree cover its probability of occurrence increased to 20% at 40% tree cover within 100 m and declined to 10% at 70% tree cover. The response was similar in wooded landscapes with a maximum probability of occurrence of 30% at 35% tree cover, declining to 5% at 90% tree cover. It preferred areas with 32-59% forest cover (Cunningham and Johnson 2016, 2019). In North Carolina, it was negatively correlated with the amount of tree canopy at the 200-m scale. As tree canopy increases, the amount of shrub coverage decreases. It was negatively correlated with the amount of exurban development at the 200-m and 1,000-m scales, although the relationship at the 200-m scale was not significant. It was significantly correlated with the amount of shrubland at the 1,000-m scale (Gilbert and Ferguson 2019). At the 400-m scale in Illinois, it was negatively correlated with agriculture and positively associated with forest (Glass and Eichholz 2023).

Sousa (1983) prepared a habitat suitability index model for the Field Sparrow. He concluded that availability of suitable perches such as shrubs, trees, and fences may be a limiting factor. In Missouri, the primary microhabitat features were canopy height and density of woody stems less than 2.5 cm DBH. Areas with canopy heights of 2-8 m were occupied but the preferred range was 2-4 m. The optimum density of small-diameter stems was 350-500 per ha, but it occupied a range of 25-1,050 per ha. Secondary habitat characteristics included density of stems larger than 2.5 cm and percent ground cover. The optimum range was 25-50 larger stems per ha (range 25-500 per ha) and 95-100% ground cover (range 85-100%). In Virginia, populations in regenerating hardwoods decreased as canopy height exceeded 4.5 m. Habitat in clear-cuts is suitable for 3-5 years on fast-growing sites and 10-15 years on slow-growing sites. Grasslands with no shrubs were considered unsuitable; more

than 75% shrub coverage was considered too dense. Habitats with 50-75% of shrubs shorter than 1.5 m were assumed to provide the optimum mix of tall and short shrubs. Grass coverage less than 50% was assumed to provide less than optimal nesting cover; more than 90% grass coverage may inhibit movement. The optimum height of herbaceous vegetation was 16-32 cm with suitability decreasing with increasing height due to increased difficulty in reaching the ground. The minimum size of habitat patches considered suitable to support the Field Sparrow was 2 ha. Scores on the habitat suitability index ranged from 0 (unsuitable) to 1.0 (optimum). For percent shrub crown cover, scores were 0 at 0%, increasing to 1.0 at 50-75%, and declining to 0 at more than 75%. For percent of shrubs less than 1.5 m tall, scores were 0.2 at 0%, increasing to 1.0 at 15-35%, and decreasing to 0.6 at 100%. For percent coverage by grass, scores were 0 at 0%, increasing to 1.0 at 50-90%, and declining to 0.8 at 100%. For average height of herbaceous vegetation, scores were 0 at 0-5 cm, increasing to 1.0 at 16-32 cm, and decreasing to 0.5 at taller than 40 cm.

Several studies defined microhabitat characteristics of Field Sparrow habitat. In Missouri, percent coverage of vegetation in 1-m^2 quadrants around nests consisted of 31.6% grasses, 52.2% forbs, 17.5% shrubs, and 6.7% bare ground (Burhans and Thompson 1998). In Illinois, territory size increased with the percentage of area covered by Indian grass, tall and early goldenrods, big bluestem, sedges, Kentucky bluegrass, black cherry and other species in the same genus, ironweed, yarrow, wild lettuce, and smooth sumac. Coverage by other species was independent of territory size. The frequency of occurrence of Indian grass and big bluestem increased significantly with territory size. The number of nesting attempts was negatively correlated with the frequency of occurrence of Indian grass suggesting that territories containing this species may become less attractive as the season progresses. Parsnip occurred significantly more in territories of yearlings than older birds. The opposite was true for the frequency of little bluestem and percent coverage by big and little bluestem, black cherry, panic grasses, and sulphur cinquefoil. This related to the extension of territories into a shrub-woodlot. All but 1 yearling territory extended into the shrub-woodland. The proportion of territory in shrub-woodland averaged 36% for yearlings and 20% for returning males. Frequency of male mating was correlated with the area covered by smooth brome, tall goldenrod, ironweed, Indian grass, and cherry. All these were used for nesting except ironweed (Best 1977a). In Pennsylvania, percent ground cover was the best model for predicting nest-site selection, with nest sites having higher ground cover than random sites (Schill and Yahner 2009). In Maine, abundance of the Field Sparrow was positively correlated with habitat patchiness and abundance of shrubs 60-200 cm tall. It was negatively correlated with bare ground. It was infrequent in areas that had been recently mowed or sprayed with herbicides (Vickery et al. 1994). In Illinois, its abundance was positively correlated with vegetation height and negatively correlated with mean grass height (Herkert 1994a). In Iowa, it was positively correlated with horizontal patchiness of saplings, vertical patchiness of trees, slope, grasses, and coniferous trees. It was negatively correlated with sapling and tree density and size, vines, and vertical stratification (Stauffer and Best 1980). In Illinois, daily nest survival was positively associated with grass cover both at the nest site and within a grassland patch (Glass and Eichholz 2023). In Texas, its highest probability of occurrence was at 74% canopy cover by woody species within 250 m (Plappert et al. 2024). Dechant et al. (2002g) summarized other microhabitat requirements. In Illinois, availability of trees, shrubs, or other potential perches was a key habitat component. Birds stayed within or near forest edge, not

venturing deep in the forest or more than 12-15 m into fields. In Wisconsin, density was correlated with percent woody cover, the total number of dead stems, and plant species richness.

Although the Field Sparrow was restricted to edge habitat in Illinois (Dechant et al. 2002g), other studies have not observed that it preferred or avoided edges. In shrub patches adjacent to forest edges in Missouri, areas within 20 m of the forest edge and those 20-40 m and more than 40 m distant from it were all used in proportion to their availability. Distance from edge did not affect predation rates and edges did not function as ecological traps (Woodward et al. 2001). In riparian wooded strips in Maryland and Delaware, there was no difference in its probability of detection in forests 50-800 m wide (Keller et al. 1993). In Tennessee and Kentucky, Lituma and Buehler (2016) found no differences in its abundance at roadsides or on transects 300 or 600 m from roads. In Illinois, nests further from edge had higher survival rates, but Field Sparrows did not avoid roads. It tended to nest near edges regardless of edge type (Glass and Eichholz 2023).

The Field Sparrow is not an area-sensitive species. In Ohio, it nested in patches smaller than 2 ha. In Illinois, it was encountered in patches smaller than 10 ha but was classified as moderately vulnerable to habitat fragmentation because it was encountered more frequently in large than small fragments. It was more strongly influenced by habitat structure than area. Absence from some small grassland areas may have been due to lack of suitable habitat rather than avoidance of small areas (Dechant et al. 2002g). In Maine, it was positively correlated with patch size, but not significantly (Vickery et al. 1994). In both Illinois and Iowa, its probability of occurrence was unrelated to patch size (Herkert 1994a; Stauffer and Best 1980). Near Ayr, 2 territorial males were present in an area of about 1 ha, near Erin a single territorial male was present in an area of 1 ha, and in Hamilton, 1-2 pairs nested annually in an area smaller than 1 ha (personal observation).

Ontario nests were on or very near the ground and elevated in shrubs, trees, plant clumps, and tangles of vines. Deciduous trees and shrubs (11 species) were somewhat preferred to conifers (5 species), with 60.5% of nests in deciduous species. The most frequently selected species were hawthorns (42 nests), spruces (15), pines (12), juniper (11), elms (8), apple (8), and white cedar (8). Nests were mostly in main crotches at the trunk, although 5 were on branches out from the trunk. Ground nests were usually in clumps of grass under small trees or shrubs (Peck and James 1987, 1998b). Mills (1981) reported 1 nest in a bracken fern and another in a red pine.

Nest height increases as the season progresses throughout the Field Sparrow's range. Nest building usually begins before foliage is well developed on trees and shrubs. During the first 1-2 weeks of nesting, nests are placed almost exclusively in dead grass litter from previous years. Once new grass growth overtops the dead grasses, this substrate is avoided. Once leaf-out has occurred, nests are placed in a mix of grasses, forbs, trees, and shrubs. Later in the season nests are predominantly in shrubs and trees. In Illinois, nest heights were 26 cm in May, 38 cm in June, 47 cm in July, and 48 cm in August with an overall range in height of 9-89 cm. Similar increases in nest height with season have been documented in many other areas. Nest height within a given substrate also increases with time. In Indian grass, mean nest heights were 29 cm in May, 34 cm in June, and 47 cm in July; mean heights in trees and shrubs were 27 cm in May, 42 cm in June, 51 cm in July, and 49 cm in August. Overall, nests have been found 0-4.4 m from the ground but most are 1 m or less from the ground. In a Christmas tree plantation in Minnesota, mean nest height was 44

cm in trees that averaged 1.42 m tall. Nests have been reported in a variety of grasses, herbaceous species, shrubs, and trees including Kentucky bluegrass, Indian grass, black raspberry, tall goldenrod, sweet clover, Canada thistle, elderberry, catnip, hawthorn, apple, cherry, oak, sumac, rose, elm, wild lettuce, Manitoba maple, lilac, dewberry, shrubby cinquefoil, red raspberry, bush-clover, black locust, blueberry, Japanese barberry, stiff-leaved goldenrod, hickory, red cedar, common juniper, ash, New Jersey tea, hazelnut, meadowsweet, alfalfa, honeysuckle, and dogwood. In Missouri, 22% of nests were in grasses, 10% were in forbs, 46% were in shrubs, and 22% were in roses. In Illinois, 41.9% of nests were in grasses, 19.4% were in forbs, and 38.6% were in trees and shrubs. Although many nests are not in woody vegetation, few are further than 40 cm from a shrub or tree. Within woody vegetation, most nests are in main crotches at the trunk where they may be supported by 2 to several branches. An exception is in common juniper where nests are often in twigs and foliage distant from the main stem. In Minnesota Christmas trees, there were no significant differences in nest heights of the Field, Chipping, and Clay-colored sparrows. In Missouri, mean nest height of Field Sparrow nests was 0.4 m, significantly lower than those of the Indigo Bunting and Northern Cardinal. In Michigan, the Field Sparrow built 94% of its nests in shrubs shorter than 1.5 m; the Chipping Sparrow built 90% of its nests in shrubs 1.5 m tall or taller. The Field Sparrow nested on the ground and in low shrubs, the Chipping Sparrow nested exclusively in trees and shrubs, and the Vesper Sparrow nested exclusively on the ground. Although Field and Chipping sparrows overlap considerably in their foraging patterns and diet, their nesting habitat is different. Food does not appear to be a limiting factor for the Field Sparrow and presence of suitable nesting locations is probably the most important factor in determining territory location. Nests are typically used only once but 1 Texas nest appeared to have been used twice in a season (Allaire 1972; Best 1977a, 1978, 1979; Buech 1982; Burhans and Thompson 1998; Carey 1990; Carey et al. 2020; Dechant et al. 2002g; Evans 1964, 1978; Judd 1901; Luscier and Thompson 2009; McChesney and Anderson 2015; Nolan 1963; Schill and Yahner 2009; Walkinshaw 1936, 1939b, 1945; Walkinshaw in Austin 1968). In Michigan, 1 nest was in a vacant lot between 2 houses (Walkinshaw 1939b).

Males may initially have larger than normal territories, but these shrink as more birds arrive. Changes in territorial configuration are common early in the season. In addition to shrinking due to new neighbours, territories may be expanded into abandoned areas. Territories in high-quality habitat tend to be contiguous; those in marginal habitat are often separated from each other. One male defended a territory in Michigan for 6 years. His territory size was 0.40 ha in the first year, 0.48 ha the second year, and 0.8 ha in the final 4 years. All 15 nests of this male and his various mates were within an area of 0.36 ha. In Illinois, the mean size of territories of returning males was 0.60 ha in the first year and 0.95 ha in the second year. After 2 or 3 years, males seem to pick an optimum size of territory to defend. Illinois territories averaged 0.76 ha (range 0.31-1.62 ha) before boundaries were changed to include abandoned territories. One male increased his territory to 3.41 ha after 2 of his neighbours abandoned their territories. Habitat quality affects territory size, with smaller territories in high-quality habitat. In Illinois, territories in grassland were significantly larger (1.02 ha) than those in shrubby areas (0.53 ha). Territories in open areas in Kansas were larger than those in shrubs. In Illinois, the best territories contained shrubland and margins of a woodlot where adults obtained much of the food for nestlings. Territories providing the most desirable nesting and foraging sites early in the spring had greater reproductive potential than those becoming desirable

later in the season when clutch size is reduced. Mean territory sizes were 0.6 ha in Indiana, 0.65 ha in Kansas (range 0.32-1.01 ha), and 0.5 ha in Iowa (range 0.3-0.8 ha). In Michigan, Field and Chipping sparrows had overlapping territories and aggression only occurred when a member of the other species approached the nest (Best 1977a; Evans 1978; Fitch 1958; Nolan 1963; Walkinshaw 1945; Yank and Dauphin in Gauthier and Aubry 1996).

Natal philopatry is very low. In Ohio, 1 of 103 banded juveniles (0.9%) returned (Lehnen and Rodewald 2009b), 6 of 1,826 nestlings (0.3%) returned in Pennsylvania, 1 of 514 nestlings (0.2%) returned in Michigan (Carey et al. 2020), and 1 of 100 fledglings (1.0%) returned in North Carolina (Fretwell 1968).

Adult site fidelity rates are high. In many areas, probably all surviving males return to breed and they tend to occupy the same territory each year. Returning males do not arrive significantly earlier than those appearing for the first time. Females have lower site fidelity than males. Some disappear within a breeding season following nest desertion and these seldom return. In Pennsylvania, some females were absent for 1 or 2 years and then returned but males never did this. When birds disperse to a different habitat patch in subsequent years, they usually move to younger patches but do not select areas with more shrubland. Dispersal patches in Ohio averaged 1 year younger than original patches. In New York over 4 years, 33 of 61 males (54.1%) returned the subsequent year. Return rates in individual years were 63.2%, 48.0%, 50.0%, and 57.1%. In Illinois, 11 of 25 males (44.0%) returned to breed in the following year. Only 3 females returned (the sample size was not specified). Females appeared to have a strong tendency to reoccupy the previous territory regardless of which male was defending it. In Ohio, 39 of 97 adults (40.2%) returned. In Pennsylvania, an average of 53% of males returned to breed in a subsequent year with annual rates of 18-80%. An average of 36% of females returned with annual rates of 18-48%. For both sexes, the rate of return was similar regardless of age. One male returned for 8 years and 1 female returned for 7 years. One study summarized results from several areas and calculated an overall return rate for adults of 49% (Best 1977a; Carey et al. 2020; Lehnen and Rodewald 2009b; Nelson 1992; Schlossberg 2009; Smith et al. 2017).

Limiting Factors

Eggs have been reported in Ontario nests from the beginning of May until mid-August, with most present from the last week of May until the third week of June (Peck and James 1987). Females usually pair with their mate 1-2 days after they arrive, but in Michigan, this occurred 9-32 days after the males arrived (average 22 days). First nests take 3-7 days to build but mostly 4 or 5 days. Later nests may be built in 2 or 3 days with some lining material occasionally added on the fourth morning. In Michigan, females invariably laid the first egg in a replacement nest 5 days after the first nest was lost or deserted. The first egg was laid in second-brood nests 6-16 days after the first young fledged (average 10.8 days). The first egg is laid the day after the nest is complete or the following day. In Pennsylvania, the first egg was laid 1 day after the nest was complete in 63.6% of cases. One egg is laid per day. The onset of incubation may occur with the laying of the first egg, the day the third egg is laid, or late in the day that the second egg is laid. During cold weather, some females delay the start of incubation for as long as 4 days after the last egg is laid. The incubation period of 1 Ontario nest was 12 days. Incubation periods of 10-17 days have been reported with most eggs

hatching in 11 or 12 days. The young usually hatch on the same day. In Michigan, 2 young usually hatched in the same hour, the third young hatched in the next 24 hours, and, if there was a fourth young, it hatched sometime the next day. Young leave the nest when they are 5-10 days old, with disturbed birds leaving earlier. In Michigan, disturbed young left the nest when they averaged 6.4 days old (range 5-7 days); undisturbed young fledged at an average of 7.5 days (range 6-8 days). In Indiana, the nestling period was 7-9 days and mostly 9 days; Pennsylvania young fledged when they were 9-10 days old (Carey 1990; Carey et al. 2020; Nolan 1963; Peck and James 1987; Walkinshaw 1936, 1939b, 1945; Walkinshaw in Austin 1968).

Ontario egg dates suggest that 2 broods may be raised. This has not been confirmed, but McIlwraith (1894) stated that 2 broods were raised. The Field Sparrow is capable of raising 3 broods in a season, but rarely does so because of predation and parasitism. In Michigan, only 2 pairs successfully raised 3 broods over an 11-year period. In Pennsylvania, 60% of nests fledged young and second broods were common. Forty-eight of 160 females (30.0%) successfully fledged 2 broods and 1% successfully raised 3 broods. Where snakes are abundant, predation rates are very high with few birds raising 2 broods and some not raising any young. It is a persistent renester, starting replacement nests 1-2 days after a nest is depredated or abandoned. One Illinois female initiated 10 nests in a season, all of which were lost due to predation and parasitism. Clutches of 3-5 eggs have been reported in Ontario (mean 3.75 eggs). Four-egg clutches were most frequent and comprised 66.3% of clutches; only 4.1% of clutches contained 5 eggs. Elsewhere, clutches of 2-6 eggs have been reported, with a normal range of 3-5 eggs. Four-egg clutches are the most abundant; most other clutches contain 3 eggs. Clutch size declines with the season. Mean clutch sizes in Michigan were 3.85 eggs in May (range 3-5 eggs), 3.54 eggs in June (range 2-5), 2.99 in July (range 2-4), and 2.75 in August (range 2-3). In Kentucky and Tennessee, clutch size was significantly reduced by 0.5 egg every 52 days; clutches of second broods averaged 0.5 egg less than first nests. Five-egg clutches usually do not occur after mid-June. Mean clutch sizes from other locations include 2.9 eggs in unparasitized nests in Minnesota, 3.53 in Michigan, 3.6 in Kentucky and Tennessee, 3.69 in Pennsylvania, 3.43 and 3.56 in 2 habitats in North Carolina, 3.4 and 3.8 in 2 years in West Virginia, and 3.96 in Missouri (Best 1974; Buech 1982; Carey 1990; Carey et al. 2020; Dechant et al. 2002g; Evans 1978; Fretwell 1969a; Giocomo et al. 2008; Nolan 1963; Walkinshaw 1936, 1939b, 1945; Walkinshaw in Austin 1968; Wray et al. 1982).

The age at first breeding is 1 year and breeding occurs every year thereafter. The presence of unmated males suggests that some yearlings may not nest. In Pennsylvania, 11.9% of territorial males were unmated. Some Illinois males remained unmated all summer. In Michigan, 2 males did not initially attract a mate but continued to defend their territories. They finally acquired mates in mid-June and nested. The mating system is predominantly monogamous but a few males are polygynous. In Pennsylvania, 4 of 156 males (2.6%) were polygynous and 1 was polyterritorial. Many pairs remain together for the entire breeding season, often through multiple nesting attempts. In Pennsylvania, 199 of 379 pair bonds (52.5%) formed at the beginning of the season remained stable throughout the season. Females may abandon their territories part-way through the breeding season in response to parasitism or predation, or after the first brood fledges. These females leave the habitat patch and probably attempt to breed in another location. Males that have been abandoned continue to defend their territories and are frequently successful in attracting another

mate. One Illinois male was mated with 5 different females in a single season. No male that was previously mated abandoned his territory if a female was in the area. All males that abandoned territories before the end of the season were unmated. Mates rarely pair again in subsequent years. In Pennsylvania, 17 of 312 pairs (5.4%) reunited in a subsequent year, significantly less than expected if surviving mates always paired with each other (Best 1977a; Carey 1990; Carey et al. 2020; Walkinshaw 1945).

Extra-pair copulations may be an important component of the Field Sparrow's mating system, and both sexes may seek them. A Michigan female copulated with her mate and 2 neighbouring males in quick succession. In Ohio, 10 of 52 nestlings (19.2%) had genotypes that were inconsistent with 1 or both behavioural parents and 5 of 17 broods (29.4%) showed mismatches. In Pennsylvania, 98 of 1,051 nestlings (9.3%) had DNA that did not match the attending male and 36 of 175 males (20.6%) had at least 1 extra-pair young in their nest. Eighty-two of 98 extra-pair nestlings (83.7%) were in nests in which the entire brood was extra-pair. Eighteen males had such broods; 13 (72.2%) were first-time breeders and 78% of their mates were also first-time breeders. Many were also late arrivals on the breeding grounds. Nesting chronology tends to be highly asynchronous with nests in varying stages. This provides opportunities for extra-pair copulations. The male does not incubate so he has 11 days to seek extra-pair copulations while the female incubates. In Pennsylvania, the frequency of extra-pair young declined steadily from 20% in 1990 to 0% in 2000-02, coincident with a decline in the population (Carey et al. 2020; Petter et al. 1990; Walkinshaw in Austin 1968). Intraspecific nest parasitism appears to be a rare behaviour. In 2 cases in Ohio, nestlings were unrelated to the social mother. In Pennsylvania, 2 of 469 nests (0.4%) received 2 eggs in 1 day and 1 of 152 nestlings (0.7%) was mismatched with the attending female. Unmated females or those that had their clutches depredated may potentially lay eggs in other females' nests (Carey et al. 2020; Petter et al. 1990).

During the breeding season, the Field Sparrow typically forages solitarily or with its mate within the territory. Some exceptions occur. In North Carolina, adults foraged for nestlings' food in adjacent alfalfa fields and shrubs bordering a watercourse. During rainy weather in Kansas, birds appeared to be reluctant to forage in the tall grasses within their territories where they usually foraged. Instead, several pairs foraged within a few square metres in open habitat along a road. No hostility was observed among these birds even though the area was within the territory of 1 pair and beyond the boundaries of the other pairs. When the weather cleared, they returned to their territories and normal aggression was resumed. In Illinois, it avoided grasslands for foraging; all foraging occurred in shrubby meadows and at the edge of a woodlot. Wooded areas provided a greater abundance of nestlings' food early in the breeding season. More open areas with low herbaceous vegetation became the preferred foraging area later in the season. The suitability of a territory for nesting and rearing young may change markedly over the breeding season. In Texas, both Chipping and Field sparrows foraged mostly within 1 m of the ground, predominantly from perches 30-40 cm up. They peered into the vegetation below and, when a non-flying insect was seen, quickly descended from the perch and tried to capture it. Field sparrows were somewhat more active than Chipping Sparrows and never spent more than 10 seconds on a perch. The Field Sparrow exhibited a greater variety of seed-gathering techniques and was more acrobatic in procuring seeds. It often flew to the top of grasses, letting its weight carry itself and the stems to the ground where it ate the seeds while

still holding onto the grass stems. It spent more time foraging from low perches than the Chipping Sparrow. It often used brush piles, fallen trees, low shrubs, and fences as perches where it reached out and ate grass seeds from the tops of stems. In South Carolina, Field and Chipping sparrows both foraged in a disturbed field of grasses, shrubs, and brush piles. The Field Sparrow foraged among the emerging flowers of a willow on 1 occasion, but all other foraging was on the ground. It spent more time flycatching than the Chipping Sparrow and did so almost invariably from the ground. In April, both species fed equally in trees and in the field, but usage of trees was very low to zero in other months. A comparison of the diet of adults and nestlings in Michigan suggested that adults spent less time on the ground and more in active flight or in higher strata when foraging for nestlings′ food. In Maryland, the Field Sparrow occasionally fed in tobacco fields with Chipping Sparrows and individually in corn fields from the time that the corn became tasselled until it was harvested. In Ohio, the Field Sparrow foraged in grasses more than their availability. In August, it visited stubble fields, feeding on oats in oat stubble and insects and weed seeds in wheat stubble, but not on wheat. All researchers agreed that food is abundant and well distributed in the breeding season and is not a limiting factor (Allaire and Fisher 1975; Best 1977a, 1977b; Carey et al. 2020; Dechant et al. 2002g; Evans 1964, 1978; Fitch 1958; Fretwell 1969a; Hebrard 1978; Judd 1901).

The nestling diet consists almost entirely of insects, with some spiders consumed. Walkinshaw (1939b) observed young being fed insects, particularly grasshoppers and caterpillars. He reported another study where nestlings were fed 154 geometer moth caterpillars, 45 grasshoppers, and 24 moths. Carey et al. (2020) reported that 237 nestling food items consisted of 65% caterpillars, 19% grasshoppers, 10% adult moths, and 6% unidentified matter. In Iowa, the nestling diet consisted of 71% caterpillars, 16% adult flies and bees, 10% adult moths, and 3% beetles. In Pennsylvania, 1,853 food items in nestlings′ diet consisted of 80% caterpillars, 10% adult flies and bees, 6% orthopterans (mostly katydids), 3% adult moths, and 1% spiders. The golden-backed snipe fly comprised a large portion of the nestling diet, but only during its emergence in early June. In Michigan, the percent occurrence of food items in the diet of 5 nestlings in spring was 20% odonates, 80% orthopterans, 40% true bugs, 80% soft-winged bugs, 60% beetles, 100% lepidopterans, 80% flies, 80% spiders, 20% snail shells, and 60% plant material. The percent occurrence of food items of 20 nestlings in summer was 30% odonates, 85% orthopterans, 100% soft-winged bugs, 60% beetles, 95% lepidopterans, 45% flies, 60% hymenopterans, 95% spiders, 10% snail shells, and 50% plant material. Larvae of lepidopterans, beetles, orthopterans, and soft-winged bugs were preferred by adults for feeding nestlings, and spiders were also important. Nestlings had significantly higher frequencies of odonates, orthopterans, lepidopterans, flies, and spiders in their diet than adults and significantly lower frequencies of true bugs and beetles. Nestlings were fed more rapidly flying insects and sluggish larvae than adults ate. Adults and free-flying fledglings ate by frequency 20.7% rapidly flying insects, 20.7% sluggish larvae, and 86.2% insects from the ground. Nestlings ate 44.0% rapidly flying insects, 96.0% sluggish insects, and 100% insects from the ground. There was no significant difference between the diets of Field and Chipping sparrow nestlings (Evans 1964). Best (1977b) examined the diet of nestlings in 2 years in Illinois. In the first year, the diet consisted of 37% caterpillars, 18% other insects, 16% soft-winged bugs, 15% orthopterans, and 14% spiders. In the second year, the diet was comprised of 30% caterpillars, 22% soft-winged bugs, 22% spiders, 18% orthopteran nymphs plus 2 adults, and 8% other insects. There was an increase in the abundance

of soft-winged bugs in the second year due to the emergence of 13-year cicadas that provided an extremely abundant food source from the end of May throughout June. In both years, caterpillars were the most important food in May and June, reached their lowest level of consumption in July, and increased again in August. Orthopterans were absent in the diet in May both years, were of minor importance in June, and the most important food item in July and August. In the first year, spiders were important in the diet but decreased to negligible use after June; usage of spiders was constant in the following year. Spiders consistently declined in the diet as nestlings aged and orthopterans increased. The larger size of orthopterans probably restricted their usage by young nestlings. Soft-winged bug usage was nearly constant as nestlings aged whereas usage of caterpillars fluctuated erratically. The size of food provided ranged from less than 0.005 cc to 0.38 cc in volume with the upper size increasing with age. The importance of items smaller than 0.005 cc decreased as nestlings grew, but even old nestlings were fed items of this size, predominantly soft-winged bugs. Nestlings were also fed walkingsticks.

Adult Field Sparrows eat predominantly seeds but also consume insects during the breeding season when they are feeding nestlings. Plant material, mostly grass seeds, dominates the spring diet. The diet gradually changes from a predominantly plant diet to a predominantly invertebrate diet in summer, and reverts to a plant diet in autumn and winter. In Texas, seeds eaten in summer consisted of 92.2% crabgrass, 0.5% panic grass, 0.5% spurges, and 6.8% unidentified. Arthropods consumed in summer included 33.3% beetles, 16.7% orthopterans, 25.0% lepidopterans, 8.3% bugs, 8.3% hymenopterans, and 8.3% spiders. Autumn seeds consumed consisted of 42.6% crabgrass, 10.7% panic grasses, 28.2% foxtails, 9.8% spinifex grass, 5.0% flatsedges, 4.5% spurges, and 0.2% unidentified. The autumn arthropod diet consisted of 11.1% termites and 88.9% lepidopterans. In Michigan, frequency of occurrence of items in the diet was 25% orthopterans, 25% true bugs, 12.5% soft-winged bugs, 50% beetles, 25% lepidopterans, 37.5% flies, 37.5% hymenopterans, 25.0% spiders, and 100% plant material including 37.5% wiregrass, 25% panic grasses, 25% Indian grass, and 12.5% sandworts. Frequency of occurrence of food items in summer was 4.8% odonates, 42.9% orthopterans, 76.2% true bugs, 90.5% soft-winged bugs, 76.2% beetles, 14.3% lepidopterans, 9.5% flies, 28.6% spiders, and 52.4% plant material including 4.8% brome grass, 19.0% poverty oat grass, 23.8% wiregrass, 4.8% fescue grass, 9.5% bluegrass, 9.5% sandworts, 4.8% thistles, 14.3% wood-sorrel, and 4.8% docks. In summer, odonates first became evident in the diet and leaf and click beetles became common in the diet. Weevils and ground beetles that were prominent in the diet in spring were also important in summer. Prior to the 20th century, the Field Sparrow was reported feeding on aphids, tent caterpillars, and geometer moth and other caterpillars. In Maryland, 175 stomachs contained 41% animal matter and 59% vegetation. Invertebrate food items consisted of 2% weevils; 2% leaf beetles; 9% ground, tiger, click, and June beetles; 4% caterpillars; 6% grasshoppers; 14% leafhoppers, true bugs, sawflies, ants, flies, and spiders; and 4% parasitic wasps. Plant food consisted mostly of grass seeds such as crabgrass, panic grasses, foxtails, broomsedge, wiregrass, and dropseed; other seeds included 4% chickweeds, lamb's-quarters, gromwell, amaranths, purslane, spurges, wood-sorrel, and knotweeds; and 4% oats. It feeds very little on seeds other than grasses and subsists on ragweed less than other upland sparrows. It occasionally shows a marked preference for wood-sorrel, chickweed, purslane, and smaller-seeded species of knotweeds and smartweeds. A flock in September fed mostly on crabgrass, but sparrows occasionally sprung up in the air and

captured a braconid wasp. Plant food of 137 birds in the northeast consisted of seeds of foxtails, crabgrass, broomsedge, panic grasses, oats, and lesser amounts of dropseeds, sheep sorrel, amaranths, ragweed, wood-sorrel, timothy, and lamb's-quarters. Thirty-eight stomachs from the prairie states contained seeds of foxtails, panic grasses, dropseeds, crabgrass, and lesser amounts of vervain, lamb's-quarters, wheat, redtop, and gromwell. In Texas, the diets of Field and Chipping sparrows were very similar but may have been partitioned because the Field Sparrow tended to forage higher than the Chipping Sparrow. The Field Sparrow tended to feed on seeds that were slightly smaller than those selected by the Chipping Sparrow. In Maryland, the consumption of parasitic wasps by Field Sparrows was the principle difference from the diet of the Chipping Sparrow. There was little difference in the diets of Field, Chipping, and Vesper sparrows in Michigan. The Chipping Sparrow ate more lepidopterans than the other 2 species and the Vesper Sparrow ate significantly more orthopterans than the Field Sparrow and significantly fewer soft-winged and true bugs than the Chipping Sparrow. Food appears to be so abundant that there is no competition for it among species (Allaire and Fisher 1975; Evans 1964; Judd 1901; Walkinshaw in Austin 1968). Browning et al. (1981) offered seeds of round-headed bush-clover, blazing-star, and 2 types of sunflowers to Field Sparrows. Bush-clover was the lowest quality food and Field Sparrows ate fewer of these seeds and more of the sunflower seeds, demonstrating that it selects higher-quality seeds.

The Field Sparrow is a common host of the Brown-headed Cowbird. It may either accept or reject cowbird eggs with nest desertion being the method of rejection. In some areas, most foreign eggs, including plastic and blue ones, are accepted; most parasitized nests are abandoned in other areas. In 1 area of Illinois, all eggs were accepted. In another area of Illinois, 14 of 29 parasitized nests (48.3%) were deserted compared with 0 of 21 unparasitized nests. In Missouri, 21 of 47 parasitized nests (44.7%) were deserted compared with 1 of more than 300 unparasitized nests (less than 0.3%). No desertion occurred in nests where a Field Sparrow egg was replaced with a real, an artificial maculated, or an artificial unmaculated cowbird egg. Sparrows may desert nests in response to a decrease in clutch size. Desertion may also occur if parasitism occurs on the first or second day of incubation. Nests may be deserted if a sparrow sees a cowbird near the nest. Of 6 cases where a cowbird was encountered near the nest during egg laying, 5 (83.3%) were deserted. All nests presented with a cowbird model in the nest-building and early egg-laying stages were deserted, 3 of 7 (42.9%) were deserted in the late-laying period, and 0 were deserted during incubation. Desertion appears to be immediate when a cowbird is observed. The reaction of Field Sparrows to cowbird models varies geographically, with higher levels of aggression in areas with higher parasitism rates. Parasitism does not appear to be a significant limiting factor to the Field Sparrow. In Illinois, 5% of sparrow eggs were lost due to parasitism, either through removal by cowbirds or nest desertion. This loss was probably mitigated by renesting. Nestling sparrows appear to be unaffected by the presence of a cowbird nestling, growing normally and fledging provided the nest is not depredated or otherwise harmed. The Field Sparrow is a poor host for the cowbird. In Iowa, only 3.4% of cowbird eggs produced a fledgling; 11.5% of Michigan eggs produced a cowbird fledgling. Parasitism rates vary considerably geographically, from 0-80%. Parasitism rates are affected by local cowbird abundance, landscape characteristics, proximity to woodlands and woody stems, and nest placement. In 2 areas in Missouri, the parasitism rate was 4.6% in an area that was 33.3% forested and 11.3% in an area with 70% forest cover. The cowbird was rare at the first site and an

order of magnitude more abundant at the second site. In Illinois and Missouri, the parasitism rates were 52.1% and 11.1% respectively; the density of cowbirds was much higher in Illinois. The cowbird tends to avoid landscapes dominated by grasslands and is more common in partially forested landscapes. It avoids landscapes that are almost completely forested. The cowbird is often concentrated near wooded areas because there is a greater density of potential hosts and bird density is higher in woodlands than grasslands. In Illinois, the mean distance of parasitized nests from woodland was 13.4 m and all but 2 were within 26 m. In Missouri, the probability of parasitism decreased with distance to the nearest tree, potential vantage points for cowbirds. In Michigan, 39% of nests in common juniper were parasitized compared with 28% in other nest substrates. In Indiana, 2 of 18 nests (11.1%) that were on the ground or in ground cover were parasitized; 0 of 43 elevated nests were parasitized. In Ontario, 63 of 378 nests (16.7%) were parasitized. Three of 10 nests (30.0%) in a Minnesota Christmas tree plantation were parasitized. In 3 Missouri studies, 14%, 11.1%, and 4.6% of nests were parasitized. In Georgia and South Carolina, 0 of 10 nests were parasitized. In extensive grassland habitat in Kentucky and Tennessee, 3 of 276 nests (1.1%) were parasitized. In different Illinois studies, 16 of 147 nests (10.9%), 6 of 93 nests (6.4%), and 37 of 71 nests (52.1%) were parasitized. Other parasitism rates include 69 of 141 nests (48.9%) in Kansas; 0 of 15 nests in New York; 16 of 20 nests (80.0%) in Iowa; 0 of 23 nests in West Virginia; 51 of 159 nests (32.1%) in Ohio; 2 of 946 nests (0.2%), 1 of 96 nests (1.0%), and 9 of 57 nests (15.8%) in Pennsylvania; and 182 of 664 nests (27.4%) in Michigan (Best 1974, 1978; Buech 1982; Burhans and Thompson 1998; Burhans et al. 2001, 2010; Carey et al. 2020; Evans 1978; Galligan et al. 2006; Giocomo et al. 2008; Hahn and Hatfield 1995; Kilgo and Moorman 2003; McChesney and Anderson 2015; Nolan 1963; Peck and James 1998b; Peer et al. 2000; Rivers et al. 2010; Strausberger and Burhans 2001; Walkinshaw 1939b, 1945; Walkinshaw in Austin 1968; Wray et al. 1982).

The most significant limiting factor for the Field Sparrow is availability of suitable nesting habitat, and habitat quantity is declining. Its shrubby habitat is frequently converted to other land uses such as agriculture and urban development. Creation of larger farm fields coupled with removal of hedgerows plus cleaner farming practices that leave minimal undisturbed areas have reduced habitat availability. Habitat suitability may be affected by natural succession; mowing, grazing, and other agricultural practices; and burning. Habitat loss is likely to continue resulting in further declines of the Field Sparrow (Carey et al. 2020; Petter et al. 1990; Walk et al. 2011).

Preferred Field Sparrow habitat is ephemeral in nature due to natural succession. When an agricultural field is abandoned, it remains unsuitable for the first year or 2 when it is dominated by annual plants. Habitat becomes more suitable as grasses and perennial herbaceous plants become established and becomes optimal when the field is invaded by scattered shrubs and saplings. Once woody stem density increases, the area becomes less attractive, and it is unsuitable once shrubs or saplings form a dense canopy. In clear-cuts in New York, the Field Sparrow appeared 2 years after the cut, peaked 3 years after cutting, and was essentially extirpated by 9 years after cutting (Keller et al. 2003). Stauffer and Best (1980) considered it to have low tolerance for habitat alteration. They predicted that it would disappear if all woody vegetation was removed and increase if woody vegetation was reduced to narrow strips, if the woody canopy was partially removed, or if the woody canopy was partly removed and shrubs and saplings were thinned.

The Field Sparrow tolerates light grazing by cattle and native ungulates. Heavy browsing that kills shrubs and saplings or makes the ground flora short and sparse is detrimental and may make the habitat unsuitable (Dechant et al. 2002g).

Cutting hay in fields used for nesting is detrimental. Prior to mowing in Arkansas hayfields, nest survival rates were similar. In fields cut 18-23 May, the nest survival rate was 0% except for 2 nests in corners of fields that were not mowed. Only 2 of 54 nests (3.9%) were destroyed when hay was cut later (7-14 July). Only 3 nests per km^2 were initiated in the 39 days following early mowing compared with 18 per km^2 in unmowed fields and 13 per km^2 in late-mowed fields during the same period (Luscier and Thompson 2009). In Iowa, the Field Sparrow nested in grassed waterways that were mowed the previous year. In Ohio, it used fallow fields, pasture, and small-grain fields grown in strips between idle croplands. In Iowa, it nested in soybean fields that were not tilled in spring or autumn and that contained year-round crop residues. Fields that were tilled in spring were not used. In Illinois, unmowed grasslands were selected over those that were high-mowed, leaving the vegetation more than 30 cm tall. In New York, fields that were mowed annually were avoided; fields were used 2-16 years after mowing (Dechant et al. 2002g). In Illinois, Graber and Graber (1963) observed large declines of Field Sparrows nesting in orchards from 1907-08 to 1957-58. In the earlier period, grasses and herbaceous species were allowed to grow in orchards but there was a tendency to mow understorey vegetation in orchards during the later period.

The effects of fire on the Field Sparrow vary depending upon timing of the burn and the intensity and frequency of burning. Intensive fires that kill woody vegetation are detrimental, unless there was excessive woody growth prior to the fire. Areas that are burned frequently have limited residual vegetation from previous years. Vegetation litter is preferred nesting substrate early in the season. Frequent burns simplify habitat heterogeneity and inhibit growth of woody vegetation. In Illinois, a prescribed burn was undertaken in grassland and shrubland habitat. After the fire, usage of shrubby habitat was higher than expected and the opposite was true for grassland and shrub-woodland habitats. Fire resulted in the preferred habitat being used more intensively. Females showed an aversion to nesting in burned areas due to the lack of cover but plant regrowth occurred in time for renesting. Some females built nests in patches of grass litter that had escaped the fire, some of which were only a few centimetres wide. Adults foraging for nestlings shifted their activities from woodland to open habitat. The fire made more grass seeds available because they were formerly hidden under the grass litter. It was concluded that infrequent fires were beneficial, allowing establishment of shrubby areas, retarding succession to forest habitat, and promoting edges and habitat heterogeneity. Frequent and complete burns would eliminate woody vegetation and the Field Sparrow. In another Illinois study area, it preferred areas that had been burned previously but was absent 5 or more years after a burn. Another Illinois study determined that its abundance was negatively correlated with prescribed burns. It preferred grasslands in later successional stages that had not been disturbed for several years. In Wisconsin, its density was correlated with the proportion of area that had been burned. In Kansas, it was absent in areas that were burned annually, probably because they did not support shrubs (Best 1979; Dechant et al. 2002g; Glass and Eichholz 2023; Walkinshaw 1945).

Predation is a significant limiting factor in the Midwestern United States where snakes are abundant. Many populations in this region do not appear to be sustainable due to high levels of predation. Predation rates have not been studied in Ontario, but are probably considerably lower because the diversity and abundance of snakes is considerably lower here. Nest placement and habitat may affect predation rates, but it is probable that these variables are site specific. In Michigan, nests in common juniper were significantly more successful than those in other locations. Predation rates in junipers were 12% during incubation and 15% during the nestling period compared with 57% and 49% respectively for other nests (Evans 1978). In Kentucky and Tennessee grasslands, predation rates were higher in smaller fields because these had more small trees per unit area that might provide perches for predators (Giocomo et al. 2008). Nest height may affect predation rates. In Indiana, higher nests had lower success rates, but only in grassland habitat. In Illinois, snake predation occurred at all heights but was most prevalent 16-30 cm above ground; predation by mammals was restricted to nests 25-60 cm from the ground. Nestlings fledged most frequently from nests located either close to the ground or at higher heights because of the foraging patterns of predators. In Missouri, higher nests were less likely to be depredated. All nests at heights above 3 m fledged young, but these were unusually high nests (Best 1978; Burhans et al. 2002; Galligan et al. 2006). Habitat type may affect predation rates. In Illinois, mammalian predation was significantly less for nests in grass litter and higher than expected in forbs, trees, and shrubs. Nests in large expanses of tall grasses never suffered from mammalian predators but predation by snakes was constant in all habitat types (Best 1978). In Missouri, higher predation rates occurred in bottomland sites than in upland old fields and pastures. Predation increased with increasing coverage by coralberry (Burhans et al. 2002).

McChesney and Anderson (2015) studied the response of the Field Sparrow to Morrow's honeysuckle. This is a nonnative invasive shrub that grows in open fields and in the understorey of forests. Nests in honeysuckle had lower survival rates as did nests where there was high coverage by honeysuckle. Fecundity decreased rapidly as more nests were built in honeysuckle but the amount of honeysuckle within the general area was a greater factor in reducing nest survival. Increasing use of honeysuckle as a nesting substrate may be because it leafs out much earlier than other shrubs and trees, thus appearing to be a high-quality nesting site.

In Texas, the Field Sparrow decreased where DDT was used to spray ticks. In New York, it did not breed for 18 years in a field where vegetation was removed by a single application of 2, 4, 5-T and kerosene. It appeared to be unaffected when shrubs were sprayed with carbaryl (Dechant et al. 2002g).

In West Virginia, the Field Sparrow demonstrated no significant response to well pads, access roads, and pipelines (Farwell et al. 2019).

Cold, rainy, or snowy weather may result in death of nestlings due to exposure or starvation. The nest is not securely anchored in trees and shrubs and may be tipped over during periods of heavy winds. The Field Sparrow is often killed by cars on roads; females are vulnerable to being killed by cats while they are on the nest (Carey et al. 2020; Walkinshaw 1936; Walkinshaw in Austin 1968).

Dechant et al. (2002g) recommended providing shrub-dominated edge habitat adjacent to grassland or providing grassland with a shrub component, both of which must include dense grass

and moderately high litter cover, and avoiding disturbances that completely eliminate woody vegetation.

Price (2004) predicted that the breeding range of the Field Sparrow might expand in southern Ontario if the average summer temperature increased by 2°C.

Status

The Field Sparrow may have reached its peak of abundance in Ontario and the northern United States during the mid-19th century when Europeans deforested the landscape (Carey et al. 2020; Walkinshaw in Austin 1968). McIlwraith (1894) reported that it was sparingly distributed in southern Ontario, which formed the northern extent of its range. In Elgin County, it was a tolerably common summer resident in 1891 but was uncommon in 1954 and 2000 (Lancaster et al. 2004). It was scarce in the Milton area in 1906. In the late 1920s, it was much scarcer in the Toronto area than it had been in the previous 2 decades. This was attributed to declines at the northern extent of its range. By the 1950s and 1960s, it was common in the Hamilton area, and continues to be so (Curry 2006). In 1909, it was fairly common in the Kingston area, where it continues to be common (Weir 2008). Baillie and Harrington (1937) concluded that the Field Sparrow was an uncommon and local breeder in southern Ontario north to Muskoka District, northern Frontenac County, and Ottawa. Mills (1981) stated that it had recently expanded its range northward to Lake Nipissing. Algonquin Park originally had much more suitable habitat for the Field Sparrow in the form of logged areas, burns, and settlements. It was not documented until 1960 but has been reported regularly since 1967 (Tozer 2012). The first atlas confirmed that the breeding range of the Field Sparrow included the area south of the Canadian Shield and the southern portion of the Shield with scattered records north to Lake Nipissing and Sudbury; there were also scattered records on Manitoulin Island. It was absent from the urbanized area of Toronto and much of the heavily forested portion of the southern Shield. It was common in areas of suitable habitat (Knapton in Cadman et al. 1987). James (1991) considered the Field Sparrow a common summer resident north to southern Georgian Bay and Ottawa, rare north to Manitoulin Island and Lake Nipissing, and a straggler north to the north coast.

The second atlas revealed that the distribution of the Field Sparrow had not changed significantly since the first atlas. Isolated breeding evidence was obtained for areas further north than during the first atlas near Sault Ste. Marie, Chapleau, and 100 km north of Cochrane. These latter 2 records were the only ones from the Boreal Forest Region. Its probability of observation decreased significantly between atlases province-wide, in the Carolinian Forest Region, and the Shield portion of the Great Lakes–St. Lawrence Forest Region. Declines in the south may be due to intensified agricultural practices; those in the Shield may be due to natural succession. There were several areas of high abundance. The most extensive area was along the southern edge of the Shield, including the Frontenac Axis and Prince Edward County. This area contains rock barrens, abandoned farmland, and red cedar savannahs on the Napanee Plain. Other areas of high density included the Carden Plain, the Flamborough Plain and Galt and Paris moraines, river valleys and sand plains from Lake Erie northwest to the Grand Bend area, and the eastern Norfolk Sand Plain (McLaren in Cadman et al. 2007).

Hanberry and Thompson (2019) compared Breeding Bird Survey (BBS) trends and forest composition over time in the eastern United States. They attributed the Field Sparrow's decline in

part to the reduction in the amount of early successional habitats and increase in the amount of closed-canopy forests. BBS results indicate annual decreases of 1.85% for Canada and 1.67% for Ontario for 1970-2021 and 0.514% for Canada and 2.06% for Ontario for 2011-21 (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

If the female initiates a second brood, the male cares for the first fledglings. If both adults feed the fledglings, brood division often occurs. For the first 1-3 days, the fledglings remain near the nest in tall grass cover and 3 or 4 days later may hide in both grasses and shrubs. One brood remained within a few metres of the nest for the first day, was 21 m distant the following day, and 2 were 61 and 82 m from the original location on the third day after fledging. The family group remained intact for the next 2 weeks and often foraged in a dry pond 137 m from the nest. During this period, the young and accompanying adults may trespass in other territories without being challenged. Family groups eventually mingle together to form larger flocks and may join flocks of Song Sparrows and Dark-eyed Juncos. Young become independent when they are 26-34 days old. Flocks tend to gather in dense thickets in the vicinity of the nest and may disperse to other similar habitats. They may also remain in favoured foraging habitat until the onset of autumn migration. Habitat used during this period may be very similar to breeding habitat. The Field Sparrow has been documented in clear-cuts 3-7 years old in Pennsylvania and Ohio. In Pennsylvania, family groups were common on a shrubby hydro right-of-way but absent in the adjacent forest (Carey et al. 2020; Fitch 1958; Stoleson 2013; Vitz and Rodewald 2006; Walkinshaw 1939b, 1945; Walkinshaw in Austin 1968; Yahner et al. 2002).

During the postfledging period in September, birds roosted at night in small trees and shrubs that were still heavily covered with leaves (Walkinshaw in Austin 1968). In Michigan, Adams and Brewer (1981) captured Field Sparrows in autumn in marshes, crop fields, and mature floodplain forest. Of 475 birds, 362 were juveniles, 71 were adults, and the age of 42 was unknown. Nine birds were recaptured during the subsequent breeding season. These included 5 juveniles, with a return rate of 1.4%, greater than reported at natal areas, suggesting that some juveniles select their breeding location prior to autumn migration. If returning adults find that their previous breeding habitat is unsuitable, they may move to sites they explored the previous autumn.

MIGRATION

The Field Sparrow migrates leisurely in both spring and autumn, spending days or weeks in the same area before moving on. In North Carolina, some males remained all winter but all females migrated south, suggesting that males winter further north than females. Birds migrate at night in small flocks but arrive on the breeding grounds a few at a time instead of all at once. Cold weather may delay the timing of spring migration. One banded at Don Mills was recovered in Texas; another banded near Cayuga was recovered in Arkansas (Black and Roy 2010; Brewer et al. 2018; Carey et al. 2020; Fretwell 1968; Walkinshaw in Austin 1968).

Males arrive on the breeding grounds 1-3 weeks before females and the earliest arrivals tend to be the oldest males (Best 1977a; Evans 1978; Walkinshaw in Austin 1968). In Ontario, a few arrive in late March, but most arrive in the second and third weeks of April with most passing through from mid-April to mid-May. Most leave the southern Shield from mid-September to late October. In the

south, migration occurs during the same period, with an influx of northern birds in the first half of October. A few remain into the first week of November (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

During spring migration, the Field Sparrow typically occurs singly but in autumn it may congregate in small loose flocks or within flocks of other sparrow species. In spring in Algonquin Park, it is occasionally found among flocks of migrating sparrows along road margins, in fields, and within campgrounds. Migration habitat is similar to that used during the breeding season and winter. It may also frequent some habitats that are avoided at other times, such as suburban yards. During spring migration in Pennsylvania, it was significantly more abundant in shrubby habitats than in forests. Detections per 100 m were 0.002 in forest and 0.130 in shrubs; captures per 1,000 net-hours were 0 in forest and 4.9 in shrubs (Carey et al. 2020; Smith and Hatch 2008; Tozer 2012; Walkinshaw 1936).

Carey et al. (2020) concluded that the Field Sparrow was an infrequent victim at towers during migration, but Walkinshaw (in Austin 1968) noted that it did strike television towers and airport ceilometers beams at airports. Although few may be killed striking tall structures, it is highly vulnerable to striking low structures during migration. Throughout the United States, it was not among the top 20 species that struck low-rises or high-rises, but was highly vulnerable to striking residences 1-3 stories high. It was 48.3 times more likely to strike a residence than average and was the eighth most vulnerable species (Loss et al. 2013).

James (1991) considered the Field Sparrow a common migrant that occasionally wanders north as far as Hornepayne and James Bay. It is a rare migrant in the Canadian Shield but may be a locally common migrant south of the Shield.

Hussell et al. (1992) reported that captures of migrant Field Sparrows at Long Point increased at a nonsignificant rate of 0.9% per year 1961-88. Trends by period were: 1961-70, +1.2% per year; 1970-79, −7.5%; and 1979-88, +8.5%.

WINTER

The winter range of the Field Sparrow is strongly determined by temperature and it can only acclimatize to the cold to a limited extent. The wintering area includes all of the eastern United States where the average minimum January temperature does not fall below −7°C, with some exceptions along major rivers in Nebraska, Colorado, and Indiana. Areas of high winter abundance occur where the temperature rarely drops below the freezing point (Root 1988). Ontario is north of the normal wintering range.

Winter habitat is very similar to breeding habitat; food availability may affect the suitability of an area to support wintering Field Sparrows. In Elgin County, it is typically observed in shrubby habitats. In North Carolina, it wintered in a field dominated by Virginia broomsedge planted with pines less than 1.8 m tall, but not in a nearby field dominated by fescue grass and bush-clover planted with pines less than 0.9 m tall. Birds that bred in the wintering habitat had higher fat levels than those that wintered elsewhere. Elsewhere in North Carolina, it favoured fields dominated by hairy crabgrass or horseweed and moved to other fields once these were depleted. In Maryland, it remained where it had bred and preferred areas with broomsedge. In Virginia, it wintered in an

agricultural field that had been fallow for 3-5 years and was dominated by broomsedge, asters, goldenrods, crabgrass, pokeweed, and deciduous saplings. Brush stations were created by placing 5-7 saplings 2-3 m tall in some plots. Plots with brush were used significantly more than those without brush. In North Carolina, it was found only in unmanaged field edges and not in fallow fields, narrow field borders, or in mowed field borders (Beck and Watts 1997; Carey et al. 2020; Fretwell 1968; Graber and Graber 1963; Judd 1901; Lancaster et al. 2004). In Maryland, its winter density was 0 in areas that had been mowed in autumn and 113 per km^2 in unmowed buffers. In winter, it uses herbaceous areas for foraging, roosting, and escape cover and autumn mowing removes this habitat (Blank et al. 2011). In Kentucky, Arkansas, and Mississippi, there were no differences in its abundance in row-crop fields with or without buffers of native grasses and forbs (Evans et al. 2015).

The Field Sparrow exhibits no territoriality in winter. No information is available on winter site fidelity but nonmigrant birds often stay year-round in the same place. In North Carolina, there was considerable dispersion from field to field. No more than 120 were ever in the studied field at any given time, but 178 were handled overall and less than 40% of birds were banded. In 1 winter, all birds migrated and the wintering birds present were those that had migrated from other areas. In Illinois, probably drifted further south as the winter progressed. Birds move to other fields if food resources become scarce in the original field (Carey et al. 2020; Fretwell 1968; Graber and Graber 1963).

In winter, the Field Sparrow frequently forages in flocks, either with conspecifics or other sparrows. Individuals often occur in Chipping Sparrow flocks and are also often associated with Song Sparrows, American Tree Sparrows, and Northern Cardinals. The Field Sparrow forages on the ground or in vegetation less than 1 m tall, mostly in open grassy or shrubby fields. In Maryland, it foraged almost exclusively from the culms of panic grass. It often foraged in open habitat 50-75 cm from cover. Its distribution on plots in Virginia was highly skewed to areas where brush had been provided. Its relative abundance in plots manipulated by adding brush or food was 80 where there was food and brush, 40 where there was food but no brush, 8 where there was brush but no food, and 1-2 where there was no brush or food. Food provided on trays was depleted at 3 times the rate where there was brush than where there was no brush (Allaire and Fisher 1975; Beck and Watts 1997; Carey et al. 2020; Dunn and Tessaglia-Hymes 1999; Judd 1901; Root 1988).

The winter diet of the Field Sparrow consists almost exclusively of seeds. Seeds found in stomach samples in Texas consisted of 29.1% crabgrass, 2.5% panic grass, 0.2% foxtail, 5.1% spinifex grass, 3.1% windmill grass, 46.0% grass #1, 14.0% grass #2, and 5.0% unidentified. Field and Chipping sparrows had similar diets, but they differed more in winter than in summer and autumn (Allaire and Fisher 1975). Pulliam and Enders (1971) examined the diet of the Field Sparrow from October to March in North Carolina. It consumed seeds 0.5-2.5 mm in length, with most about 1.5 mm. Two thirds of foraging birds fed from a standing plant while they were standing on the ground, one third fed while perched on a plant, and none fed from the ground. As the winter progressed, it initially fed only in horseweed fields, then in aster fields, and finally in broomsedge fields. The most abundant seed in the horseweed field was crabgrass and it fed almost exclusively on it, indicating that it was the preferred seed. Seeds were scarce by mid-March and there was a significant correlation between the abundance of seeds and Field Sparrows. It was concluded that it was

limited by winter food supplies. In winter, it is not a common feeder visitor, either in the number of feeders visited or the frequency of sightings. More feeders are visited in midwinter and spring and its abundance declines somewhat throughout the winter. Favourite feeder foods are mixed seeds, cracked corn, and probably millet. Infrequent choices include striped and black oil sunflowers, water, canary seed, and milo (Dunn and Tessaglia-Hymes 1999).

Graber and Graber (1979) analyzed the effects of a severe winter storm on the Field Sparrow in Illinois. Densities per km^2 prior to the storm were 7.5 in bottomland forest, 0 in upland forest, and 9.5 in urban residential. No birds were observed after the storm and the authors believed that it had suffered 100% mortality.

James (1991) considered the Field Sparrow rare in winter in the south north to Manitoulin Island and there are records of winter vagrants as far north as Lake Superior.

Fox Sparrow

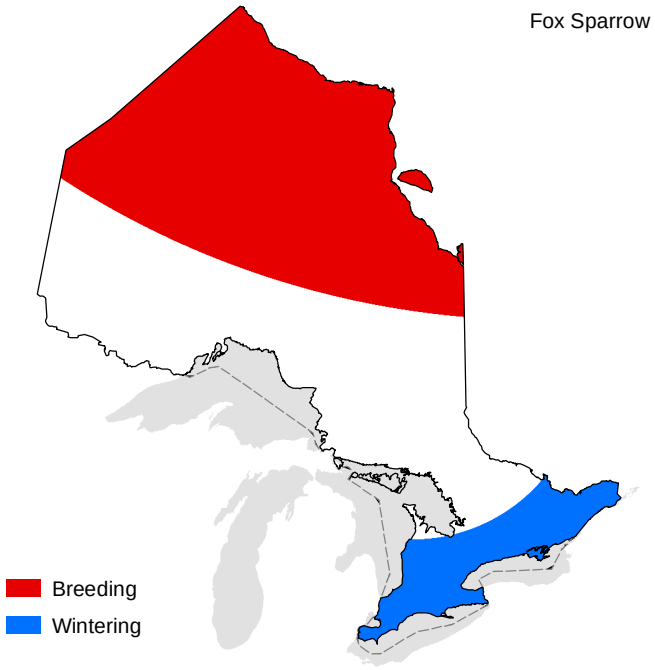
Passerella iliaca

BREEDING SEASON

Habitat Requirements

Ontario Fox Sparrow nests were in a balsam poplar thicket; in a muskeg with stunted tamarack and black spruce; in an open area interspersed with ponds and with growths of black spruce, tamarack, poplar, dwarf birch, and willow; and in a black spruce muskeg with growths of Labrador tea and swamp laurel (Peck and James 1987).

Along the Hudson and James bay coasts, the Fox Sparrow always occurred in deciduous thickets and was common in willow thickets at York Factory (Manning 1952). From the Pickle Lake area northwestward, McLaren and McLaren (1981) observed it in deciduous forest, coniferous forest with an understorey, and mixed, coniferous, and deciduous scrub. It was absent in coniferous forest without an understorey, heath, and tundra. Wilson and McRae (1993) reported several territories in areas of large willow scrub on islands in the Moose River near Moosonee. On the east side of James



Bay in Quebec, it was most frequent where there was a mixture of alder patches and open or stunted spruce, or dry rocky ground. It was not seen in tall patches of alder growing in otherwise barren areas (Manning and MacPherson 1952). Rising (in Cadman et al. 1987) concluded that it nested in Ontario in moist rank growths of black spruce, tamarack, poplar, birch, and especially willow and alder. McLaren (in Cadman et al. 2007) characterized its Ontario habitat as dense stands of stunted conifers in taiga areas and dense thickets of conifers, willows, birches, and alders in regenerating burns along shores of lakes, rivers, and streams. It tends to avoid open tundra, occurring only locally in riparian shrub thickets.

The most important habitat requirement for nesting for the Fox Sparrow is dense shrubby cover where it can nest and scratch for food while remaining concealed. Early in the season, patches of ground that are snow-free are important and are incorporated within territories (Terrill in Austin 1968; Threlfall and Blacquiere 1982). In Newfoundland, it nests in balsam fir–black spruce–white spruce, balsam fir–black spruce, and balsam fir forests; regenerating areas of balsam fir and black spruce; wind-blown stunted forests and scrub forests; successional old fields, clear-cuts and burns; rocky and alpine coastal barrens; brushy forest edges; in mixed farms and wasteland at edges of towns; and historically in gardens in villages. On an island, habitat consisted of climax balsam fir–black spruce–white spruce forest with mountain maple, white birch, American mountain-ash, and alder in open places, with a dense understorey of spinulose woodfern, skunk currant, mosses, bunchberry, and starflower. It used areas with high white birch densities in the shrub layer; it used areas of low birch density on the mainland. Occupied areas on the island were significantly more open with less canopy cover but a taller canopy (8 m compared with 5 m) than mainland habitat. Despite the differences in habitats occupied on the island and mainland, there were no significant differences in its densities in the 2 areas. In 1 Newfoundland study, habitat consisted of harvested and uncut balsam fir and black spruce forest. There was no difference in its probability of occurrence in the 2 landscapes. Its probability of occurrence declined with increasing amounts of forests in both landscapes. In harvested landscapes, it had 80% occurrence at 20% tree cover, 50% occurrence at 40% tree cover, and 20% occurrence at 100% tree cover. In natural landscapes, it had 70% occurrence at 20% tree cover, 90-100% occurrence at 40% tree cover, and 20% occurrence at 100% tree cover. At the landscape level, it was negatively correlated with the amount of tree cover, Within a radius of 12.5 m, it was positively correlated with the amount of scrub, bog, regeneration, recent cut, and dense gnarled conifers. It was considered an edge species. Another study that included both natural and harvested landscapes captured 62% of Fox Sparrows in harvested landscapes.

Other researchers considered it ubiquitous rather than a forest generalist, a forest-interior species, a riparian species, or an open-edge species. Another Newfoundland study in balsam fir stands determined that it was associated with young stands with some deciduous cover on nutrient-poor sites. Young stands (40-60 years old) had a more closed structure with higher tree and small tree density, fewer gaps, more small deciduous trees, less varied tree height profile, taller small trees, and less dead wood on the ground than more mature stands. In Labrador, it preferred scrub spruce and rather open spruce-fir forests, but also occupied pockets of black spruce on barrens, fringes of swamps, and deciduous forests in river valleys (Taylor and Krawchuk 2006; Terrill in Austin 1968; Thompson et al. 1999; Threlfall and Blacquiere 1982; Vassallo and Rice 1981; Weckstein et al. 2020; Whitaker and Montevecchi 1997, 1999; Whitaker et al. 2008).

In Quebec, the Fox Sparrow breeds in coniferous and mixed forests where it prefers thickets and edges; it also occurs in shoreline scrub. It rarely strays from low dense tree and shrub cover, including shrubby woodlands and streamside thickets of willow and alder. It favours rocky shores, particularly on islands and the coast where there is stunted and gnarled coniferous growth that is almost impenetrable. It also occurs in clear-cuts regenerating to conifers. In 1 study area, it was absent in recent clear-cuts and burns where the vegetation was less than 2 m tall, absent in logged areas with saplings 2-5 m tall, significantly more abundant in logged than burned forest where the vegetation was 5-11 m tall, and absent in stands burned 120 and 200 years previously. The eastern part of its Quebec range is characterized by higher elevation, a damp climate, more abundant precipitation, and forest cover consisting primarily of balsam fir with some yellow birch, white birch, white spruce, or black spruce. It is particularly abundant in the stunted coniferous forests of the islands and shorelines of the Gulf of St. Lawrence. On the Magdalen and Anticosti islands, it is associated with dense coniferous growth in the interior and stunted white spruce along the shorelines. In the lower North Shore, it is attracted to the characteristic alternating patches of stunted forests and open rocky areas. In boreal habitat, it is found in edges and clearings and often nests in regenerating rank dense scrub in mountainous areas. In the Great Whale River area, it is abundant in slightly wet areas vegetated with Labrador tea, other low shrubs, and scattered spruce (Bisson and Limoges in Gauthier and Aubry 1996; Imbeau et al. 1999; Terrill in Austin 1968). In Ungava Bay at the extreme northern extent of its range in Quebec, 1 pair nested in a clump of alders in a dry sandy barren on a bluff about 10 m above the Koksoak River. Habitat adjacent to the opening consisted of an open stunted black spruce forest with an understorey of lichens and mosses (personal observation).

Near Churchill, the Fox Sparrow is fairly common in wet willow thickets and wooded areas. It appears to require large blocks of continuous woodland and is absent in clumps of spruce near the coast (Jehl 2004). In the Prairie Provinces, it was associated with riverine sites where there were willows and alders. It occurred in areas with moderate wetness and nutrient status (Kirk et al. 1996). In the Mackenzie Delta in the Northwest Territories, it is one of the most abundant species where it breeds well beyond the limit of trees (Porsild 1943). In the Yukon, it occurs most frequently in shrubby areas of open forests, wetlands, and burns, and along lakeshores and streams. It inhabits white spruce, white birch, and willow along streams and also nests in alder thickets on hillsides and in ravines, alder and willow within spruce forests, and occasionally in black spruce forests (Austin 1968; Sinclair et al. 2003). In Alaska, it was most abundant in hill or bluff habitat followed by subalpine areas, alpine areas, lowlands, and floodplains and terraces where it did not occur in measurable

densities. Floodplains and terraces were highly disturbed with varied vegetation including tall and low shrubs, spruce forests, deciduous forests, and mixed forests. Lowlands consisted of black spruce woodlands and spruce forests. Hillsides were covered with deciduous forest in previously burned areas and mixed forest in unburned areas. Bluffs were steep slopes rising directly from a river with steppe communities, deciduous and mixed forests, scree, and exposed rock. Subalpine habitats included wet sedge and graminoid meadows with low shrub thickets of willow or birch, tall alder thickets, and spruce forests. Alpine habitats consisted of low or dwarf shrubs, wet graminoid meadows, and exposed rock (Handel et al. 2009).

In boreal forest habitat in New York, Vermont, Maine, Nova Scotia, and Newfoundland, presence of the Fox Sparrow was closely clustered in relation to principal components indicating more specialized habitat requirements. It was restricted to colder high latitude sites, suggesting that it could be adversely affected by warming due to climate change (Ralston et al. 2019).

The 3 Pacific groups of the Fox Sparrow use a variety of habitats, many of which do not occur within its eastern range, but presence of dense shrubby habitat is still essential. In 1 region of British Columbia, a requirement appeared to be damp, but not marshy or swampy, ground with a litter of dead leaves rather than a heavy growth of forbs. It required a dense growth of low shrubs that were mostly willows, with occasional elevated perches for singing. Breeding habitat includes sphagnum bogs; subalpine habitats of spruce, willow, and birch; high elevations where forests have been logged or burned; coastal spruce forests; clear-cuts and early stages of regrowth 5-10 years old where it is often confined to this age class; deciduous thickets, alpine spruce, and fir krumholtz; subalpine meadows and forests; dense tangles of willows and alders near streams and lakes; trembling aspen stands with an understorey of Saskatoon and silverberry; tall old-growth balsam poplar with a dense shrub understorey of prickly rose and red-osier dogwood; and drowned muskeg with standing dead snags and black spruce (Campbell et al. 2001). In British Columbia coniferous forests, Wiebe and Martin (1998) considered it a riparian species during the breeding season. Eighty percent of observations were in riparian willow-alder habitat rather than coniferous forest. In Wyoming, it occupied grassy glades surrounded by a circle of willows 3-3.6 m tall. The Fox Sparrow sang from the tall willows and fed in the grass of the glades and the low willows around them (Salt 1957). In Colorado, its abundance was significantly correlated with willow height. Its relative abundance was 0 at 0 cm willow height, increasing linearly to 1.0 at 200 cm height; it preferred to reside and nest in taller shrub habitat (Olechnowski and Debinski 2008). In California, it nested in both burned and unburned forest but was more common in burned areas (Bock and Lynch 1970).

Two Ontario nests were on the ground, one at the base of a sphagnum moss hummock and the other under a small black spruce. Two other nests were 0.5 m and 0.6 m from the ground, with the higher nest in a small black spruce and the other between a balsam fir and a stump (Peck and James 1987).

Nests may be either on the ground or elevated a short distance above it in a shrub or tree. The incidence of elevated nests decreases as the season progresses; earlier nests may be elevated to avoid snow or wet ground. In Newfoundland from 27 April to 13 May, 75.0% of nests were elevated compared with 63.6% 14-30 May, 33.3% 31 May to 16 June, and 0% 17 June to 3 July. Ground nests are under conifers, in clumps of willows or alders, among roots of upturned stumps, on grassy

hummocks, or under herbaceous plants. Most elevated nests are in conifers, especially spruce and balsam fir, but the Fox Sparrow has also nested in willow, yellow birch, currant, and other deciduous species. Most nests are 1 m or less from the ground, but have been reported 4.6-6.0 m up. One nest was on a dead branch leaning against a spruce sapling, 60 cm from the ground. Two nests were in white spruce 1.5 m from the ground. Some females build more than 1 nest before selecting one to lay eggs in (Austin 1968; Burns and Hackett 1993; Campbell et al. 2001; Linsdale 1928; Mailliard 1921; Ryan 1974; Sinclair et al. 2003; Terrill in Austin 1968; Threlfall and Blacquiere 1982; Weckstein et al. 2020).

The Fox Sparrow is territorial but very limited information is available on its territory size. Three territories in regenerating balsam fir–black spruce on the mainland of Newfoundland were about 1 ha in size. Territories on a nearby island averaged 0.25 ha (Threlfall and Blacquiere 1982).

No information is available on natal philopatry and limited information exists on adult site fidelity. In Newfoundland, 12 of 51 adults (23.5%) returned the following year. Nine (75.0%) were recaptured in exactly the same location they were captured the previous year; the other 3 were found within 50 m of their banding locations (Threlfall and Blacquiere 1982).

Limiting Factors

Males establish territories within a day of arriving on the breeding grounds, even when they return 3 weeks prior to snowmelt. Pair formation occurs within a week of territory establishment. Nests typically take 2-3 days to construct, but 1 was built in a single day. Egg laying begins at the rate of 1 a day as soon as the nest is complete. Incubation may begin with the laying of the last egg, start before the clutch is complete, or start with the laying of the first egg. The incubation period has been reported as 12 days 4 hours to 14 days, with hatching spread over a period of at least 35 hours. The nestling period is 9-10.5 days; young may not be capable of flight when they leave the nest (Linsdale 1928; Mailliard 1921; Ryan 1974; Threlfall and Blacquiere 1982; Weckstein et al. 2020).

Double brooding has been confirmed only in Alaska but has been suspected in British Columbia, Quebec, Newfoundland, and the Magdalen Islands. One Newfoundland study concluded that there was no evidence of second broods. The long breeding season and observations of fresh eggs late in the season suggest that double brooding may be widespread. If the first nest is lost, the Fox Sparrow readily renests in a new nest that may be started 2-4 days after the first one is lost. Ontario nests contained either 3 or 4 eggs. Clutches elsewhere may contain 2-5 eggs. In British Columbia, 64% of clutches contained 3 or 4 eggs. Mean clutch sizes were 4.11 eggs in Alaska and 3.24 eggs in Newfoundland (Campbell et al. 2001; Peck and James 1987; Terrill in Austin 1968; Threlfall and Blacquiere 1982; Weckstein et al. 2020).

The age at first breeding is unknown. No information is available on the mating system or duration of the pair bond (Weckstein et al. 2020).

The Fox Sparrow forages predominantly on the ground in either leaf litter or bare ground using a double-scratch technique, moving both feet simultaneously to disturb the substrate. It may also glean insects off vegetation and occasionally flies from a perch to capture flying insects (Terrill in Austin 1968; Weckstein et al. 2020).

Young are fed insects almost exclusively, especially caterpillars. Adults are thought to subsist mostly on insects during the breeding season. The breeding season diet consists of weevils and other beetles, fly larvae, caterpillars, ants and bees, scale insects, spiders, millipedes, and small molluscs. Along the coast of Newfoundland and Labrador, it feeds abundantly on minute crustaceans and may peck at dead and dying fish. Some vegetable matter may be consumed in summer including seeds and fruits of sedges, raspberries, cinquefoils, buttonweed, and juneberries (Terrill in Austin 1968; Threlfall and Blacquiere 1982; Weckstein et al. 2020). On an island off the coast of British Columbia, Hipfner et al. (2013) used stable isotopes to compare the diets of Song and Fox sparrows. The 2 species could compete for food resources because they were the most abundant songbirds and only sparrows on the island and both fed predominantly on insects, fruits, and seeds as well as amphipods captured in the intertidal zone. The Fox Sparrow was dominant to the Song Sparrow in interspecific encounters for food. The Fox Sparrow fed at a lower trophic level, probably consuming more plant material and less animal material than the Song Sparrow. These differences may allow the 2 species to coexist. In May, the Fox Sparrow ate insects almost exclusively in Nevada (Salt 1957). Linsdale (1928) collected 10 stomachs in Nevada. It ate predominantly animal food, with the percentage of animal food in stomachs ranging from 90% to 100% (average 98.1%). The animal food consisted of 70.8% hymenopterans (mostly ants), 15.7% beetles (ground, scarab, and rove beetles, and weevils), 9.9% flies (crane flies and anthomyiid flies), 2.3% small bivalve molluscs, 0.1% spiders, and a trace of caterpillars and millipedes. The vegetation consumed consisted mostly of sedge seeds, but a few cinquefoil and buttonweed seeds were eaten.

There are no records of cowbird parasitism of the Fox Sparrow in the east, where the breeding ranges of the Brown-headed Cowbird and Fox Sparrow do not overlap. There are only 2 records of other subspecies of the Fox Sparrow being parasitized (Weckstein et al. 2020).

There appear to be no significant limiting factors to the Fox Sparrow during the breeding season, but some factors may affect individual birds or local populations. Early nests are vulnerable to being covered by snow during storms. These nests are typically abandoned and a replacement clutch is laid (Threlfall and Blacquiere 1982).

The abundance and distribution of the Fox Sparrow may be affected by logging and human-induced fires (Weckstein et al. 2020). In Newfoundland, breeding season survival rates were slightly lower in harvested than natural landscapes, but not significantly. It appeared to be resilient to moderate levels of clear-cutting (Whitaker et al. 2008). In Alberta, there was no difference in its abundance along seismic lines and pipelines and at well pads than in adjacent forest interior. These energy-sector disturbances appeared to have no effect on it (Bayne et al. 2016).

In the western portion of its range, the Fox Sparrow can be negatively affected by intensive elk grazing, and it may also be affected by moose grazing. Grazing reduces the height of willows, making them unattractive to the Fox Sparrow (Anderson 2007; Olechnowski and Debinski 2008).

In central Quebec and Labrador, DesGranges and LeBlanc (2012) determined that the Fox Sparrow occurred mostly in stands with lower summer temperatures and high rates of summer precipitation. This suggests that it could be adversely affected by climate change in that area.

Status

The first Ontario Fox Sparrow nest was found at Moose Factory in 1860 (Baillie 1958; Peck and James 1987). Manning (1952) considered it common in willow thickets at York Factory. The first atlas demonstrated that it was widespread in the Tundra Zone, Hudson Bay Lowland and the northern portion of the Boreal Forest Region, south to about 70 km north of Cochrane and the Pickle Lake area (Rising in Cadman et al. 1987).

The second atlas indicated that there had been no change in the distribution of the Fox Sparrow. Its probability of occurrence increased significantly province-wide and in the Hudson Bay Lowland and Boreal Forest Region between atlases. The reason for the increase was unclear because there was no significant change in its habitat and northern areas were surveyed by experienced individuals during both atlases (McLaren in Cadman et al. 2007).

POSTFLEDGING PERIOD

All information for the postfledging period is from Newfoundland. Young remain in family groups in or near the natal territory until they are well grown. A male was observed feeding a young in his territory 21 days after it fledged. In late summer, the Fox Sparrow may be seen in groups of 2-6 that include fully grown juveniles and adults. These may feed on dead or dying fish on beaches, or perhaps on insects on the fish (Linsdale 1928; Terrill in Austin 1968; Threlfall and Blacquiere 1982; Weckstein et al. 2020).

MIGRATION

The Fox Sparrow is a nocturnal migrant that usually arrives on the breeding grounds during early morning darkness. Spring migrants may travel together in groups of 8-12 that remain together until migration is resumed. It moves through quickly in spring. It is an early migrant, often appearing when there is still snow on the ground. Snowstorms do not appear to affect the timing of migration; numbers of birds may fluctuate annually but arrival dates are fairly consistent. In Newfoundland, both sexes arrived on the breeding grounds at the same time (Bisson and Limoges in Gauthier and Aubry 1996; Brewer et al. 2018; Terrill in Austin 1968; Weckstein et al. 2020).

In Ontario, spring migrants are often observed in late March but the main movement occurs in the first 2 weeks of April. Migrants may remain south of the breeding range until mid-May, although most leave in late April (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

In British Columbia, the median capture date for juvenile and adult autumn migrants was identical, suggesting that both age classes migrate at the same time. Departures began to occur shortly after the young were out of the nest. In Alaska, approximately 10% of birds undertook part of their moult during autumn migration. In Kansas, a flock of autumn migrants remained at 1 site for 13 days (Benson and Winker 2015; Campbell et al. 2001; Evans Ogden et al. 2013; Fitch 1958).

Migrants occur in the southern Shield from late September to late November, with peak numbers in the second and third weeks of October. In southern Ontario, Fox Sparrows usually arrive in early October and depart in early November, with stragglers to late November (Black and Roy 2020; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

At Delta Marsh in Manitoba, Murphy-Klassen et al. (2005) studied spring arrival dates from 1939 to 2001. The Fox Sparrow's arrival was significantly negatively correlated with mean monthly temperature. It arrived 3.3 days earlier in 2001 than in 1939.

The Fox Sparrow prefers shrubby habitat during migration, but may also occur in open hardwood forests with little to no ground cover. It occurs in swampy thickets, streams bordered by dense herbaceous species or shrubs, thickets near ponds, heavy shrub cover along forest edges, clear-cuts in early stages of regeneration, coastal wind-pruned trees, tamarack and spruce muskeg, bogs, treed floodplains, rocky pastures, hedgerows, weedy grain fields, weedy and shrubby roadsides, and urban and rural gardens. It often occurs near water including estuaries, lagoons, ponds, rivers, lakes, sloughs, and bogs and may occur among beach wrack on marine shores. Autumn migrants may feed more often in open weedy areas instead of within thick cover, but seldom stray far from dense cover (Campbell et al. 2001; Fitch 1958; Linsdale 1928; Terrill in Austin 1968; Weckstein et al. 2020). In British Columbia, migrants inhabited willow-alder riparian habitat but not adjacent coniferous forest (Wiebe and Martin 1998).

During the nonbreeding season, the Fox Sparrow is more omnivorous than during the breeding season. In addition to arthropods, it eats a mix of seeds and fruits and occasionally plant buds. It is probable that most fruit is consumed during autumn migration. If snow is on the ground during migration, it often appears at winter bird feeders. In the eastern United States, 127 stomachs collected during the nonbreeding season contained 86% vegetable matter and 14% animal matter. The vegetable matter consumed by the Fox Sparrow differs from that of most sparrows with fewer grass seeds (1%), less grain, and more fruit and seeds of ragweeds and smartweeds, which comprise about 50% of the diet. Twenty-eight percent of the diet consisted of seeds of berries and fruit skin, including those of blueberries, elderberries, grapes, and blackberry. Blueberries may be an important food source for autumn migrants in alpine areas. It also eats berries of red cedar and pokeweed and buds of peach and pear trees. In April, it began eating millipedes, which constituted 20% of the diet for that month; 10% of the April diet consisted of ground beetles. Two stomachs collected during spring migration in Ottawa contained mostly insects, especially beetles, but also spiders, millipedes, and seeds of gromwell. Birds collected in October in Toronto had eaten witch-hazel buds, beetles, firefly and crane fly larvae, spiders, millipedes, and seeds of hound's-tongue. One in Wisconsin had eaten 50 chinch bugs. Ten stomachs collected in Nevada in May contained 71% hymenopterans and 16% beetles. Two April stomachs were almost completely filled with seeds but contained a few ground beetles (Bisson and Limoges in Gauthier and Aubry 1996; Evans Ogden et al. 2013; Judd 1901; Terrill in Austin 1968; Weckstein et al. 2020).

If it snows during migration, the Fox Sparrow leaves thickets to search for food in places such as streambeds and feeders. Mass mortality may occur during severe snow and freezing rain storms. Severe weather during migration and winter may be its greatest limiting factor (Terrill in Austin 1968; Weckstein et al. 2020).

The Fox Sparrow does not appear to be highly vulnerable to striking objects during migration. At the Lennox generating station chimneys near Kingston, no mortalities were detected out of thousands of birds killed (Weir 2008). In British Columbia, 2 Fox Sparrows were killed at a single house out of 118 mortalities (Campbell et al. 2001).

James (1991) considered the Fox Sparrow an uncommon to locally common migrant. Regional bird books concur with this assessment, except that it is a rare migrant in Niagara Region (Black and Roy 2010).

Hussell et al. (1992) reported that captures at Long Point Bird Observatory declined at a nonsignificant rate of 3% per year 1961-88. Trends by period were: 1961-70, –6.7% per year; 1970-79, +3.2% per year; and 1979-88, +9.5%.

WINTER

Wintering Fox Sparrows tend to remain in small groups that stick closely to their particular bit of cover. Winter habitat includes dense thickets and underbrush on edges of woods, dense willows or tall herbaceous species along streams, and rural and suburban yards that have bird feeders. In California, it occurred close to shrubs, roads, and streams, more distant from trees, and far from fields (Kalinowski and Johnson 2010; Terrill in Austin 1968; Weckstein et al. 2020; Wiebe and Martin 1998).

In Indiana, wintering birds roosted overnight in thick red cedar and yew hedges (Weckstein et al. 2020).

In California, Sandercock and Jaramillo (2002) banded 1,139 juveniles and 493 adults over 12 years to determine winter site fidelity. This study was done on a subspecies that does not occur in the east and is a very short-distance migrant. The recapture rate was 60.3% for juveniles and 49.6% for adults. The probability of survival was 10.8% for juveniles after their first capture, 27.4% for adults after their first capture, and 35.2% for adults in later years. Juveniles may have had higher mortality rates because of competition, poor condition, or greater risk taking. Alternatively they may have migrated to different areas in subsequent years. Migratory sparrows are known to change wintering areas after their first year.

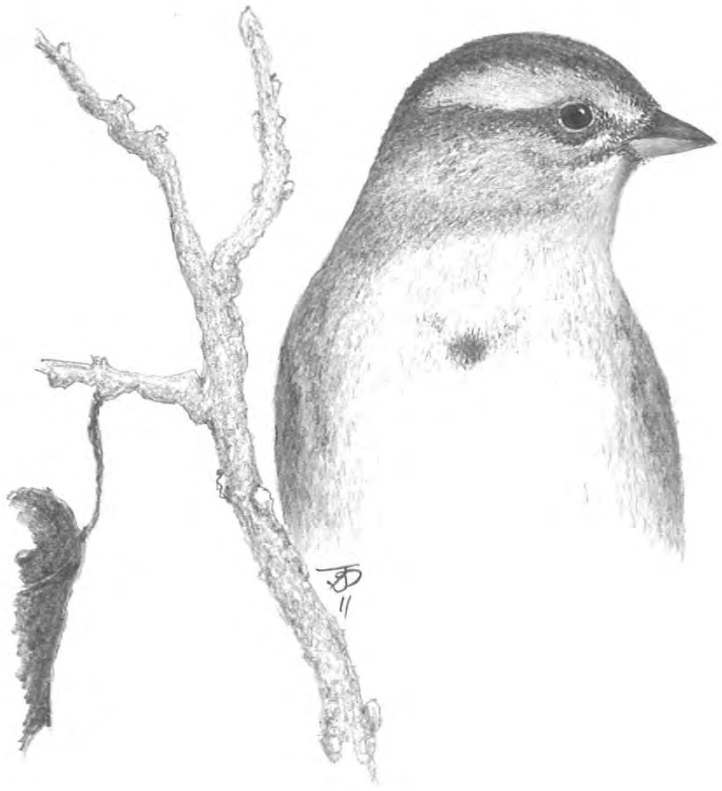
Most observations of Fox Sparrows at bird feeders are of spring migrants with 3 times as many feeders visited in spring than autumn; it also visits feeders in winter. It typically occurs for only a few weeks at a given feeder. It eats numerous berries in winter. At feeders, it often ignores sunflower seeds and selects millet or cracked corn instead. It also prefers mixed seeds and milo. It infrequently takes sunflowers, niger, suet, water, and possibly canary seed and whole corn (Dunn and Tessaglia-Hymes 1999).

Severe weather has the potential to decimate wintering populations. In British Columbia, the population declined 63% during a period of severe weather. The decline was attributed to mortality rather than dispersal (Weckstein et al. 2020). Thousands died in Massachusetts during the severe winter of 1894-95 (Linsdale 1928).

James (1991) considered the Fox Sparrow occasional and rare during winter in the south, north to Bruce and Renfrew counties.

American Tree Sparrow

Spizelloides arborea

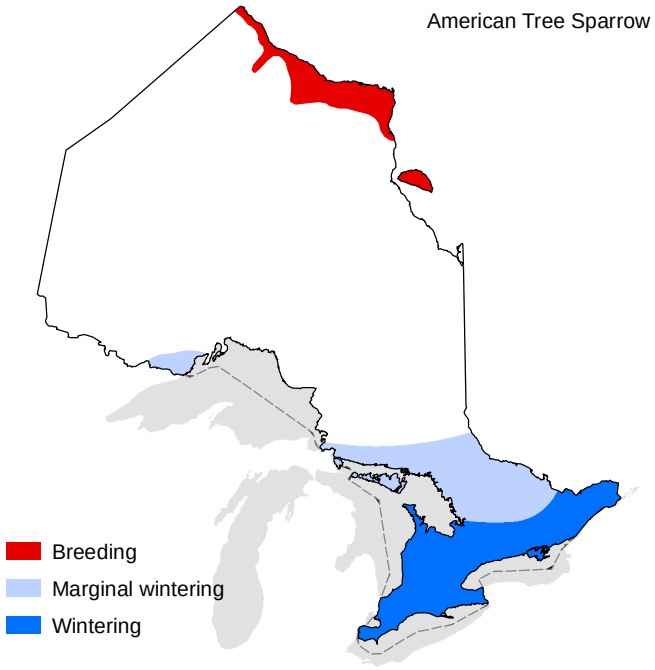


BREEDING SEASON

Habitat Requirements

In Ontario, the American Tree Sparrow nests near the treeline north to the Hudson Bay coast. Nests were in tundra or on old beach ridges covered with lichens, herbaceous species, and small shrubs (Peck and James 1987, 1998b).

In the Boreal Forest Region from North Caribou Lake north to the Manitoba border, it was most abundant in tundra followed by heath, with lesser numbers in deciduous scrub, coniferous forest with an understorey, and coniferous and mixed scrub. It was absent in deciduous and mixed forest and coniferous forest without an understorey (McLaren and McLaren 1981). At Cape Henrietta Maria, it nested in areas of dwarf birch and arctic willow (Peck 1972). It was common in low scrub at the



edge of the treeline along the Hudson and James bay coasts. It also inhabited edges of willow thicket swamps and appeared to nest in patches of dwarf willow and birch (Manning 1952).

Throughout its range, the American Tree Sparrow nests in tundra north of the treeline, in ecotones between tundra and the Boreal Forest Region, and in high altitude subalpine and alpine meadows above the treeline. Less frequently, it nests within spruce forests, but typically in shrubby forest openings. Shrubs, such as willow, birch, and alder, are an important habitat component. Most territories contain water or have water nearby. Erskine (1977) considered it characteristic of tundra and alpine habitats. On the Twin Islands in James Bay, it usually occurred in or near willow thickets where it favoured tall willows; it avoided the shoreline (Manning 1981). On the east side of James Bay in Quebec, it probably nested in considerable numbers along the edge of the treeline and in patches of alders on the barrens. On the barrens, it preferred taller patches of alder and was frequently seen in or near small patches of spruce, but never in the main spruce forest (Manning and MacPherson 1952). Near Churchill, it is common to abundant near the treeline and in willow thickets and is much less common south of the treeline (Jehl 2004; Jehl and Smith 1970). Near Churchill, it is one of the most abundant breeding species in tundra interspersed with patches of scrub birch and willows. Most nests (76.9%) were in dwarf willow–birch thickets, 15.4% were in open tundra near a patch of shrubs, and 7.7% were in spruce near the treeline (Baumgartner in Austin 1968). In the same area, West (1973) reported that melting typically occurred soon after birds arrived, at which time they occurred singly or in pairs around margins of partially melted ponds. Nesting habitat included spruce-tundra ecotones, ponds bordered by alder and willow, and dense willow thickets along a river. Most available habitats were used for nesting except the sea coast, continuous spruce woods, and acid mountain avens tundra. Water or moisture appeared to be important. It occurred most often along margins of small ponds, lakes, marshes, streams, and rivers. In British Columbia, characteristic nesting habitat is near the altitudinal limit of trees in subalpine meadows and marshy wetlands that are interspersed with willow thickets a few cm to 2 m tall. A few conifers or scrub birch are often present in territories. Of 117 nests, only 1 was associated with a building. Seventy-seven percent of nests were in shrub thickets (predominantly willow), 11% were in other low vegetation, and 9% were in unspecified habitats (Campbell et al. 2001). In the Yukon, it is a common breeder in open shrubby habitat at or beyond the treeline. It is the most common species in upland and subalpine shrubs. It typically nests in shrubby tussock tundra with scattered shrubs or a dense cover of shrubs; scattered trees are occasionally present. It also nests well below the treeline in open shrubby habitat with scattered

trees, usually at or near wetlands (Sinclair et al. 2003). In Alaska, it nested in 3 main vegetation types within subarctic tundra: open tundra, low shrubs, and tall shrubs. Open tundra consisted of plants less than 15 cm tall. Low shrubs were predominantly dwarf birch, willow, and bog bilberry 0.15-1.2 m tall. These formed a dense impenetrable mat that was seldom used except along edges or as song posts. Tall shrubs consisted of alder and willow taller than 1.2 m. These thickets often had a herbaceous layer, providing both food and cover; the tall plants also functioned as song posts. Each vegetation type supported isolated spruce trees 3-12 m tall that were used as song perches (Weeden 1965).

During the breeding season, males roost 6-15 m from the nest, often in a conifer. The female roosts on the nest (Naugler et al. 2020).

Twelve of 13 Ontario nests (92.3%) were on the ground; the other was on the lowest branch of a black spruce 30 cm from the ground. Ground nests were at bases of small black spruce or deciduous shrubs such as willows and among grasses near willows. One was under a piece of partially buried scrap metal (Peck and James 1987, 1998b). Schueler et al. (1974) reported 2 nests near Winisk that were on the ground near bases of small deciduous trees. Two nests near Fort Severn were on the ground under small spruces (Baillie 1961).

Throughout the tree sparrow's range, most nests are on the ground, but a few are a short distance above ground, usually in a small coniferous tree or deciduous shrub, but occasionally in a clump of dead grass. In British Columbia, 93% of 94 nests were on the ground; the maximum height above ground was 1.4 m. In the Yukon, 37 of 38 nests (97.4%) were on the ground; the other was 5 cm above ground. In Alaska, most of 200 nests were on the ground, but a few were 0.3-1.2 m up in dwarf willow. A nest near Churchill was 1.5 m from the ground in a small spruce, the highest nest reported. Nests may be partially sheltered by overhanging grasses or leaves, but most are at the base of a shrub or small tree such as Labrador tea, willow, birch, and spruce. Nests may also be in sedge tussocks, clumps of grass, in depressions in mossy hummocks, under grasses, or under debris. One elevated nest was built in an old Redpoll nest. Reuse of nests has not been reported (Baumgartner in Austin 1968; Campbell et al. 2001; Heydweiller 1935; Jehl 2004; Jehl and Smith 1970; Naugler et al. 2020; Sinclair et al. 2003; Walkinshaw 1948b).

Weeden (1965) studied the territoriality of the American Tree Sparrow in Alaska. It is rarely required to defend its territory except in very dense populations. Fights were not confined to birds' typical boundaries and frequently covered an area many times larger than the area in which other daily activities took place. Much fighting appeared to be over females and not a specific area. Frequently-used areas were termed activity spaces rather than territories. Activity spaces included a series of 3 concentric areas: the inner-most core of intensive use, an area of moderate use, and an outer area of low use. Females' activities spaces were always within those of the males' and it is probable that the location of the female dictated the location of the male. Activity spaces occasionally overlapped, usually in areas of moderate or low utilization. Part of the overlap was due to shifts in areas throughout the season, so some of the overlap was not simultaneous. Overlap of activity spaces was 5% for females and 7.2% for males. Where female spaces did not overlap, male spaces overlapped by only 2.6% indicting that overlap of male spaces was more pronounced when female spaces overlapped. Maximum space was used during courtship when males were

establishing territories and acquiring mates. There was a gradual reduction in the size of the activity space through the incubation and nestling phases. Activity spaces were smaller in years of high density. Smaller activity spaces tend to be used more intensively; larger ones had outer cortexes with less intensive use. Females spent much of their time on or near the nest and had smaller activity spaces than males. Nests were frequently not in the centre of activity spaces but were never in areas of overlap with other pairs. Mean sizes of activity spaces for males over 3 years were 1.8, 2.2, and 1.2 ha compared with 0.9, 1.1, and 0.8 ha for females. Mean daily activity spaces were 0.7, 1.1, and 0.7 ha for males. Females wandered throughout the area, stopping in 1 male's territory for a while then moving on to the next. At Churchill, Heydweiller (1935) considered areas occupied by pairs to be territories. Territories ranged in size from 0.29 to 0.65 ha. A pair isolated from other birds had a territory of 2.6-3.6 ha.

No information is available on natal philopatry. In Alaska, 5 of 24 adult males (20.8%) returned in a subsequent year; 3 were present in all 3 years of the study (Weeden 1965).

Limiting Factors

Eggs have been reported in Ontario nests from 21 June to 9 July (Peck and James 1998b). Five to 6 days may elapse after pairing before nest construction begins. At Churchill, nest construction took 9-10 days: 7 days to build it and 2-3 days of rest. The first egg is laid 3-5 days after the nest is complete. Typically 1 egg is laid per day; a day may be rarely skipped. Incubation usually begins with the laying of the last egg, but occasionally with the penultimate egg. The incubation period is 10.5-13.5 days but mostly 12-13 days. All young hatch within a period of 1-30 hours. The nestling period ranges from 8 to 10 days (mean 9.2 days). Undisturbed birds tend to leave the nest when they are 9-9.75 days old, but may leave when they are only 8 days old if disturbed (Allen 1939; Baumgartner in Austin 1968; Heydweiller 1935; Jehl 2004; Naugler et al. 2020; Walkinshaw 1948b; Weeden 1966).

A single brood is raised in a season. At Churchill, there was circumstantial evidence for renesting after loss of a nest, but replacement nests have never been confirmed. In another year at Churchill, all nests were lost during a severe storm and there was no evidence of renesting or resumption of territorial behaviour (Allen 1939; Baumgartner in Austin 1968; Heydweiller 1935; Jehl and Hussell 1966a; Jehl and Smith 1970). Clutches of 5-6 eggs have been reported in Ontario (average 5.25 eggs, mode 5 eggs; Peck and James 1998b). Clutches of 3-7 eggs have been reported, with 5-egg clutches most frequent. Seven-egg clutches have been reported only from Alaska; 4-6 eggs appear to be typical in Manitoba and Ontario (Baumgartner in Austin 1968; Campbell et al. 2001; Heydweiller 1935; Naugler et al. 2020; Sinclair et al. 2003).

The age at first breeding is unknown, but it is probable that both sexes can breed when they are yearlings. The mating system is presumed to be monogamous (Naugler et al. 2020). In Alaska, Weeden (1965) observed numerous unidentified females in territories of mated pairs. Resident males tended to court them and copulation occurred frequently. He assumed that some polygyny and polyandry occurred where activity spaces overlapped. These observations may represent extra-pair copulations rather than polygyny and polyandry. One possible case of intraspecific nest parasitism has been documented, suggesting that female tree sparrows occasionally lay eggs in other females' nests (Naugler et al. 2020).

When feeding on seeds, the American Tree Sparrow usually forages on the ground or a short distance above it in herbaceous plants or shrubs. When feeding nestlings, it gleans insects from tiny leaves of willows and birch, often only 3-4.6 m from the nest. Early in the nesting season, both sexes may feed together in grassy edges of small pools, frequently picking off fresh buds of willow and birch. Buds are obtained by perching on the branch or hopping up a few centimetres from the ground. Occasionally it jumps into the air to hawk mosquitoes or moths (Baumgartner 1937; Heydweiller 1935).

Young are fed almost exclusively animal food until they are 3-4 weeks old, with a trace of leaves from plants in the rose family. Nestlings are fed predominantly caterpillars, but also flies, mosquitoes, and other insects. Once juveniles are capable of feeding themselves, seeds and fruits are taken to a limited extent, with their proportions gradually increasing in the diet. Nestlings are not fed sedge seeds, although these are the main food item of adults throughout the summer and are also important in the diet of juveniles (Baumgartner 1937; Heydweiller 1935; Weeden 1966).

The proportion of animal and vegetable food items in the diet changes seasonally. In winter, the diet is approximately 95% vegetable matter. In late April and May during spring migration, the diet transitions to animal material. The tree sparrow arrives on the breeding grounds to winter-like conditions, and once again reverts to a diet that is almost exclusively vegetation. A staple at this time is sedge seeds from the previous year's production which are typically collected around margins of partially melted pools. The importance of animal material in the diet increases as the season progresses and insects become more available (Baumgartner 1937). Near Churchill, the composition of the diet by period included 64.6% vegetation and 35.4% animals from 25 May to 15 June, 69.15% vegetation and 30.85% animals from 16 to 30 June, 11.59% vegetation and 88.41% animals from 1 to 15 July, 50.83% vegetation and 49.17% animals from 16 to 31 July, 71.2% vegetation and 28.8% animals from 1 to 15 August, and 87.62% vegetation and 12.38% animals from 16 to 24 August. After mid-July, fruits of ericaceous shrubs became available and were important in the diet. For the entire summer, the diet averaged 59.17% plant material and 40.84% animal material. In summer, seeds of 6 species of sedges comprised 46% of identifiable food items. Most other plant foods were heaths and included 7.3% crowberry seeds and 13.2% mountain cranberry seeds and flowers. Of 41 plant taxa available as food, only 9 represented more than 1% of the diet. Seeds (22.1%) and berries (28.4%) of crowberry comprised half the available plant food. Plants that were abundant yet seldom or not used included black spruce, white spruce, 1 sedge species, sweet gale, cloudberry, crowberry seeds and especially berries, and berries of blueberries and cranberries. Bulrushes, 1 sedge species, mustard seeds, and amaranth seeds were consumed roughly in proportion to their availability. Preferred plants included 4 species of sedges, whitlow-grass seeds, blueberry and cranberry seeds, and cotton-grass seeds. It may select smaller seeds that are more easily husked; the large seeds of spruce and cloudberry were not preferred. Only 4 animal orders constituted at least 1% of the diet: 7.6% snails, 3.1% adult flies, 1.2% springtails, and 1.0% beetles; 22 of 53 available taxa (41.5%) were consumed. The tree sparrow was also selective in the animal foods that it ate. The abundant snails and springtails were seldom taken compared with their availability. Scarce items such as beetle larvae and caterpillars were selected. Most other insect taxa and spiders were taken in proportion to their availability. Other animal material consumed included hymenopterans, flies, bugs, adult and larval lepidopterans, and mites (West 1973). Baumgartner

(1937) also studied the diet of the tree sparrow near Churchill. Sedge seeds were the main food item and seeds of 6 different species often occurred in a single stomach. In late July and August, seeds of crowberry and mountain cranberry and bulblets of alpine smartweed became important in the diet. Grass seeds were strikingly scarce in the diet, occurring in only 1 of 39 stomachs in late August. Besides seeds, stomachs contained soft bits of wood or wood chips, fibres, leaf fragments, galls, and unidentified debris. The most conspicuous animals in the diet were spiders, beetles (especially leaf beetles), ichneumonid wasps, lepidopterans, sawflies, and caddisflies. It consumed mostly adult insects, but also eggs, larvae, and pupae.

In a laboratory experiment, Robel et al. (1997) offered tree sparrows different-coloured and different-flavoured food pellets. It preferred brown and yellow pellets and avoided blue and orange ones. Butter- and nut-flavoured pellets were eaten at equal rates and significantly more than lime-flavoured pellets. Flavour discrimination was not as great as visual discrimination.

Water is as essential to the American Tree Sparrow as food (Baumgartner in Austin 1968). This may explain why most territories contain water or have water nearby. Water may also be obtained from succulent plants. Captive birds consumed an average of 29.6% of their body weight of distilled water per day. Birds that were offered salty water increased their water consumption with increasing salt concentrations. Those drinking the 0.15 mole salt solution initially lost weight but recovered. On the 0.2 mole salt solution, 5 of 12 tree sparrows died; the remaining 7 maintained their weight and 2 gained weight. The test with 0.3 mole salt solution was terminated early after 8 of 12 died and the remaining birds exhibited drastic weight loss. It may be able to maintain body weight only on salt solutions that do not exceed 0.15 mole (Ohmart and Smith 1970). Water in oceans averages 0.599 moles of sodium chloride, so it could not survive drinking ocean water.

Habitat loss and degradation on the breeding grounds is not an issue. At Churchill, Sammler et al. (2008) investigated whether intensive grazing by geese affected populations of other bird species. The American Tree Sparrow was 1 of 5 willow-nesting passerines. Over a 15-year period, there was no evidence for a decline of this guild.

Severe weather during the nestling period can result in extensive loss of young. Jehl and Hussell (1966a) reported the effects of a severe wind and rain storm at Churchill that lasted 5 days while young were 3-6 days old. All young died of exposure and there was no evidence of renesting. Prolonged cold and wet weather during the nestling period may result in no young being produced in an entire breeding season.

Status

The American Tree Sparrow was not known to breed in the province until 2 nests were found at Fort Severn on 1 July 1940. Approximately 100 were seen that day on the tundra (Baillie 1961). Manning (1952) considered it common along the Hudson Bay coast. He stated that it was absent at Cape Henrietta Maria although Peck (1972) reported it breeding there. The first atlas demonstrated that it bred throughout the Tundra Region from the Manitoba border east to Polar Bear Provincial Park and south along the James Bay coast almost to Attawapiskat. It was not documented at Cape Henrietta Maria. Some squares supported substantial populations (Knapton in Cadman et al. 1987). James (1991) considered the tree sparrow a common summer resident along the Hudson Bay coast and the northern James Bay coast.

The second atlas revealed little change in the distribution of the American Tree Sparrow. It was rediscovered at Cape Henrietta Maria and nesting evidence was obtained on Akimiski Island, slightly further south than during the first atlas. It is restricted from nesting further south on the mainland due to extensive coverage by forests, bogs, and fens and a general lack of habitat. There was no change in its probability of observation. It was most abundant within 30-40 km of the Hudson Bay coast, particularly between Winisk and Cape Henrietta Maria (Harris in Cadman et al. 2007).

POSTFLEDGING PERIOD

If the nest is not within a dense shrubby area, young are led to one as soon as they fledge. One fledgling took 20 minutes to travel 30 m to a thicket. Once in a thicket, newly fledged young may perch as high as 15 cm from the ground in a small spruce or tamarack. Young are fed by the adults for about 2 weeks after fledging. By the end of July, young at Churchill were flying freely within the thickets. About the third week of August, young emerged from the thick cover and merged with flocks that foraged in open grasses and mosses on river flats. These larger flocks contained both adults and juveniles and remained intact until autumn migration. In Ontario, juveniles were found mostly in patches of dwarf willows and birches, but a few were among spruce. On the eastern James Bay coast, juveniles remained hidden in dense alders (Baumgartner in Austin 1968; Heydweiller 1935; Manning 1952; Manning and MacPherson 1952).

In the latter part of July and most of August after the young had fledged, adults still maintained territories of 0.29-0.65 ha near Churchill. In early August when young were capable of feeding themselves, 3 broods ranged through a 1.4-ha patch of thicket (Baumgartner in Austin 1968).

MIGRATION

Allen (1939) stated that the American Tree Sparrow migrates mostly by day, but other authors concluded that it was a nocturnal migrant (Baumgartner in Austin 1968; Naugler et al. 2020). One bird banded in Edmonton was recovered in Ajax (Brewer et al. 2018). It migrates in flocks of 5-10 or even hundreds, occasionally with other species. At spring migration sites in the Yukon, it initially occurred in small groups of 2-10 and later in flocks of several hundred. As flocks grew, they became multispecies, mostly mixed with Dark-eyed Juncos, but also with Savannah, Fox, Lincoln's, and White-crowned sparrows. No individuals were caught more than 2 days after their initial capture. Migration appeared to be affected by local weather. The initial wave of migrants occurred after a front with heavy wind moved northward. Individuals pursue their own migration schedule and arrive and leave locations independent of each other. Those in the same physiological state probably depart together but the association is transient with some individuals stopping to feed before others. At the Yukon stopover site, the ratio of males to females was 12.3:1. This suggested that females moved along a different route, migrated after 10 May when the bulk of migration was over, or did not stop in the study area. Northward migrating flocks break up before the breeding grounds are reached (Baumgartner in Austin 1968; Naugler et al. 2020; West and Peyton 1972). Morbey et al. (2025) captured tree sparrows during winter and spring at Long Point and Guelph and tracked them using the Motus system. Fifty of 71 departures (70.4%) were nocturnal, with most occurring soon after sunset. The remaining 21 departures were diurnal and 2 of these occurred within 30 minutes of sunrise. Birds were detected nocturnally at Motus stations from 4 February to 4 May and were moving in a northerly direction. Nocturnal movements were strongly associated

with weather conditions, with the likelihood of departure increasing with higher temperatures, higher pressure, and less cloud cover. Departures also increased with more easterly winds, or birds avoided departure during strong westerly winds. Nine birds were detected in southern Ontario in autumn between 17 October and 20 November. Only 1 bird returned to its capture location. Results suggested broad fidelity to the nonbreeding area but limited precise nonbreeding site fidelity. In Alaska, only 8% of the moult occurred during autumn migration, the lowest of the 17 species studied. Because the tree sparrow had the shortest distance to the wintering area and the second-longest duration of time on the breeding grounds, most birds had time to moult prior to migration (Benson and Winker 2015).

In spring, most wintering tree sparrows have departed by mid- to late April in southern Ontario. Some remain until mid-May or rarely into late May or early June. Numbers increase in late March when wintering birds are joined by spring migrants. Northward migration peaks by mid-April. In the southern Shield, it is mostly seen in April during spring migration with stragglers into mid-May (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). James (1980) saw as many as 6 on 3 occasions in mid-June near Pickle Lake. It is likely that these were unusually late migrants. No information is available on when it reaches its Ontario breeding grounds.

At Delta Marsh, Manitoba, Murphy-Klassen et al. (2005) examined spring arrival times over a 63-year period in relation to temperature. Arrival date was significantly related to temperature in the month of its arrival. The tree sparrow arrived an average of 8.1 days earlier in 2001 than in 1939, but this difference was not significant.

Wilson and McRae (1993) observed 5 tree sparrows at Ekwan in late July, but these had probably been raised nearby. Two seen there on 3 September were the first migrants and 5 seen at Longridge in September were also migrants. In the southern Shield, most arrive in early October, but migration extends from late September to late November. In the south, it typically arrives in mid-October but may occur as early as mid-September (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

During migration in forested landscapes in Ontario, the American Tree Sparrow inhabits wet areas such as alder swales, borders of beaver ponds, and margins of marshes. It also uses weedy and shrubby areas; areas dominated by asters and goldenrods may be favoured in autumn (Mills 1981; Tozer 2012). It frequently visits bird feeders in rural and even urban areas during migration. In British Columbia, it frequents a variety of clearings with an abundance of dried herbaceous stems, low deciduous shrubs, and open ground for foraging. These include weedy edges of agricultural fields, willow thickets, around sewage lagoons, abandoned farmsteads, hedgerows, abandoned roadways, utility rights-of-way, stubble fields, grasslands, road verges, and cabin and cottage clearings in forested areas (Campbell et al. 2001). These habitats and marshes may be used during migration in Ontario. In the Yukon, it is widespread during migration in open shrubby lowland habitats where it is associated with wetlands, forest edges, and settlements (Sinclair et al. 2003).

James (1991) considered the American Tree Sparrow a common migrant in Ontario and abundant along the James Bay coast. Wilson and McRae (1993) confirmed that it was a common migrant at Moosonee.

WINTER

Temperature is the main factor determining the winter range of the American Tree Sparrow. The northern limit of its range coincides with the –23°C average minimum January isocline. Factors determining the southern boundary of its range are not as obvious, but may be related to interactions with the Chipping Sparrow (Root 1988). Twomey (1936) compared the temperature and humidity in areas of its breeding and wintering ranges and determined that they were similar in winter in Illinois, Missouri, and Tennessee to conditions during the breeding season at Churchill, Moosonee, and Ungava Bay.

Males winter further north than females. A sample of 16 collected in Ontario consisted entirely of males. In February and March in New York, the male to female ratio was 2:1 whereas there were 3 females for every male during spring migration in April (Heydweiller 1935).

When the ground is covered in snow, the tree sparrow frequently congregates near winter feeders. It is more abundant at rural than urban feeders. It is an open-habitat and edge species in winter, occurring in weedy fields, pastures with some shrubs, cattail marshes (particularly those with some shrub cover), hedgerows, weedy margins of cultivated fields, corn stubble, brush piles, woodland edges (especially those with thickets or weeds), watercourses with weedy or shrubby margins, prairie remnants, and savannahs (Black and Roy 2010; Campbell et al. 2001; Dunn and Tessaglia-Hymes 1999; Fitch 1958; Graber and Graber 1963; Grundel and Pavlovic 2007a, 2007b; Lancaster et al. 2004; West 1967). Smith (2003) considered it a field species in Ontario and used results of Winter Bird-Population Studies to determine its relative abundance in different habitats. Densities per km^2 averaged 10.5 in urban natural parks larger than 10 ha, 7.9 in mixed rural habitat, 4.8 in urban natural parks smaller than 10 ha, 4.4 in rural forests, 1.4 in urban natural areas with open water, and 0 in cities and cropland or pasture with no significant vegetation except hedgerows; differences among the habitats were significant. In Indiana, Grundel and Pavlovic (2007b) reported densities per km^2 of 58 in open habitat with little woody vegetation such as prairie remnants and areas disturbed by farming and mining; 10 in woodland, which was similar to savannah but with greater canopy cover, 4 in oak savannahs, and 0 in forest and dense regenerating oak sprouts following a fire; differences among habitats were significant. It was in the open habitat guild. In Ohio, its abundance was positively correlated with the amount of forest edge. Doherty and Grubb (2000) considered it an edge and generalist species. In Pennsylvania, it was absent in uncut forest and occurred in low density where 50% and 75% of trees had been cut. Cutting created greater availability of early successional vegetation. It preferred edges or brushy vegetation (Yahner 1993).

In winter, the tree sparrow roosts on or near the ground. It mostly roosts solitarily and prefers cattail marshes where they are available. It typically creeps into little cavities in clumps of grasses or cattails in marshes but may also roost in weedy fields and haystacks. It has roosted in dense growths of white pine that offer shelter similar to roosts used on the breeding grounds (Baumgartner in Austin 1968; Heydweiller 1935). During severe weather, it may roost under the snow, either singly or communally. Thompson (1934) observed one near Toronto that burrowed 20 cm into the snow at the base of a small shrub at dusk during a winter snowstorm. McNicholl (1987a) documented communal roosting under snow at Long Point. The overnight temperature was –18°C with a wind chill of –32°C. He observed 18 tree sparrows and a Song Sparrow emerge from 2 small caverns under

the snow formed by the accumulation of snow over arched-over clumps of grass at the base of some red-osier dogwoods. When he retreated, they crowded back into the cavities, filling all the available space. In New York, one roosted in a dense low-growing shrub covered in deep snow (Naugler et al. 2020).

In winter, the American Tree Sparrow typically occurs in flocks. Flocks as large as 250 have been observed in Elgin County and it is likely that flocks of this magnitude occur in many locations. Flocks are often accompanied by Dark-eyed Juncos and occasionally by other sparrow species. Flocks may either remain in 1 general area all winter or wander considerable distances, especially during snow storms. Flocks inhabiting open country wander more widely than those in denser cover such as marshes. A New York marsh supported 2 flocks at either end and there appeared to be an invisible line through the centre of the marsh that flocks never crossed. Birds in the discrete flocks roosted within their diurnal home range; no birds ever roosted in the centre of the marsh. In Kansas, flocks of several hundred tree sparrows mixed with juncos and a few Song Sparrows moved and foraged together. One flock of several hundred stayed within an area of about 11.2 ha all winter. Winter ranges included a weedy fallow field, thickets, a field of milo bordered by an intermittent creek with weeds and shrubs, and debris from a bulldozed hill. Flocks tended to remain together, concentrated in a small part of the range, moving about slowly usually by following shrubs along field edges. Flocks in open habitat may move as far as 10 km during snow storms. Although flocks remain discrete over the winter, their composition may change daily. Individuals may move freely from 1 flock to another. Occasionally large flocks break up into several smaller ones and coalesce later. In New York, 38 birds moved a maximum of 300 m over the winter, 21 moved as far as 600 m, 4 moved 600-760 m, and 17 moved 914-2,073 m. In Kansas, the average distance between successive captures was 115 m indicating a home range of approximately 4.0 ha over the winter. Some birds are fairly sedentary all winter whereas others may wander freely; some birds move as far as 10 km. Winter territories are not defended, but winter flocks may form linear dominance hierarchies (Baumgartner in Austin 1968; Fitch 1958; Heydweiller 1935; Lancaster et al. 2004; Naugler et al. 2020; West 1967).

Many birds exhibit site fidelity to their wintering areas and some return for several years. At a feeder south of Guelph, about a third of birds returned in subsequent years (Brewer et al. 2018). At Prince Edward Point, 34 of 189 birds (18.0%) returned the following year, 9 of the 34 (26.5%) returned the third year, and 3 of 9 (33.3%) returned for the fourth year (Weir 2008). In New York, Brooks (1985) banded a bird of unknown sex and age and recaptured it 41 times over a period of 9 years. In New York, 34% of birds banded the previous year returned, compared with 31.7% in Missouri and 21% in Massachusetts (Dowling 1956; Heydweiller 1935). In Pennsylvania, where the tree sparrow occurs only in the severest part of the winter, Middleton (1943) banded 604 birds over 17 years and 77 (12.8%) returned in subsequent years; 9 were present in 5 winters. Of the 77 that returned, 12 did not return until 2 years after banding, 5 returned 3 years later, 1 returned 4 years later, and 1 returned 6 years later. Of the 77 returning birds, 38 (49.4%) returned a second year. Of the 38 that returned a second year, 15 (39.5%) returned a third year. Of the 15 that returned a third year, 9 (60.0%) returned a fourth year. Of the 9 returning a fourth year, 5 (55.6%) returned a fifth year. Of the 5 returning a fifth year, 2 (40.0%) returned a sixth year.

In winter, the tree sparrow feeds mainly on the ground where it scratches at the substrate or hops up at bent-over herbaceous species. It may also sway from the top of a herbaceous plant and forage as high as 12-15 m in order to obtain berries or catkins. In Missouri, it perched on wild bergamot stems, beat its wings rapidly, and bounced up and down. This dislodged seeds that otherwise would have been unavailable, allowing it to feed on them on the ground. This may be a common foraging technique (Baumgartner 1937; Goldman 1976; West 1967). Gaines (1989, 1990), with a review by Tome (1990), concluded that it did not select high-quality plots and remain in them until high-quality and low-quality patches produced the same energy gain rate. In Pennsylvania, Nastase and Linville (1995) provided seeds at 4 different heights (0, 2, 4, and 6 m). It conducted 16.4% of its foraging on the ground, 20.9% at 2 m, 38.3% at 4 m, and 24.2% at 6 m. It foraged significantly more on the ground than the White-breasted Nuthatch, House Finch, and American Goldfinch and significantly less than the Black-capped Chickadee, Tufted Titmouse, and Dark-eyed Junco. At 2 m, its foraging frequency was significantly different from only the titmouse, junco, and goldfinch, foraging less than them at this height. The tree sparrow foraged significantly more than all species at a height of 4 m. At 6 m, it foraged significantly more than the chickadee, titmouse, and junco and significantly less than the nuthatch and House Finch. The tree sparrow and junco did not differ in their seed choices but differed in their elevation choices, with the tree sparrow preferring to forage at 4 m and the junco preferring to feed at 2 m.

In Ontario, Dance (1986, 2008) observed the American Tree Sparrow eating seeds of black alder, tall goldenrod, gray goldenrod, broad-leaved goldenrod, catnip, Virginia wild rye, and meadow fescue. Mills (1981) observed a flock of 75 feeding on evening-primrose seeds in Muskoka District. Judd (1901) analyzed 517 stomachs collected in the United States in winter. The diet was comprised of 98% seeds, 2% animal matter, and minute amounts of fruit. Grass seeds constituted about 50% of the seeds consumed, with those of panic grasses and foxtails preferred. Other grass seeds in the diet included those of Virginia broomsedge, wiregrass, crabgrass, timothy, bluegrasses, and ensheathed dropseed. Important herbaceous plant seeds included ragweed, lamb's-quarters, amaranths, and smartweeds; these comprised about 40% of the diet. Another 10% of the diet consisted of miscellaneous vegetable matter such as red maple flowers and buds, alder seeds, cultivated grain, a wide variety of miscellaneous seeds, and fruits of red cedar, common juniper, privet, sand cherry, blackberry, blueberry, and nannyberry. Animal foods were predominantly beetles (ground and scarab beetles, and weevils), ants and other hymenopterans, caterpillars, flies, and bugs. Of 549 stomachs examined by the United States Department of Agriculture, 14 (4.3%) contained insects and spiders (Knappen 1934). The animal food of 45 tree sparrows collected in winter consisted of beetles (ground, leaf, rove, and click beetles, and weevils), winter stoneflies, spiders, bugs, leafhoppers, ichneumonid wasps and other hymenopterans, house flies, caterpillars (especially owlet moths), orthopterans, deer flies, and common earthworms (Baumgartner 1937). In Illinois, the winter diet consisted of 98.37% plant material and 1.63% animal material. Grass seeds comprised 77.7% of the identifiable food items. Important grass seeds included those of foxtails (giant, green, and yellow), crabgrass, satin grass, cutgrass, and wheat. Other important seeds included those of lamb's-quarters, amaranths, and asters. It consumed seeds of 36 of 87 available plant species (41.4%). Virginia wild rye, switch grass, Pennsylvania smartweed, climbing false buckwheat, spotted jewelweed, black snakeroot, and giant ragweed were abundant but seldom, if ever, eaten. They may

not be used because of their large size, hardness of the outer seed coat, or unpalatability. Species used in proportion to their availability included wheat, hairy crabgrass, giant foxtail, lamb's-quarters, amaranths, and Pringle's aster. Selected species included nimblewill, rice cutgrass, green foxtail, yellow foxtail, and Pennsylvania pellitory. Approximately 30% of the species consumed were nonnative and most of these were used in proportion to their availability. Animal food consisted of beetles, spiders, and a trace of hymenopterans (West 1967). In Missouri, tree sparrows foraged preferentially in a patch of lamb's-quarters rather than in adjacent plantings of millet and sorghum (Dowling 1956). In New York, a flock fed in the terminal panicles of common reed. No insects were detected in the flower heads so it was concluded that they were either feeding on the seeds or other parts of the dried inflorescence. Seeds of common reed are a rather poor source of food that are rarely consumed by wildlife (Russak 1956). Water remains an essential component of the diet in winter; birds may consume snow to obtain it (Baumgartner in Austen 1968; Naugler et al. 2020).

The American Tree Sparrow may be absent or scarce at feeders when there is no snow on the ground, but common when snow covers the ground. Favoured feeder foods include mixed seeds, millet, and cracked corn. It infrequently selects canary seed, sunflowers of any type, peanut butter mixes, and baked goods (Dunn and Tessaglia-Hymes 1999). Nastase and Linville (1995) offered tree sparrows striped sunflowers, niger seeds, cracked corn, white millet, and canary seed. They ate 46.7% millet, 33.8% canary seed, 12.8% corn, 5.2% niger, and 1.5% sunflower seeds. In a laboratory study, it preferred short and thin sunflowers (less than 12 mm long and 4.7 mm wide) to larger ones (Naugler et al. 2020). A total of 6,644 observations of tree sparrow food selections determined that it preferred white proso millet in hopper or platform feeders (Horn et al. 2014).

Stuebbe and Ketterson (1982) demonstrated that the tree sparrow could survive without eating an average of 30 hours with extremes of 21-40 hours. A bird that ate in late afternoon prior to roosting could be expected to survive overnight and the following day but not a second night. It is highly at risk of starving when severe snow or ice storms make food unavailable. In 1907, 358 were found dead within 3 hours on the shoreline of Lake Huron following an October snow storm (Baumgartner in Austin 1968).

The amount of suitable wintering habitat for the tree sparrow is declining. The old-field habitats that it prefers are being lost as a result of natural succession, tree planting, agricultural intensification, and urbanization (Naugler et al. 2020).

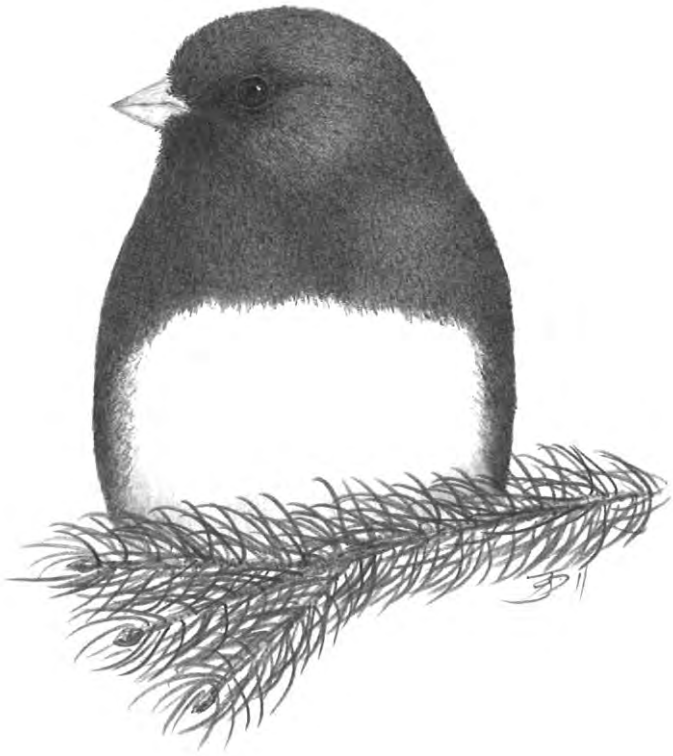
James (1991) considered the American Tree Sparrow common in winter in southern Ontario and rare in the north at Thunder Bay. In Algonquin Park, it is irregular in winter and varies from absent to very common. This is probably due to scarcity of suitable habitat. Early in the 20th century, it was common when many weedy fields were present, but declined as forests matured and eliminated open areas (Tozer 2012). Mills (1981) reported that it was irregular in winter in Muskoka and Parry Sound districts.

It is difficult to determine trends in winter populations due to the American Tree Sparrow's habit of dispersing throughout the landscape when there is no snow and concentrating near feeders when there is snow on the ground. Over the long-term, it is likely that it benefitted from deforestation by the settlers and by the increasingly popular practice of feeding birds. More recently, forest maturation may have eliminated some suitable open habitats, particularly in the southern

portion of the Shield. Results of Christmas Bird Counts are highly variable. Peaks on this survey in 1977, 1980, and 1985 were associated with substantial snow cover. Low counts in 1979, 1984, and 1987 occurred when there was little or no snow. Long-term declines in Pennsylvania were attributed predominantly to the detectability of the species related to snow cover (Hess 1989a, 1989b; Limoges and Barrette in Gauthier and Aubry 1996; Naugler et al. 2020).

Dark-eyed Junco

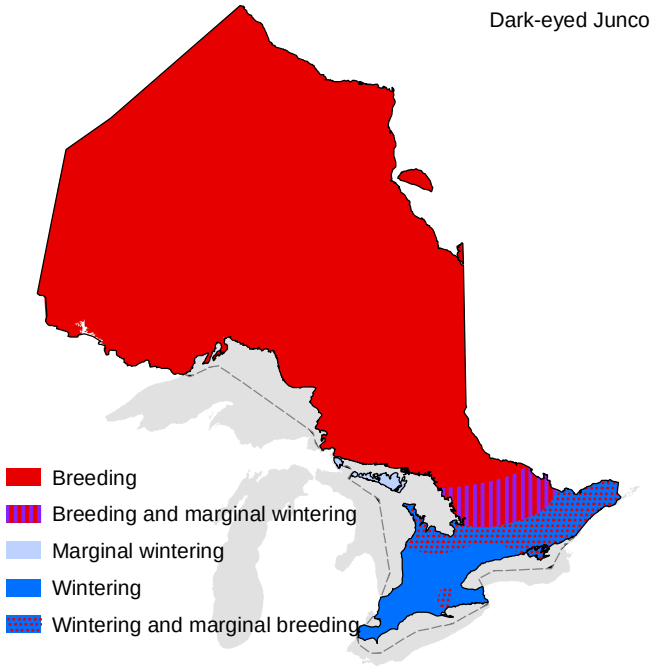
Junco hyemalis



BREEDING SEASON

Habitat Requirements

In Ontario, 59.0% of Dark-eyed Junco nests were in forested habitats, with coniferous (40.0% of nests) preferred to mixed (17.0%) and deciduous (2.0%) stands. Nine percent of nests were in burns or clear-cuts, 19.0% were in bare or sparsely treed bedrock outcrops, 6.0% were in wooded parks or cottage areas, 4.0% were in residential gardens, 2.0% were in open grassy areas, and 1.0% were on a golf course. Wooded areas used for nesting were usually semiopen, or nests were placed at forest edges or clearings. Several nests were at edges with roads and railways, near paths, along shorelines, and in ditches. It preferred to have open areas near the nest. Nesting areas were more often dry than wet. A significant number of nests were on slopes, embankments, and vertical rock faces (Peck and James 1987).



In the Hudson Bay Lowland, the Dark-eyed Junco was very common in burned areas near Hawley Lake (Schueler et al. 1974). Manning (1952) observed it along the Hudson Bay and James Bay coasts, but concluded that it probably nested only in its preferred habitat of dry open spruce forest. Wilson and McRae (1993) also reported it along the northern coasts except at Brant where it did not occur in the tundra habitat.

In the Boreal Forest Region from Pickle Lake northward, the Dark-eyed Junco was most abundant in mixed scrub, followed by coniferous scrub, coniferous forest with an understorey, heath, coniferous forest without understorey, and deciduous and mixed forests. It was absent in deciduous scrub and tundra (McLaren and McLaren 1981). At Pickle Lake, it occurred irregularly in small numbers in disturbed mixed woods or open black spruce stands (James 1980). In jack pine stands near White River, it was most abundant in stands 3-5 years old, but not significantly. It was strongly negatively correlated with vegetation structure 0.5-2.5 m from the ground (Venier and Pearce 2005). In mixed-wood stands near Manitouwadge, it was equally abundant in stands 1-21 and 60-223 years old but absent in 24-36 year-old stands (Venier et al. 2009). Near Hearst, Welsh and Fillman (1980) reported it in a 24-year-old lowland coniferous forest and an upland uncut mixed forest. They did not detect it in deciduous clear-cuts or coniferous clear-cuts younger than 24 years. In the Clay Belt, it was most common in black spruce stands followed by stands dominated by jack pine, tamarack–white cedar, trembling aspen, birch–white spruce, and balsam poplar. It occurred in stands that ranged from wet to dry and nutrient-poor to nutrient-rich (Welsh and Lougheed 1996). Zimmerling et al. (2017) compared its abundance in forests disturbed by fire and logging and in different age classes. It was slightly more abundant in early regenerating stands that were harvested than burned. In mid-successional regenerating stands, it was significantly less abundant in harvested than burned stands. Relative to mature stands, it was significantly more abundant in early regenerating stands and slightly but nonsignificantly more abundant in mid-successional regenerating stands. In the Boreal Forest Region of Ontario, it nested in stands dominated by spruce, balsam fir, hemlock, red and white pine, jack pine, tamarack, and poplar–white birch (Erskine 1977).

In Quetico Park in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, there was little difference in the Dark-eyed Junco's abundance in stands 1-23 years old, 67-73 years old, 112-176 years old, and 367-370 years old, although it was most abundant in the oldest and youngest stands (Apfelbaum and Haney 1985). Near Gogama, it was a common and characteristic species of jack pine forests. It first colonized forests when they were approximately 10 years old and attained maximum density when trees were about 20 years old. It avoided deciduous forests and,

to a lesser extent, mixed forests. Territories were in forests that were very uniform with a continuous canopy or where only small openings or gaps were present. Low shrubs were numerous wherever it occurred, but tall deciduous shrubs were sparse to absent (James and Peck 1995a). In jack pine stands near Parry Sound, it occurred in low density in young open stands mixed with a variety of deciduous tree species (James 1979a). In Parry Sound and Muskoka districts, it nested on embankments, among tree root systems, on rock ledges, and on more conventional ground sites (Mills 1981). In Algonquin Park, it was abundant in mixed and coniferous forests, uncommon in sugar maple stands, and rare in settlements (MacLulich 1938). Martin (1960) did not report it in bogs in Algonquin Park, but it inhabited black spruce, black spruce–white cedar, white birch–poplar, poplar and birch mixed with spruce and balsam fir, immature white pine, and hemlock stands. In black spruce–white cedar forests, it occurred from the ground to a height of 18 m, above the top of the cedars but not to the top of the spruce. In white birch–poplar stands, it occupied the ground and shrub layer to a height of 3 m. In hemlock stands, it occurred from the ground to the top of the canopy at 24 m. Also in Algonquin Park, Kingsley and Nol (1999) studied its abundance in white pine stands harvested by the shelterwood method. It occurred in 16.7% of cuts 2-9 years old, 0% and 27.3% of 10-16 year-old cuts in 2 years, and 7.1% and 13.3% of stands with no recent history of cutting. Differences among age classes were not significant. In Algonquin Park, it breeds in open coniferous and mixed forests, often where there is dense ground cover, and favours forest edges, clearings, lake margins, hillsides, and talus slopes below cliffs (Tozer 2012).

Historically, the Dark-eyed Junco was a widespread breeding species south of the Shield. In the Carolinian Forest Region, McIlwraith (1894) stated that it demonstrated a preference for rocky ravines, quarries, and stone piles. Small numbers still nest on talus slopes along the Niagara Escarpment, on the Bruce Peninsula, and in mature plantations (Rising in Cadman et al. 2007).

Throughout its range, the Dark-eyed Junco nests predominantly in forests and appears to prefer coniferous and mixed forests to deciduous forests in most regions. It also nests in treed fens and bogs, subalpine and alpine meadows, and recent clear-cuts and burns. Some western subspecies often breed in open treed natural and landscaped plantings; it may nest on university campuses and in well-treed suburban neighbourhoods. In many cases, it prefers open-canopied forests, small gaps in the canopy, or forest edges.

Numerous studies examined the habitat of the Dark-eyed Junco in Canada and Alaska. In Quebec, it nested in dense spruce forests along the eastern coast of James Bay and in the interior. Most were observed in the drier portions of spruce forests (Manning and MacPherson 1952). Lessard and Limoges (in Gauthier and Aubry 1996) stated that it was one of the most common species in Quebec mixed and coniferous forests where it favoured forest edges, clearings, and other semiopen areas rather than forest interior. It was common in both deciduous and coniferous clear-cuts in Quebec, but absent to uncommon in strip-cuts (Falardeau et al. 1999). In New Brunswick, it occurred in spruce plantations and natural coniferous forests. It tended to be more common in natural forests. In plantations, it was most common in stands 3 years old and those 13-21 years old with lesser numbers in stands 4-8 years old (Freedman and Johnson 1999). In Nova Scotia northern hardwoods, it was most abundant in clear-cuts and was one of the dominant species. It was one of the most abundant and characteristic species in stands 12 years or less in age. It was positively correlated with

young stands with high slash cover and low development of horizontal and vertical plant structure. It was common in strip-cuts in northern hardwoods and mature forests. It was absent in shelterwood cuts (Freedman and Johnson 1999; Freedman et al. 1981; Morgan and Freedman 1986). At Churchill, it nested in drier spruce forests (Jehl 2004; Jehl and Smith 1970). In the same general area, it nested in white spruce–tamarack–black spruce forests and in jack pine stands. These forests had a discontinuous shrub layer of dwarf birch, willows, Labrador tea, crowberry, and blueberries with sedges and lichens. Some of these forests bordered tundra (Gillespie and Kendeigh 1982). In the Prairie Provinces, it exhibited a pronounced gradient of increased abundance from deciduous to coniferous stands. It was associated with dry nutrient-poor sites, mostly with burned areas. It occurred in all age classes of forest, but tended to be associated with older stands (Kirk et al. 1996). In Alberta, it nested in a treed fen dominated by tamarack with a minor component of black spruce. The understorey shrub layer consisted of swamp birch, bog willow, and Labrador tea with a ground flora of creeping sedge, water horsetail, and mosses (Johnson 1988). In Alberta, it preferred coniferous forests. In aspen forests, there was no difference in its abundance in different forest age classes; it tended to be most abundant in old-growth forests (Schieck et al. 1995). Erskine (1977) noted that it tended to be associated with scattered trees or clumps of conifers in deciduous stands, especially white spruce or balsam fir, and was associated with either an open canopy or small trees. In British Columbia, the junco inhabits a variety of forested sites at higher elevations, particularly forest edges and openings, but also occurs deeper in the forest. It nests in alpine meadows and in open subalpine forests interspersed with heath tundra or herbaceous meadows. In the north, it nests in spruce–tamarack bogs and muskeg. In boreal forests, it nests in spruce woodland edges, edges of spruce–hardwood stands, trembling aspen stands, balsam poplar floodplains, black spruce muskeg, and riparian wooded creek areas. In Vancouver Island aspen stands, it was most abundant in clear-cuts and stands 15-20 years old but occurred in all ages of stands except those 50-60 years old. Its abundance was positively associated with elevation and negatively associated with canopy closure. In fir stands, it was most abundant in climax forests dominated by conifers taller than 10 m with an open understorey of scattered snowberry and grasses. It also occurred in young coniferous stands with trees shorter than 10 m and some snowberry and bearberry in the understorey. Other important nesting habitats include recent burns, well-drained shrubby avalanche chutes, and open subalpine fir forests with an understorey of rhododendrons and bilberry. Sixty-nine percent of nests were in forested habitats, 22% were in human-influenced areas, 4% were in alpine areas, and 3% were in riparian areas. Thirty-four percent of forested sites were coniferous, 17% were mixed, and 6% were deciduous. Human-influenced habitats included 10% rural and 7% urban sites; 6% cultivated farmland, orchards, and vineyards; and 4% regenerating cuts and burns and urban and recreational areas. Its abundance was significantly greater in young than old clear-cuts. Presence of slash piles appeared to be an important habitat component of trembling aspen clear-cuts. Riparian sites were associated with swamps, marshes, sloughs, lakes, ponds, bogs, muskeg, and bottomlands (Campbell et al. 2001). In the Yukon, the Dark-eyed Junco is one of the most common song birds. It breeds in a variety of forest types, usually at low altitudes but is occasionally found above the treeline. It nests in dense mixed or coniferous forests, open spruce-deciduous woodlands, edge habitat, trembling aspen–coniferous woodlands, and pine forests (Sinclair et al. 2003). Erskine (1977) stated that it was dominant in all forest types in the southwestern Yukon, whether the site was coniferous or deciduous or successional or climax. It is absent from tundra habitat in this area (Nolan

et al. 2020b). In Alaska forests, it occurred in stands ranging from early succession to old growth and was absent only from stands with a closed dense canopy, low light penetration, and scant ground cover. It was most abundant in shrub-forb growth, sapling-shrub-stage forests, lakeshore old growth, and muskeg (Nolan et al. 2020b). Eaton (in Austin 1968) stated that it inhabited more open woodlands and forest edges or openings in the canopy created by streams, logging roads, or clearings.

Several studies summarized the habitat of the Dark-eyed Junco in the eastern United States. In Maine, it was common in a coniferous forest dominated by balsam fir and spruce with only 7% coverage by deciduous trees. It was absent in a mixed forest dominated by spruce with 38% deciduous tree cover (Morse 1978). In spruce–balsam fir forests in Maine, Titterington et al. (1979) found it only on recent clear-cuts no more than 2 years old and in mature forests. It was absent in mid-successional habitats. Clear-cuts that it used were characterized by dense slash and abundant open ground. Mature stands had a dense coniferous canopy and an open forest floor with some windthrown trees and branches and twigs that had fallen from the overstorey. In subalpine areas of New Hampshire, it occurred mostly in the high krummholz area and extended above this into the tundra (Sabo 1980). In an extensive stand of northern hardwoods in New Hampshire, it was patchily distributed and occurred consistently in areas with a more open understorey and relatively dense herbs and ferns compared with less occupied areas (Holmes and Robinson 1988). Holmes and Sherry (2001) considered this habitat marginal for the junco. It occurred in only 16 of 30 years, predominantly at the start of the study, and may have been attracted to the area by an outbreak of the saddled prominent. In subalpine New Hampshire stands, it was common at elevations of 750-1,150 m in tall mixed, second-growth deciduous, and coniferous forests (Morse 1979). In the White Mountains of New Hampshire and Maine, it was significantly correlated with cover type and structure but not tree-size class. It was most abundant in stands dominated by white pine followed by spruce–balsam fir, white birch, and hemlock stands. It was uncommon in northern hardwoods and swamp hardwoods and absent in aspen stands (DeGraaf et al. 1998). In Vermont, some territories encompassed both northern hardwoods and clear-cuts but it tended to avoid cuts, particularly their centres (Lent and Capen 1995). It was common in New York clear-cuts. It was more abundant in cuts 2-18 years old and declined 24-120 years after cutting (Keller et al. 2003). Several studies summarized its habitat preferences in forested areas of the northeast. In northern hardwoods, it occurred in 10% of plots in mature undisturbed habitats and 37% of disturbed and successional habitats. It occurred at low density in a 3-year-old burn in aspen–white birch but was absent in sapling-pole and pole-mature stands. In red, white, and jack pine forests, it was most abundant in seedling-sapling stands and mature forests; it occurred in low density in pine-hardwood stands and was not observed in pole-sized pine stands. It has not been reported in pitch pine stands. It was associated with small openings, edges, and forests, but not with large openings (Back 1979; Capen 1979; Noon et al. 1979; Taylor and Taylor 1979; Temple et al. 1979). In Wisconsin, it is rare in diverse barrens and absent in other types of pine-oak barrens (Mossman et al. 1991) and rare in northern mesic forests dominated by sugar maple, hemlock, yellow birch, beech, white pine, basswood, and elm. In these forests, it occurs predominantly in coniferous saplings, pole-sized coniferous stands, and mixed forests (Hoffman 1989a). In Minnesota, Niemi and Hanowski (1984a) reported it in closed-canopy spruce forests but not in open spruce stands, low shrubby areas, or

fens. In Virginia, it is the most common breeding species above elevation 1,000 m. It nests there in all available habitats including woodlands, forest edges along hydro corridors and roads, and openings around human habitation (Chandler et al. 1994a).

In Utah, the junco nested in mixed subalpine meadows, trembling aspen forests, and spruce-fir forests (Smith and Andersen 1982). In California, it was the most abundant species in clear-cuts. Large amounts of logs and slash were important in providing cover until shrubby vegetation became established (Hagar 1960). In California coniferous forests, it was common in both unburned and burned forest and comprised more than 50% of the ground-brush nesting guild in unburned forest (Bock and Lynch 1970). In Arizona, it nested in open pine forests and savannahs with an understorey of native grasses (Walsberg 2005).

Some studies characterized habitat of the Dark-eyed Junco at the landscape scale. In Minnesota, it was positively associated with the amount of black spruce within 200 m, the amount of non-forest within 1,000 m, and the density of streams within 200 m. It was negatively correlated with the amount of mortality due to the eastern larch beetle within 500 m. It was associated with black spruce forest and was not common in pure tamarack stands (Zlonis et al. 2017). In Alaska, it was most abundant on hills or bluffs, followed by lowlands, subalpine areas, floodplains and terraces, and alpine areas (Handel et al. 2009). Near Seattle at the 1-km^2 scale, it was most abundant in open developed areas and at forest edges (Marzluff et al. 2007). In Saskatchewan, it was randomly distributed among fragmented and contiguous forested landscapes. It was more common within large forest patches with low percent forest cover within 5 km, but its abundance was not significantly correlated with forest size. It was more common than expected in pure white spruce stands and was uncommon in trembling aspen and mixed stands (Hobson and Bayne 2000). Near Quebec City in second-growth balsam fir forests mixed with black spruce, white spruce, and white birch, it was not significantly associated with forest cover, amount of core area, or edge (Drolet et al. 1999). In Newfoundland balsam fir and black spruce stands, natural landscapes contained a mix of age classes and natural openings created by wetlands and water bodies. Cut landscapes contained these features but at least 5% of the forest had been clear-cut. Its rates of occurrence were 38% in cut landscapes, 34% in natural landscapes, and 36% overall. Its occurrence rate was similar across levels of forest cover within cut landscapes but not within natural landscapes. Lower levels of occurrence in natural landscapes occurred primarily at low levels of forest cover suggesting that natural openings such as bogs and barrens did not provide adequate resources. The proportion of sites occupied in cut landscapes was 20% at 20% forest cover, increasing to 40% at approximately 45% forest cover and remaining constant to 100% forest cover. In natural landscapes, the proportion of sites occupied was less than 10% at 50% forest cover, increasing to 30% at 65% forest cover, and to 40% at 80-100% forest cover. Incidence at the 300-m scale increased with increasing forest cover in natural landscapes but decreased in cut landscapes. Taylor and Krawchuk (2006) concluded that the junco preferred early successional habitats based on its preference for harvested areas and ecotones. In the Boreal Forest Region, Erskine (1977) considered it characteristic of tundra and alpine ecotones with boreal forest. It is one of the most typical boreal species, particularly in black spruce stands. It is common in spruce–balsam fir stands, is found in most jack pine stands, is among the species detected in black spruce and tamarack bog forests with more tree cover than average or taller scattered trees, and is common in burns and clear-cuts.

Several studies detailed microhabitat preferences of the Dark-eyed Junco. In the northeast, it was in a guild that was common in mature upland and lowland conifers; rare to uncommon in alder, mature deciduous upland forests, disturbed shrub areas, young plantations, aspen regeneration, and recent clear-cuts; and absent in grasslands. Its abundance was not associated with the density of low shrubs, saplings, or trees (Niemi and Pfannmuller 1979). In clear-cuts in Maine, it was positively correlated with slash above and below 1 m and the number of conifers larger than 20 cm diameter at breast height (DBH), which was the largest size of trees. It was negatively correlated with raspberries. Its presence was closely associated with dense slash (Titterington et al. 1979). In the White Mountains of Maine and New Hampshire, it was not positively associated with any habitat parameter, but was negatively associated with the percent ground cover and foliage volume of deciduous trees 2-10 cm DBH (DeGraaf et al. 1998). Mean habitat characteristics of territories in subalpine areas of New Hampshire included occurrence on the exposed upper slope of the mountain, usually no water present, mean canopy height 4.0 m, 42% canopy coverage, 72% conifer foliage volume, 38% conifer foliage volume 0-2 m above ground, 15% deciduous foliage volume above 5 m, and average tree DBH 7 cm. It used dense shrub clumps with a rock outcrop or exposed banks for nesting (Sabo 1980). In Vermont, average habitat variables for 6 territories included 84.0% ground coverage by green vegetation, 7.9% coverage by slash, 35.8% canopy cover, 9.5 m canopy height, 6.1 m canopy depth, 8.4 m^2 basal area (BA) of deciduous trees, 4.1 m^2 BA of conifers, mean DBH of deciduous trees 8.3 cm, mean DBH of conifers 6.5 cm, and 20 snags per 0.08 ha. It was in the intermediate canopy–dense understorey guild. The junco was associated with pole-sized hardwoods with a canopy closure of 55-80%, high understorey density, and a mean DBH of 8-15 cm. Plots with these characteristics included a stand that had been clear-cut 20 years previously and stands where recent logging opened the canopy and allowed a dense understorey to regenerate. It preferred denser understorey than other species in the guild (Thompson and Capen 1988). In Vermont northern hardwoods, it was associated with increasing successional age, decreasing numbers of dead trees, and increasing numbers of conifers (Lent and Capen 1998). In New York, it was in an edge-associated guild that was also associated with conifers. It was most abundant in young clear-cuts but also occurred in pole-sized to timber forests. Tree gaps in these forests provided canopy openings that allowed regeneration of the understorey (Keller et al. 2003). In North Carolina, it was significantly associated with the number of houses and buildings within 200 m. It was also associated with an increase in the amount of forest canopy, but not significantly (Lumpkin and Pearson 2013). In western aspen stands, its abundance was correlated with ground cover; it preferred stands with dense herbaceous cover. Despite this preference, few nests were found in areas of dense ground cover. Most occupied stands had an understorey dominated by either grasses or forbs, but it appeared to select habitat on the basis of ground cover density rather than type (Flack 1976). In Colorado, it nested in trembling aspen woodlands bordered by meadows. It was a nonriparian nesting species that was unaffected by proximity to willows, water, or meadows (Glass and Floyd 2015).

The Dark-eyed Junco tends to be most abundant in very young stands and mature forests and less common in intermediate-aged stands. In many forest types, it is most abundant in recent clear-cuts and burns and declines with increasing age of stands. Older forests tend to have gaps in the canopy as a result of treefalls; they provide the microhabitats that it prefers for nesting. In Quebec

black spruce stands, older stages of forest were codominated by the junco and Yellow-rumped Warbler. The junco occurred in all age classes of forest from recent burns and cuts where the vegetation was less than 2 m tall to stands 200 years old (Imbeau et al. 1999). In Newfoundland balsam fir stands, it was most common in 80-year-old stands and significantly more abundant than in 40-year-old stands. The difference in its abundance in 80- and 60-year-old stands was not significant. The 80-year-old forest had a more open structure with lower tree and small tree density, more gaps in the canopy, fewer dead small deciduous trees, a more varied tree-height profile, shorter small trees, larger diameter dead and live trees, and more dead wood on the ground. The junco was associated with communities containing few deciduous species (Thompson et al. 1999). In Pennsylvania mixed woods, it occurred in 100% of old-growth forests, 27.1% of forests statewide, and 52.8% of forests in the Appalachian Plateau. Haney (1999) considered it to have a positive affinity with old-growth forests. Erskine (1977) concluded that it was more common in young than mature coniferous forests in the Boreal Forest Region.

Although the Dark-eyed Junco nests in forest interior, it is more of an edge species. In Newfoundland, it was considered an open-edge species. It was significantly more abundant at nonriparian edges of balsam fir forests where the opening was a clear-cut or a road than in forest interior or riparian edges. It was uncommon in riparian buffers between water bodies or watercourses and clear-cuts but absent within 30 m of riparian edges when the adjacent forest was intact (Whitaker and Montevecchi 1997, 1999). In balsam fir–white cedar forest in Quebec, it occurred in nonriparian stands and riparian stands that included a narrow wetland composed of alder, reed grass, and sweet gale along an aquatic shoreline. There was no difference in its abundance in riparian and nonriparian stands (LaRue et al. 1995). In British Columbia coniferous forests, Wiebe and Martin (1998) studied the influence of a strip of riparian vegetation consisting of a dense understorey of deciduous vegetation that was absent in the main forest. It was negatively associated with the riparian strip, but not significantly. The dense woody vegetation was probably unsuitable nesting habitat. Battin and Sisk (2011) studied its response to edge in coniferous forests in Arizona. The treatment involved a combination of thinning and prescribed burning that reduced basal area by 45% and pine stem density by 80%. It was significantly more abundant in treated than control forests. The junco was the only species that responded to an edge in the treated habitat. Its probability of occurrence peaked at the edge in both habitats. It displayed an edge-exploiting response, seeking out territories that encompassed both treated and untreated forest.

Coniferous trees are used for nocturnal roosts even where deciduous trees are more common. In Virginia, the junco always roosted in hemlock, pine, or spruce trees 2-25 m tall. If trees were tall enough, roosts were several metres above ground. When the female was fertile, both members of the pair roosted together, both on the territory of the male and on those of neighbours. Males usually select a different tree each night for roosting. Over 12 nights, 6 of 13 males (46.2%) roosted on a neighbour's territory rather than their own (Nolan et al. 2020b).

Most Ontario nests were on the ground, often well hidden in depressions in the ground, in hollows in moss, in rock crevices, and various other cavities. Fourteen elevated nests were reported: 9 in crevices on cliff faces, and 1 each in a cedar tree, Labrador tea, a hanging flower basket, a 15-cm cavity in a boulder, and a depression in a stump. Nine nests were 0.2-1.7 m from the ground and 2

nests on cliff faces were 3 and 9 m above water. Ground nests were under shrubs, vines, or trees (27.3% of nests); in or under grass clumps, ferns, and other plants (21.4%); in moss and lichen hummocks (16.9%); beside or under branches, fallen logs, fence rails, and stumps (12.3%); under earthen bank overhangs (7.8%); under rocks (6.5%); in rock crevices (4.5%); beside buildings and walls (1.3%); and 0.6% each in the end of a hollow log, under a metal barrel, and in a vole tunnel (Peck and James 1987). In Algonquin Park, 1 nest was under a dome of dead mown grass on the visitor centre tile bed (Tozer 2012).

Quebec nests are usually on the ground, sometimes in a shallow depression and occasionally in a shallow scrape where the ground is soft enough. They are often at the edge of a forest and usually well concealed under some type of shelter, in dense shrubbery or forbs, or abutting a stump or root. One nest was in a cavity 10 cm underneath a dead stump with the opening concealed by a clump of club-moss (Eaton in Austin 1968; Lessard and Limoges in Gauthier and Aubry 1996). The junco has a tendency to nest on slopes in shallow depressions or cavities overhung by vegetation and sod. It nests on hillsides, talus slopes, cliffs, and road and railway cuts, often under protruding rocks, among roots (especially of windthrown trees), under fallen tree trunks, at bases of saplings or shrubs, and in or at bases of clumps of grasses, forbs, or ferns. Many nests in mountains in the eastern United States are under polypody ferns on the very edges of cliffs. One Alberta nest had a tunnel 10 cm long through the side of a hummock of sphagnum moss to the nest, which was about 15 cm below the top of the hummock and the same distance above water. A small proportion of nests are elevated either in trees or shrubs, or in or on buildings. Most elevated nests were in the west or mountainous areas of the eastern United States. In British Columbia, 86% of nests were on the ground. Nests in trees and shrubs were usually in a crotch or fork of a branch. Maximum nest height there was 10 m but in Virginia, nests were as high as 15 m and were not placed in forks or branches. One nest was 2.1 m from the ground on the back wall of a shallow cave. In the western and eastern mountains, it may nest under, in, or on buildings. It has nested on ledges of buildings, among vines on sides of buildings, on beams and light fixtures, in hanging flower pots, in flats of flowers in a greenhouse, on rafters in barns, under eaves of buildings, and in an attic. There are 3 records of it nesting in old woodpecker holes or tree cavities and 2 records of it using nest boxes attached to sides of houses. There are several records of it relining and using old robin nests. Unusual nest locations include in a bait bucket hanging on a garage wall, in a bicycle helmet, in empty cans lying on their sides, in a bird feeder, in the corner of an empty box, and in discarded rubber tires. It typically builds a new nest for each clutch but there are at least 3 records of nests being reused; 1 was used 3 times (Bailey and Sherwood 2017; Butler 1980; Campbell et al. 2001; Chandler et al. 1994a; Eaton in Austin 1968; Flack 1976; Johnson 1988; Michael 1992; Nolan et al. 2020b; Phelps in Austin 1968; Sinclair et al. 2003; Smith 1964; Sprunt in Austin 1968; Thatcher in Austin 1968; Walsberg 2005). In Arizona, nests were in significantly more open sites with fewer total stems than random sites; predation was less likely at open sites (Nolan et al. 2020b). In Montana, it preferred to orient nests to the north (average 36°); nests with a northern orientation had cooler mean temperatures. This area had been burned at varying intensities. Females were more likely to have burrow nests (with more than 50% of the bowl under a roof of rock or soil) in high-severity burns where canopy cover was the lowest. They were less likely to burrow nests in the second year postfire when the amount of ground cover was significantly greater. Nesting success was unrelated to nest type, orientation, or

burn severity. Birds nesting in postfire sites exhibited a preference for nest sites with the most moderate microclimates: exposed and north facing (Robertson 2009a). In California burned sites, it often placed nests in unburned patches and also used non-traditional nesting sites. Two nests were on mats of pine needles more than 10 m from the ground in trees and many were under overhanging rocks or in burned root holes. These types of nest sites were not observed in unburned areas or in the burned area prior to the fire. Regardless of whether a site had been burned, nests were significantly more likely to be placed in areas of downed wood created by windthrow (J.H. Sperry et al. 2008).

Males sing from the tops of the tallest trees in the territory, often at heights of 15-23 m. Territories often include an opening in the forest canopy surrounding a rock outcrop or exposed soil bank. In Montana, territories occasionally partly overlapped and did not encompass all available habitat (Eaton in Austin 1968; Nolan et al. 2020b; Robertson et al. 2010). North of Lake Nipigon, 3 territories averaged 1.47 ha (range 1.05-1.90 ha; Kendeigh 1947). In Algonquin Park, 19 territories averaged 0.52 ha (range 0.08-1.46 ha; Martin 1960). Eaton (in Austin 1968) reported that territory sizes varied greatly in size, but most were 0.8-1.2 ha. Average territory size reported in Quebec is 1.6 ha (range 1.4-1.9 ha; Lessard and Limoges in Gauthier and Aubry 1996). Average territory size in New Hampshire subalpine forests was 1.1 ha (Sabo 1980). In Maine mainland white spruce forests, 6 territories averaged 1.67 ha; the junco did not nest on adjacent 0.1-4.0-ha islands (Morse 1977). In Minnesota, it nested on the mainland but not on islands 0.04-1.1 ha in size (Howe 1979); most or all these islands may have been smaller than its territory size. In Montana, there was no difference in territory sizes in areas subjected to different intensities of fire, or in the year of the fire compared with the following year. Territory sizes averaged 1.52-1.88 ha (Robertson et al. 2010). The mean home range of 7 females in Virginia during the nestling period was 0.83 ha (range 0.16-2.45 ha). Previous studies determined that the mean home range of females during the fertile period was 2.44 ha, significantly larger than during the nestling period and slightly larger than for males (2.11 ha). During the fertile period, the female seeks copulations, often leaving her mate's territory. During the nestling period, the female focuses on parental care and nest defence, staying closer to the nest. The home range of males during the nestling period averaged 1.31 ha, larger than for females but not significantly. Home ranges of males did not change over the nesting cycle. The large variation in the size of females' home ranges may have been related to differences in the distribution of hemlocks, which were used for roosting (Reichard and Ketterson 2012). In Virginia, Chandler et al. (1994a) implanted some males with testosterone and radiotracked them and control birds. Testosterone males had significantly larger home ranges during both the incubation (6.36 ha compared with 1.96 ha) and nestling (3.31 ha compared with 1.31 ha) periods. The 95% activity core during incubation was 1.51 ha for testosterone males and 0.33 ha for control males; respective results during the nestling period were 0.83 ha and 0.20 ha. Testosterone males often ranged more than 150 m from the nest and were occasionally found 550 m away on neighbouring territories.

Natal philopatry of migratory populations appears to be low. In northern Utah, 0 of 102 nestlings returned (Smith and Anderson 1982). In a resident population in Virginia, 26 of 265 nestlings (9.8%) were in the breeding area the following spring. Twenty-three of 253 nestlings (9.1%) that were known to have fledged and 19 of 123 fledglings (15.4%) that reached independence were present

the following spring (Wolf et al. 1988). Also in Virginia, 99 of 795 juveniles (12.4%) returned. Of 321 additional young first banded as juveniles, 73 (22.7%) returned (Nolan et al. 2020b).

Adult site fidelity rates are considerably higher than natal philopatry rates. In Ontario, 53% of males returned in the following year; at Rutherglen, 1 male returned in 3 years. In Oregon, 7 of 26 adults (26.9%) returned in the following year. In a resident Virginia population, 48 of 77 territorial males (62.3%) were present the following year and reoccupied their former territories; 44 of 104 females (42.3%) returned (Lawrence 1956; Nolan et al. 2020b).

Limiting Factors

Eggs have been found in Ontario nests from mid-April until the end of July, with most present in June (Peck and James 1987). In Algonquin Park, nests are under construction early May to early July, eggs are present mid-May to late July, nestlings are present late May to early August, and fledglings have been seen from early June to early September (Tozer 2012).

Pairing occurs as soon as females arrive. North of Lake Nipigon, this appeared to happen when spring flocks broke up. Severe weather may delay or suspend pair formation, with birds leaving their territories to assemble at feeding areas. During the interval between pairing and nest-site selection, the pair wanders aimlessly while actively feeding. During this period, considerable chasing and fighting occurs, with the male defending an area of 0.9-1.2 m around his mate. A nest site is finally selected during the wandering period; movements of the pair stabilize and they establish a territory. One nest in Algonquin Park took 2 days to build. First nests in Virginia took 3-7 days to build (average 4.5 days). Later nests were usually built in 2 days and occasionally in 1 day. In Virginia, the interval between nest completion and egg laying was 1-11 days for the first nest and 4-5 days for subsequent nests; there is usually no delay between nest completion and egg laying or a maximum of 1 day. Eggs are laid at the rate of 1 a day. Incubation is initiated with the laying of the last egg in 3-egg clutches and with the penultimate egg in larger clutches. Ontario incubation periods were 11-12 days. Elsewhere, incubation periods of 11-14 days have been reported, with most eggs hatching in 12-13 days. Because of when incubation is initiated, hatching of 3-egg clutches is synchronous and hatching in larger clutches is asynchronous. In Utah, 0% of 3-egg clutches, 58.6% of 4-egg clutches, and 77.8% of 5-egg clutches hatched asynchronously. Asynchronous hatching allows brood reduction to occur if food is scarce. Young leave the nest when they are 8-13 days old, with shorter nestling periods usually due to disturbance of the chicks (Allan 1979; Ball and Bayne 2012; Campbell et al. 2001; Eaton in Austin 1968; Kendeigh 1947; Nolan et al. 2020b; Peck and James 1987; Phelps in Austin 1968; K.G. Smith 1988; Smith and Andersen 1982; Sprunt in Austin 1968; Thatcher in Austin 1968; Wolf et al. 1988, 1991).

The Dark-eyed Junco raises 2 broods in Ontario and in much of its range, including northern British Columbia and the Yukon. In alpine areas, only a single brood is raised but in more southern areas, 3 or even 4 broods may be raised. Of 88 cases where the female successfully raised 1 brood in Virginia, 43% had 2 clutches, 44% had 3 clutches, and 13% had 4 clutches. Females usually lay a replacement clutch if one is lost. Clutches of 3-7 eggs have been reported in Ontario, with most containing 4 eggs. Six- and 7-egg clutches are rare. Mean size of 137 clutches was 4.04 eggs. Elsewhere, clutches of 1-5 eggs have been reported but 3 British Columbia nests contained 6 nestlings. Four-egg clutches are most frequent and the normal range of clutch sizes is 3-5 eggs.

One- and 2-egg clutches are rare. Most may be a result of partial depredation but there are some authentic records of single-egg clutches. In most areas, initial clutches contain 4 or 5 eggs and 3-egg clutches usually occur later in the season. Five-egg clutches have lower hatching success rates than smaller clutches but are still the most productive clutch size. Mean clutch sizes from other areas include 4.24 eggs in Colorado and Utah, 4.0 eggs in South Dakota, 4.25 eggs in the Yukon, and 3.92 eggs in California, Oregon, and Utah (Campbell et al. 2001; Eaton in Austin 1968; Nolan et al. 2020b; Peck and James 1987; Phelps in Austin 1968; Robertson 2009b; Sinclair et al. 2003; K.G. Smith 1988; Smith and Andersen 1982; Sprunt in Austin 1968; Thatcher in Austin 1968; Wolf et al. 1991).

Both sexes are capable of breeding when they are 1 year old. In Montana, all males paired successfully but floater males occur in other populations; these are probably all yearlings. Some floater males are successful in obtaining a territory later in the year (Nolan et al. 2020b; Robertson et al. 2010).

The mating system is typically monogamous but some cases of polygyny have been documented. In Virginia, 2 of more than 200 males (less than 1%) were mated to 2 females simultaneously. Polygyny also occurred occasionally when a female lost her mate. In some of these cases, a neighbouring male mated with the female. These males typically retained their existing mate and rarely cared for the young of the secondary female. Most pairs remain together for the entire breeding season. If a female's mate dies, he is typically replaced within a few hours. Replacement males rarely help raise the female's brood but most provide no assistance. When a male loses a mate, it may take weeks to replace her. Some of these males remain unmated for the remainder of the season. In established pairs in Virginia, 2 of 65 females (3.1%) dispersed within the breeding season and mated with another male. In Virginia, most pairs remain mated in subsequent years; 82% of 22 pairs that returned the following year reunited. This population is resident and any migration that occurs is altitudinal. This rate of mate retention in subsequent years may not be typical of migratory populations. In Virginia, 21-56% of young were sired extra-pair. In these studies, males were injected with testosterone so the results may not be typical. There is no evidence of intraspecific parasitism by the junco (Allan 1979; Chandler et al. 1994a; Ferree 2019; Nolan et al. 2020b; Reichard and Ketterson 2012; Wolf et al. 1991).

The Dark-eyed Junco forages predominantly on the ground, but also in low shrubs, saplings, and trees. The male may forage while he sings from treetops; therefore his average foraging height is higher than for females. On the ground, it kicks simultaneously with both feet to disturb the litter area and uncover food items. It often leaps from the ground to capture flying insects. It may forage on skid roads and other areas of bare ground when seeking conifer seeds. It may swarm finch-like at the tops of conifers to feed on seeds. In logged areas, it often forages in fallen slash. Early in spring or shortly after snowfall, it seeks snow-free areas for foraging such as the bases of trees, under dense vegetation, and south-facing slopes (Hagar 1960; Howe 1979; Nolan et al. 2020b; Phelps in Austin 1968).

Several studies described the junco's foraging techniques and substrates and some compared its foraging techniques with other species. In Ontario, foraging occurred 92.0% of the time in conifers, 42.0% in foliage, 29.8% by aerial attacks with an average attack distance of 22.7 cm, 0% by hanging, 10.0% by hovering, 10.7% by reaching, with foraging occurring at 45.0% of tree height at

an average height of 6.2 m. In Mackenzie District, foraging occurred 82.1% of the time in conifers, 66.0% in foliage, 26.1% by aerial attacks with an average attack distance of 35.0 cm, 6.4% by hanging, 0% by hovering, 8.5% by reaching, with foraging occurring at 47.0% of tree height at an average height of 3.8 m (Greenberg et al. 1999). In Vermont, foraging was 95% by gleaning, 5% by aerial attacks, and 0% by hanging and hammering. Foraging substrates consisted of 22% foliage, 0% air, 3% branches, 53% the ground, 0% trunks, and 22% twigs (Lent and Capen 1995). When foraging above ground in Arizona, 84% of observations were at 12 m or below in the lower two thirds of the vegetation (Nolan et al. 2020b). In northern hardwoods in New Hampshire, the junco was in the ground-foraging guild. Its prey attacks were 64.7% 0-0.2 m from the ground, 20.4% on shrubs at heights of 0.3-2 m, 12.5% on saplings 2.1-8 m tall, 3.1% in the subcanopy at 8.1-14 m, and 0.2% in the canopy above 14 m. It directed 37.4% of its prey attacks on the ground or in litter, 18.7% on a forb or fern, 34.6% on foliage, 4.6% on bark, and 4.7% in the air. Prey-attacking manoeuvres consisted of 6.9% probing, 62.7% gleaning, 20.5% jumping and hovering, 5.7% hovering, 0% diving and gleaning, and 4.2% hawking. The forest floor was the most common foraging substrate for all species studied except the Winter Wren which foraged in the shrub layer. All 6 ground-foraging species (Swainson's Thrush, Hermit Thrush, Wood Thrush, Veery, junco, and Ovenbird) differed in one or more aspects of their use of space, foraging behaviours, and diet (Holmes and Robinson 1988). In subalpine areas of New Hampshire, Sabo (1980) classified the junco as a forest-floor forager. Its foraging techniques consisted of 0% aerial flycatching, 17.2% leaf gleaning, 5.0% leaf hawking, 0.3% leaf hovering, 20.2% twig pecking, 21.5% twig gleaning, 5.7% hawking and hovering, 1.5% branch pecking, 1.7% branch gleaning, 0.3% bole pecking, 0.2% bole gleaning, 21.4% litter picking, 3.8% litter gleaning, and 1.4% fallen log manoeuvres. Twenty-three percent of foraging occurred distal to the trunk, 48.1% proximal to the trunk, 57.9% on coniferous tree foliage, 13.6% on deciduous tree foliage, 3.0% on herbaceous foliage, and 25.7% on the forest floor. Foraging height included 13.0% in the understorey at height 0.1-2 m, 35.7% in the midstorey at 2-5 m, 16.8% in the midcanopy at 5-8 m, and 8.8% in the upper canopy above 8 m. Lima (1988) provided juncos with 3 sizes of crushed millet bits and whole millet seeds. Whole seeds took significantly longer to handle, so bits were more profitable to consume. Scanning for predators and handling were mutually exclusive for bits but not for whole seeds. All birds ate both bits and whole seeds. Males ate significantly more whole seeds than females, possibly because males are dominant. The proportion of whole seeds in the diet decreased with an increase in flock size when individuals would not need to be as vigilant. The foraging strategy was a trade-off between the need to be vigilant and to maintain a high rate of energy intake. If predators were not a concern, the junco would be unlikely to eat whole seeds. In an aviary, Goldstein and Baker (1984) offered juncos canary and niger seeds that were natural as well as in pellets and seeds. When offered as pellets, most birds significantly preferred canary seed to niger seed, but natural niger was preferred to natural canary seed. Of 12 birds that had significantly different handling times, 11 preferred the seed (10 niger, 1 canary) that they handled the quickest. Birds did not exhibit an absolute preference for a seed type and usually ate some of the less preferred seed. In an aviary, sparrows, including the junco, were more efficient handling seeds smaller than 0.74 mg; finches were more efficient at handling seeds larger than 1.44 mg (Benkman and Pulliam 1988).

When the male fails to feed the nestlings or dies, the female is capable of raising the entire brood. Although females without assistance can successfully fledge their broods, they may not be able to raise all their fledglings to independence. When nestlings are young, they may be fed regurgitated or partially digested food as well as moths and caterpillars. Older nestlings are fed yellow grubs, owlet moths, spruce budworms, caterpillars, caddisflies, crane flies, soft parts of grasshoppers, and millet. During several hours of observation, young were fed nothing but large numbers of smooth green caterpillars (Eaton in Austin 1968; Nolan et al. 2020b; Thatcher in Austin 1968; Wolf et al. 1988, 1991).

The adult diet consists mostly of insects during the breeding season and vegetable matter the remainder of the year. Eaton (in Austin 1968) reported that adults ate mostly caterpillars, beetles, and ants in the summer, but also wasps, bugs, grasshoppers, other insects, and spiders. In early spring, it feeds on swarming springtails, catches emerging gnats on the snow or in the air, and preys on hatches of winter stoneflies. In late summer and autumn, it eats caterpillars of fall webworms. Seeds the Dark-eyed Junco consumes in autumn and winter include those of ragweeds, foxtails, dropseeds, crabgrasses, amaranths, and goosefoots. Thatcher (in Austin 1968) stated that adults eat dandelion seeds and those of brome grasses and amaranths. In winter, it may feed on spruce seeds in trees with the Pine Grosbeak, Red and White-winged crossbills, and Pine Siskins. Phelps (in Austin 1968) reported that it fed at sapsucker wells, but it was unknown if it was feeding on insects or sap. In spring in Ontario, it has been documented feeding on sugar maple sap icicles (Simpson 2025). In spring, it eats plant galls and seeds of goosefoots, knotweeds, melic grass, and lesser amounts of seeds of pines, catchflies, wheat, annual bluegrass, knapweed, mayweed, scarlet pimpernel, sheep sorrel and wood-sorrel. Twenty-five stomachs collected in the breeding season contained leafhoppers, bugs, beetles, adult and larval lepidopterans, a fly, ants, a spider, and several seeds including those from sunflowers. In California, cultivated and wild oats constituted 10-25% of the autumn and winter diet; seeds of common chickweed were equally important. Cultivated and wild barley comprised 5-10% of the diet during this period; seeds of amaranths were also prominent in the diet. Judd (1901) analyzed the contents of 299 stomachs collected in every month but May, mostly from the Atlantic seaboard but also from the central United States and California. The annual diet consisted of 22% animal matter and 78% vegetable matter. The animal matter consisted of 7% miscellaneous insects that were mostly true bugs, 6% beetles, 3% hymenopterans, 2% orthopterans, 2% lepidopterans, and 2% spiders plus a few snails and other invertebrates. Sixty-five stomachs collected from June to August in California and North Carolina contained 49% animal matter and 51% vegetation. Beetles were important insect food items, including 1% ground beetles, 2% leaf beetles, 8% weevils, 6% click and long-horned beetles, and 16% insects that were mostly small dung beetles and ants. Other animal foods included 4% caterpillars, 5% grasshoppers, and 5% parasitic wasps. The vegetation consisted of 49% seeds and 2% fruits of blueberries, blackberries, strawberries, and elderberries. Important seeds included 9% violets, 8% smartweeds, 5% grass seeds, and smaller amounts of sedges, sheep sorrel, wood-sorrel, purslane, and chickweed. The winter diet consisted of 9% animal matter and 91% vegetation. The vegetable matter could be divided into 3 almost equal parts. The first consisted of seeds of timothy, broomsedge, foxtails, crabgrasses, panic grasses, and paspalum, with small amounts of grain and ensheathed dropseed. The second part consisted of ragweed and smartweed seeds and the third part was comprised of seeds of various

plants, mostly amaranths, lamb's-quarters, chickweed, purslane, tick-trefoil, vetches, gromwell, wood-sorrel, sedges, sheep sorrel, wild sunflowers, and Russian thistle. Seeds of amaranths and lamb's-quarters were by far most important in the diet. Few other sparrows eat as many of these seeds as the junco and it feeds on them mostly in March. Beal and McAtee (1912) analyzed the contents of more than 500 stomachs collected in the United States in all months. They contained 23% animal matter and 77% vegetation; their results also included the stomachs that Judd (1901) analyzed. The principal food was weed seeds (61.8% of the diet) that were eaten in every month and comprised 95% of the September diet. Grain (oats, wheat, barley, and corn) constituted 8% of the diet. Animal foods included 6% beetles, 2% hymenopterans that were mostly ants and a few wasps, 9.4% caterpillars, and 7.3% bugs, grasshoppers, other insects, and spiders. Smith and Andersen (1982) examined the contents of 3 adult stomachs collected during the breeding season in Utah. Major food items included ants, 6 unspecified families of beetles, leafhoppers, and spiders. Juncos also ate lacewings, leaf bugs, and several wasps that were mostly ichneumonids. Only a single beetle larva was found in the stomachs, but they observed adults feeding many beetle larvae, caterpillars, and orthopteran nymphs to nestlings. Hagar (1960) analyzed the contents of 460 stomachs collected in California, mostly from birds foraging in clear-cuts but some were collected in forests. It preferred seeds of Douglas-fir when they were available. In spring, insects, especially small beetles, were a substantial component of the diet complemented by seeds of early successional plants that invaded clear-cuts. By June, these seeds comprised 21-32% of the volume of the food. In summer, the junco depended heavily on seeds of a great variety of weeds and grasses, with the most important being those of bull thistle, fescues, bluegrasses, wiregrass, knotweeds, and willow-herbs. Fruits of raspberries and strawberries were of some importance in late summer. The autumn and winter diet varied considerably annually depending upon the availability of different foods. In 1 winter, fruit of the arbutus tree was used extensively along with forb and grass seeds. Douglas-fir seeds were a minor component of the diet in 1 year but more than 50% of the food volume during 1 autumn and winter and into the next spring. In spring, it also ate germinating seeds and very young fir seedlings. Consumption of fir seeds decreased by June and no new seeds were produced, so it reverted to eating grass and weed seeds. Insects were less important in the diet in the year that fir seeds were abundant, but still comprised 60% of the food volume. Nolan et al. (2020b) reported that 269 juncos collected in California had eaten 24% animal matter and 76% vegetation. In order of decreasing frequency in the diet, the animal food consisted of beetles, moths and butterflies and their caterpillars, ants and wasps, flies, and miscellaneous insects and spiders. The diet was comprised of 62% seeds, with important groups including chickweeds, amaranths, knotweeds, and sorrel. In another sample of 248 stomachs, the diet consisted of 76% vegetation from November to March, 40% in April and May, 93% from June to August, and 92% from September to October. Ragweed and various grass seeds were important in the diet. During the same periods in California, the amount of vegetation consumed was 74%, 52%, 95%, and 91%. Chickweed seeds were important but it frequently ate grama grass and crabgrass seeds. The junco drinks from streams, ephemeral pools, and moisture on vegetation and also eats snow.

The Dark-eyed Junco frequently eats budworms and may or may not increase its population in response to outbreaks. In New Brunswick, it exhibited the highest mean consumption rate of black-headed budworms of the species studied. It was one of the most effective predators of budworms

and increased in density in response to increasing budworm populations (Gage et al. 1970). Near Manitouwadge, Venier et al. (2009) observed no numerical response of the junco to spruce budworm numbers, but it was uncommon within the area. Morris et al. (1958) also observed no response in New Brunswick. In Maine spruce–balsam fir forest, Mitchell (1952) determined that it frequently ate spruce budworms but did not study its population response. In New Hampshire and Maine, Crawford and Jennings (1989) reported that it consumed an average of 1.7 budworms per stomach, a moderate consumption rate for the bird species examined. It responded positively and ate more budworms as their population increased. They did not observe an increase in junco numbers in response to the budworm outbreak but acknowledged that the population could have increased over several years as numbers of budworms increased. In northern hardwoods in New Hampshire, density of the junco was higher during years of an outbreak of the saddled prominent moth (Holmes and Sturges 1975).

The Dark-eyed Junco is an uncommon host of the Brown-headed Cowbird in the east. Parasitism rates may be higher in the west, particularly for populations of juncos that nest near human habitation. The junco accepts cowbird eggs. No detailed studies have been done on the effects of parasitism, but cowbirds in Virginia removed junco eggs in about half the nests they parasitized. An average of 1.7 cowbird eggs were laid in parasitized nests and 1.2 junco eggs were removed by cowbirds. In Ontario, 7 of 177 nests (4.0%) were parasitized, 1 of 75 Quebec nests (1.3%) was parasitized, 25 of 840 British Columbia nests (3.0%) were parasitized, and adults have been observed feeding cowbird fledglings in the Yukon. In the United States, 40% of Virginia nests, 25% of Sierra Nevada nests, 1 of 3 Michigan nests (33.3%), and 1 of 48 California nests (2.1%) were parasitized (Campbell et al. 2001; Nolan et al. 2020b; Peck and James 1998b; Sinclair et al. 2003; Turner et al. 2022).

Extreme habitat loss occurred south of the Canadian Shield due to deforestation around the turn of the 20th century. South of the Shield, the junco is now confined to extensively forested landscapes in areas such as the Bruce Peninsula, the Norfolk Sand Plain, and southeastern Ontario. Populations in these areas may be at risk due to habitat fragmentation.

The junco may exhibit a neutral or positive response to forest management, with positive effects usually associated with the removal of a higher proportion of trees. In California coniferous forests, biomass thinning removed small-diameter low-quality trees, opened up the canopy, and increased understorey cover. There were significantly more nests in thinned plots and they were significantly more successful (Siegel and DeSante 2003). In mature trembling aspen forests in Colorado, it was initially abundant in clear-cuts; 5 years after cutting, it was equally abundant in cut and uncut forest. In British Columbia coniferous forests, it was more abundant in tracts with greater tree removal (Nolan et al. 2020b), and readily colonized 60-100 year-old trembling aspen stands after they were clear-cut (Campbell et al. 2001). In California, it was equally abundant in clear-cut and uncut forest in the first year. Once weedy vegetation became established in cuts, the junco population increased to 2-3 times that in virgin forest, peaking 3-6 years after cutting when shrubs and sapling were the dominant vegetation (Hagar 1960). In the Boreal Forest Region of Ontario, it increased by 50% when 20% of tree cover was removed (Vanderwel et al. 2007). In Maine spruce–balsam fir forests, the junco was most abundant in clear-cuts for 2 years following cutting. It was less abundant in closed-canopy

forest and absent in intermediate stages of forest (Titterington et al. 1979). In northern hardwoods in Nova Scotia and New Brunswick, it was most abundant in clear-cuts, intermediate in abundance in mature forests and strip-cuts, and absent in stands that were thinned by shelterwood or single-tree logging (Freedman and Johnson 1999; Freedman et al. 1981). Falardeau et al. (1999) reported similar findings in Quebec. In Idaho, it was equally abundant in uncut forests and those cut by single-tree selection (Medin and Booth 1989). In New York northern hardwoods, it did not appear to respond to logging where 25-100% of the merchantable timber was removed. Even in 100% removal, residual areas were still forested because non-merchantable timber was retained. The lack of response may have been because it was scarce, representing 2-3% of birds detected in all treatments (Webb et al. 1977). In Pennsylvania, timber stand improvement involves removing dead, dying, diseased, suppressed, or low-quality trees. It was more abundant in improvement stands where snags were retained. Snag-retention areas had a more patchy and open canopy and greater availability of low-growing vegetation and woody plants (Stribling et al. 1990). In Newfoundland, Whitaker et al. (2009) captured 67% of birds in landscapes that contained clear-cuts and 33% in landscapes without clear-cuts. There were no differences in survival rates of birds in cut and natural landscapes. Harrison et al. (2005) studied its response to partial harvest of forests in Alberta. It increased in deciduous stands when 100% of trees were cut, increased in deciduous stands with an understorey when 90% of trees were cut, increased in mixed forests when 20% and 50% of trees were cut, and increased in coniferous forests when 100% of trees were cut. It colonized deciduous forests where it was previously absent when 25-100% of trees were removed but the increase was significant only when 100% of trees were removed. It colonized or increased wherever trees were cut regardless of forest type.

The Dark-eyed Junco appears to be little affected by fire and any effects typically last less than a year (Nolan et al 2020b). In Oregon, Stephens et al. (2015) found that it demonstrated no clear response to fire; its abundance did not vary with fire intensity. In the Sierra Nevada, it was equally abundant in burned and unburned forests (Bock and Lynch 1970). In California, J.H. Sperry et al. (2008) found no difference in its abundance in unburned areas and where prescribed burning removed small-diameter trees. Potentially negative effects due to reduction in litter and an increase in the amount of bare ground were offset by increased food availability and novel nesting strategies such as nesting in small unburned patches and selecting non-traditional nest sites that offered better concealment. In Montana, it was equally abundant in burns of low, intermediate, and high intensity. Nest-predation probability was significantly less in intermediate-intensity burns than in low- and high-intensity burns. Females in intermediate-intensity burns had larger clutch sizes. In high-intensity burns, females were more likely to select nest sites that were concealed by overhanging rocks or turf (Robertson 2009a, 2009b).

In Arizona, grazing by cattle in forests had adverse effects on the Dark-eyed Junco. Grazing resulted in a 75% reduction in fledging success, mostly due to cattle cropping the vegetation overhanging nests; other nests were trampled (Walsberg 2005). On Anticosti Island, grazing by white-tailed deer had no significant effect on the junco (Cardinal et al. 2012). Grazing is unlikely to be an issue in Ontario. The main range of the junco is outside areas of high density of livestock and deer.

Marzluff et al. (2007) examined habitat use by the junco in relation to predator distribution. At larger scales of 1 km and 0.5-70 ha, it was positively associated with corvids and members of the squirrel family but was negatively associated with squirrels in forest patches. Although it co-occurred with nest predators at larger scales, it strongly avoided areas within forests that were rich with a single predator or all predators combined.

The junco responded favourably to energy sector disturbances in Alberta forests. It was significantly more abundant at seismic lines, pipelines, and well pads than in forest interior adjacent to these features (Bayne et al. 2016). In Quebec, Rail et al. (1997) used playbacks of the junco's song to determine the effects on territoriality of gaps 3-100 m wide. Its response did not seem to vary abruptly at any gap width, suggesting that gaps in contiguous forest did not have a strong effect on its territorial response. There was no difference in its probability of crossing different types of gaps, including power lines, roads, ski trails, and clear-cuts. There may have been no discernible effect because the junco nested in most of these gaps.

Gutzwiller and Anderson (1999) studied the effects of human intrusion on juncos nesting in Wyoming subalpine forests. A researcher walked within a 1.0-ha plot for an hour. There was no difference in its abundance inside and outside disturbed areas.

The junco may benefit from reforestation of farmland (Lessard and Limoges in Gauthier and Aubry 1996). This is the case in the Norfolk Sand Plain where reforestation over a century ago resulted in natural-appearing pine-oak forests and stands of mature pine. This area supports one of the few breeding populations in the Carolinian Forest Region.

Birds nesting at high altitudes or in northern areas may experience nest loss as a result of late-season storms (Phelps in Austin 1968). Where the junco raises a single brood, this has the potential to significantly reduce annual productivity. Where more than 1 brood is typically reared, storms may eliminate the possibility of more than 1 brood.

Price (2004) predicted that the Dark-eyed Junco might be excluded from breeding in southern Ontario if the average summer temperature increased by 2°C. In southern and central Quebec and Labrador, it occurs mostly in stands with low summer temperatures and high precipitation. Consequently, it is vulnerable to climate change (DesGranges and LeBlanc 2012; DesGranges and Morneau 2010).

Status

Prior to the 20th century, the Dark-eyed Junco was a common resident that bred throughout the province (McIlwraith 1894). Lancaster et al. (2004) reported that it was a common resident that bred in Elgin County in 1891. It bred in Halton in 1906 and was a scarce nester in Wellington County at approximately the same time (Brewer 1977; Curry 2006). In 1901, it was a common breeding species in Muskoka and Parry Sound districts; it was abundant in southwestern Parry Sound in 1928 and at Lake Muskoka in 1906. By the turn of the 20th century, it was disappearing south of the Canadian Shield as a result of extensive deforestation. There was no evidence of it breeding within the Hamilton area from 1925 to 1956. Baillie and Harrington (1937) considered it a common summer resident of the entire province that nested everywhere except in the extreme southern counties. By 1954, and probably much sooner, it occurred in Elgin County only as a migrant and winter resident

(Lancaster et al. 2004). Mills (1981) reported that it was still widespread in Parry Sound and Muskoka districts, but less common than formerly. Tozer (2012) noted that it had decreased in recent decades in Algonquin Park. It was more numerous in the 1930s in young forests created by fire and logging. The decline was attributed to maturation of trees and filling in of open forests. The first atlas demonstrated that it nested throughout the Canadian Shield to the Hudson Bay coast, with the exception of Cape Henrietta Maria. Its distribution became spotty in the southern portion of the Shield south of Algonquin Park. In the Great Lakes–St. Lawrence Forest Region south of the Shield, it was confined to heavily forested areas such as the Bruce Peninsula, the Oak Ridges Moraine, and scattered areas in extreme southeastern Ontario. The only records from the Carolinian Forest Region were from Long Point and Simcoe where it bred in tracts of conifers (Rising in Cadman et al. 1987).

The second atlas revealed that there had been no change in the range of the Dark-eyed Junco. Province-wide, its probability of observation increased significantly, with significant increases in the Boreal Forest Region and Hudson Bay Lowland, but a significant decline in the Shield portion of the Great Lakes–St. Lawrence Forest Region. Breeding evidence was obtained at Cape Henrietta Maria during the second atlas. Reasons for the decline in the southern portion of the Shield may be related to forest maturation and canopy closure. It was most abundant in the northern portion of the Hudson Bay Lowland. It was also common in the remainder of the Hudson Bay Lowland and the northern portion of the Boreal Forest Region (Rising in Cadman et al. 2007).

In Ontario, the Breeding Bird Survey (BBS) does not cover the area where the junco is most abundant, so it may not be a reliable indicator of population change. During 1970-2021, BBS data indicate that the junco decreased annually by 1.13% in Canada and 2.5% in Ontario. The trends 2011-21 were annual decreases of 0.864% in Canada and 3.96% in Ontario. All results were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young are poorly developed when they fledge and incapable of flight for 3-4 days. They run or hop from the nest and move upward in the understorey and lower canopy, where they behave cryptically. Until age 23-28 days, brood mates are scattered and do not associate with each other. They become independent 14 days after fledging at age 25-27 days, although feeding by adults may occur until 24 days after fledging. After age 30 days, they increasingly occur in flocks. In Virginia, many fledglings began dispersing from the natal home range at age 30 days. The maximum distance travelled from the natal site before age 40 days was 2.2 km. Nonetheless, many birds 50-60 days old were caught on the natal territory. It was unknown if they had remained there all the time or if they had dispersed and returned. Fledglings 31-40 days old averaged 50 m from the nest, those 51-60 days old averaged 700 m from the nest, and 71-80-day-olds averaged 500 m from the nest (Bailey and Sherwood 2017; Eaton in Austin 1968; Nolan et al. 2020b; Smith and Andersen 1982; Thatcher in Austin 1968; Wolf et al. 1988, 1991).

Thatcher (in Austin 1968) studied a pair that raised 3 broods. Shortly after leaving the nest, young of the first 2 broods moved out of the nesting territory. The third brood remained in the territory until they had almost completed their moult. The adults left the territory together before the fledglings did. Members of the third brood mixed with other broods once the adults left and left the territory together after autumn migration was well underway.

Late summer and early autumn is an important period for juveniles. At this time, they congregate in flocks that wander around on the breeding grounds, with much mixing of flocks. Later in the season, birds that remained near the natal site are joined by juveniles that were raised elsewhere. During this period, young begin familiarizing themselves with potential breeding sites and this makes them more successful in obtaining a territory the following breeding season. In Virginia, 76 of 122 juveniles (62.3%) that had been present in the previous summer or autumn were successful in obtaining a territory compared with 5 of 46 (10.9%) that were not present the previous year. Individuals' status within flocks is determined during the postfledging period. It is possible that this is an important determinant of winter survival (Hagar 1960; Leary et al. 1999; Nolan et al. 2020b).

The junco uses a wide variety of habitats during the postfledging period. In Pennsylvania, Stoleson (2013) captured adults and juveniles in clear-cuts and adjacent mature deciduous forests; both habitats had a dense shrub understorey. Major and Desrochers (2012) captured juncos in young clear-cuts in balsam fir–black spruce stands in Quebec. In Washington, fledglings that had been raised in a nest box on a house in a rural residential area remained around the property for 2 weeks after leaving the nest (Bailey and Sherwood 2017).

Both adults feed the fledglings, although females attempting second broods leave care of fledglings of the first brood to the male once they begin incubation. In Virginia, male care of fledglings was extremely important in raising juveniles to independence. The number of young reaching independence was 2.5 times greater in broods where both adults fed the fledglings than in broods fed only by the female (Wolf et al. 1985, 1991).

MIGRATION

All northern populations of the Dark-eyed Junco are migratory, and breeding and wintering birds do not overlap. In mountainous areas, it may undertake altitudinal migration, moving to lower elevations during the winter. Some western populations are resident. It commonly migrates at night. Kills at towers in December and January in Florida suggest that it makes facultative southward movements to avoid adverse weather conditions. Flocking at night is unlikely, but simultaneous departure of flock mates at dusk has been documented. Members of a diurnal group may gather independently at sites that provide food and shelter, or bottlenecks such as water crossings, then depart as an apparent flock. Family members do not travel together because of dispersal of young and differential timing and distance travelled by the sex and age classes. East of the Mississippi River, sex and age classes winter in different areas. In the northern states, the wintering population is comprised of 20% females; in Texas, 75% of birds are females. The percentage of females at differing wintering areas were 28.0% in Washington, 23.8% in Utah, 19.9% in Michigan, 34.6% in Ohio, 27.9% in Indiana, 53.1% in South Carolina, and 72.5% in Alabama. Females travel further south than males and young of both sexes tend to concentrate further north than adults. Young males are the most prevalent age class at latitude 40°N, adult males have a bimodal distribution, peaking at latitude 40°N and outnumbering juvenile males at latitude 35°N, young females peak and outnumber any other group at latitude 35°N, and adult females are most abundant at latitude 33°N. Temperature was consistently a better predictor of sex ratio than latitude or the amount of snowfall. Spring migration appears to be triggered by photoperiod. Spring migration is usually more rapid than autumn migration, with spring migrants making fewer stopovers and staying shorter periods during

stopovers. In Michigan, average stopover periods were 9.7 days in spring and 13.6 days in autumn. Recaptures of birds in Michigan in subsequent years revealed that certain individuals used the same migration route in spring and autumn (Ketterson 1979a; Ketterson and Nolan 1979, 1982; Nolan and Ketterson 1990; Nolan et al. 2020b; Sprunt in Austin 1968; Stack and Harned 1944). Of birds banded or encountered in winter in Ontario, almost two thirds wintered in the province. The remainder wintered across the Great Lakes states eastward to Pennsylvania and North Carolina. Recoveries indicated a wide range of direction of travel suggesting that Ontario migrants may breed both east and west of the province (Brewer et al. 2018).

Males migrate before females in spring and usually arrive on the breeding grounds 10-14 days earlier than females. At Rutherglen, a female arrived 11 days after her mate. Over a 63-year period in Manitoba, there was no significant change in its arrival date in relation to climate change (Chandler and Mulvihill 1990; Lawrence 1956; Murphy-Klassen et al. 2005; Nolan et al. 2020b). Because the junco is a winter resident in much of southern Ontario, it can be difficult to determine when spring migrants arrive; for some areas, only spring departure times are known. Most depart in late April and early May with some remaining until late May. There is a peak in numbers in April when migrants move through, with migrants arriving in mid-March in the south and late March or early April in the southern Shield (Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). Manning (1952) observed 3 migrants at North Point north of Moosonee on 6 June. At Shagamu, Wilson and McRae (1993) observed migrants from 28 May to 9 June.

During autumn migration in Indiana, the age and sex classes tended to arrive together. When there were differences in timing, females predominated among early arrivals. In Pennsylvania, females moved south before males and adult females moved before juvenile females. In Indiana, birds that stayed to become winter residents did not arrive earlier than those that continued to migrate. Adults were caught earlier than juveniles. The median capture dates of the sex and age classes were arranged according to the north-south order of their winter destination. Those that had the furthest to travel passed through or settled in for winter the earliest (Ketterson 1979a; Nolan and Ketterson 1990; Nolan et al. 2020b).

Wilson and McRae (1993) observed autumn migrants at Shagamu 20-30 August. In the southern Shield, migration begins in earnest in mid-September and peaks in mid-October, with some birds remaining into early November. Most arrive in southern Ontario in mid-September, with some arriving in early September or as early as mid-August (Black and Roy 2010; Curry 2006; Easton in Austin 1968; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

During migration, the Dark-eyed Junco prefers tree or shrub habitat adjoining open areas. In Algonquin Park, it occurs in clearings, roadsides, campgrounds, and around feeders. It may use a variety of habitats during migration, including wetlands, backyards (especially if a feeder is present), alpine tundra, hedgerows, edges of woodlands, cemeteries, brush tangles and piles, riparian vegetation along streams and water bodies, orchards, weedy country roadsides, pastures, fallow fields, beach edges and spits, meadows, clear-cuts, open burns, utility rights-of-way, bogs, marshes, willow thickets, and harvested croplands. The earliest autumn migrants arrive in Kansas when the weather is warm. These birds tend to remain in deep shade in cool and sheltered areas and forage

mostly in open fields when the ground is snow-free (Campbell et al. 2001; Fitch 1958; Nolan et al. 2020b; Phelps in Austin 1968; Sinclair et al. 2003; Tozer 2012).

In Kansas, autumn migrants usually roosted at night in flocks in dense grass, often in smooth brome (Fitch 1958). In Illinois, autumn migrants commonly roost in tall or fallen grass (Gottfried and Franks 1975).

Flocks of migrants form in autumn. At a California site, 2 clear-cuts separated by a timbered ridge each supported a flock of 30-40 birds. Birds from each flock readily mixed with birds of the other flock. Some birds left the area entirely and 2 wandered at least as far as 3.2 and 4.8 km. Although wandering and mixing of flocks occurred freely during October and early November, flock sizes in each clear-cut did not change appreciably. Individuals did not become committed to a single flock or foraging area until December. Once this occurred, flocks remained constant through the winter except during periods of heavy snow (Hagar 1960).

There is evidence that at least some individuals exhibit fidelity to migratory stopover sites in subsequent years. In Michigan, 14 of 5,369 birds (0.3%) were recaptured in a subsequent year and 1 bird returned twice. Some birds were banded in autumn and recaptured the following spring and some banded in spring were recaptured in autumn of the same year. One bird was recaptured 3 years after it was banded (Stack and Harned 1944). Michael (1994) reported a bird at a Washington feeder 16-21 March in 1 year and on 19 March the following year.

In Ontario, the junco has been observed eating seeds of giant ragweed and black alder in autumn and winter (Dance 2008; Dance et al. 2012). In Idaho, Carlisle et al. (2012) compared the diet of autumn migrants with the availability of insects. Prey consumed by the junco more frequently than its abundance included, in decreasing order of preference, beetles, ants, hymenopterans, and leafhoppers. Prey consumed less than its availability, in order of decreasing avoidance, included jumping plant lice, true bugs, spiders, stilt bugs, hornets, wasps, flies, stink bugs, lepidopterans, and spittle bugs.

In the east, small numbers are killed during migration by nocturnal collisions with television towers and other tall structures. In 1 night in Kansas, 2,000 were killed at a tower in October, but the rate is typically low at less than 1-2 per year at different locations (Nolan et al. 2020b).

James (1991) considered the Dark-eyed Junco a common to locally abundant migrant. In the south, spring flocks often number 500-1,000 birds; flocks of 2,000 or more occur in autumn (Curry 2006; LaForest 1993; Weir 2008).

Hussell et al. (1992) reported that captures of the junco at the Long Point Bird Observatory decreased at a nonsignificant rate of 0.1% per year 1961-88. Trends by period were: 1961-70, –1.6%; 1970-79, –4.0%; and 1979-88, +4.5%.

WINTER

In the east, the Dark-eyed Junco avoids areas that have a minimum January temperature less than –18°C to –12°C. It is absent in winter from southern Texas, areas along the Gulf Coast, and from peninsular Florida. High concentrations occur throughout much of its winter distribution. The western extent of where it occurs appears to be determined by precipitation, with highest

concentrations occurring where the annual rainfall exceeds 61 cm. Areas of high concentrations extend southward only as far as where the minimum January temperature is less than 4°C. The highest numbers are largely in riparian habitats (Root 1988).

In southern Ontario, Smith (2003) summarized results of Winter Bird-Population Studies to determine the abundance of the junco in different habitats. Densities per km^2 were significantly different among habitats: 27.6 in urban natural areas smaller than 10 ha, 20.5 in larger urban natural areas, 8.7 in urban natural areas with water, 7.9 in forest, 0.6 in urban commercial and residential areas, and 0 in croplands, some of which had hedgerows. In suburbs of California, it occurred far from fields and close to trees and shrubs (Kalinowski and Johnson 2010). In forest fragments in Ohio, it was less likely to be present as woodlots became more isolated (Doherty and Grubb 2000).

Habitat used in winter is similar to that used during migration. The junco is most common in landscapes fragmented by agriculture and urbanization. Within these landscapes, it inhabits weedy fields, utility rights-of-way, roadsides, forest edges, hedgerows, shrubby areas, orchards, fallow fields, grasslands, agricultural fields with waste grain, urban residential areas, and feeding stations in all types of habitats. In Illinois, fallow fields, ungrazed grasslands, pastures, and cornfields were favoured habitats. In British Columbia, it concentrated in urban areas in winter (Black and Roy 2010; Campbell et al. 2001; Fitch 1958; Graber and Graber 1963; Nolan et al. 2020b). In Ontario, birds south of the Canadian Shield occupy a wide range of habitats. Those in the Shield are often restricted to areas with feeders. In Indiana, it was most abundant in savannahs, followed by prairie remnants disturbed by fire, anthropogenically disturbed areas, woodlands, scrub, and forest. Densities per km^2 ranged from 0 in forests to 119 in savannahs but differences were not significant (Grundel and Pavlovic 2007b).

In Colorado, housing density was the greatest factor in determining abundance of the junco. It increased significantly as the density of housing within 100 m increased. It probably benefitted from bird feeders and ornamental seed-bearing plants. Its abundance also increased as the average height of understorey vegetation increased (Miller et al. 2017).

In Maryland, Blank et al. (2011) studied the effects of mowing grassy buffers interspersed with wildflowers on numbers of wintering juncos. The buffers were between forested wetlands and row-crop fields and were mowed to heights of 10-15 cm in late summer or autumn. Mowing significantly reduced winter junco populations from 34 per km^2 in unmowed buffers to 7 in mowed buffers. In Arkansas, Kentucky, and Mississippi, it was more than 3 times abundant in fields with buffers than those without buffers. It was more abundant in buffers wider than 23 m than in narrower buffers, but not significantly (Evans et al. 2015).

Most juncos remain in fairly stable flocks over winter. In North Carolina, birds inhabiting open weedy fields remained in large stable flocks. Birds in mature woods occurred in small groups or individually (Fretwell 1969b). Flocks tend to maintain a stable home range but do not defend them from other flocks. Home ranges may shift in response to snow accumulations or other factors, and individuals may switch flocks (Nolan et al. 2020b). In Illinois, Gottfried and Franks (1975) observed 2 winter flocks. Flock 1 of 11 birds remained within an area of 27 ha. Flock 2 used 2 home ranges. The first was 33 ha that was used from flock formation in mid-December until 30 January when the flock broke up due to an accumulation of 10-15 cm of snow. The birds reunited a month later when the

snow melted. For the first week after the flock broke up, members stayed in 5 groups of 2-4 birds, with each group occupying a non-overlapping foraging area within the original home range. After the first week, 4 of the groups abandoned their foraging area and congregated with other sparrows at nearby cattle pens where food was available. The fifth group remained where a large tree prevented the accumulation of deep snow. All 3 winter ranges had specific areas used day after day for certain activities. Each contained an area where intensive feeding occurred in the morning and late afternoon and an area where most non-feeding activities occurred at midday. Scrub areas were used for intensive feeding by 1 flock; the other flock used short-grass pasture. Midday activities occurred in trees and shrubs adjacent to cultivated fields. Birds usually fed in areas with trees, shrubs, or tall forbs, including short-grass pastures and soybean fields bordered by shrubs. Birds flew to shrubs when disturbed and perched there between foraging bouts. The occurrence of such vegetation probably determined to some extent which feeding areas were used within the home range. Areas lacking taller vegetation, such as hayfields and centres of large cultivated fields, were rarely used and tallgrass pastures were never used. Flocks spent most of the day in scrub and short-grass pastures. Flock 1 spent about 82% of its time in scrub and 18% in cultivated fields. The second flock spent 58% of its time in scrub, 21% in short-grass pasture, 16% in cultivated fields, and 4% in woods while it was intact. After it broke up, it spent 35% of its time in scrub, 51% in short-grass pasture, 5% in woods, and 4% in hayfields. Daily movements in each home range followed a consistent pattern, especially on clear cold days. Flocks perched on trees adjacent to the roost shortly after sunrise. After leaving the roosting area, birds followed a feeding circuit that extended 0.5-1 km from the roost. The furthest locations from the roost were used from midmorning until late afternoon. Birds followed a similar route back to the roost. On days with snow accumulation, high winds, or low temperatures, movements from and to the roost were irregular because many birds left the flock for varying amounts of time. In flock 1 and the dispersed flock 2, birds gradually worked across a large field as they moved from the roost, although there were some reverse movements. In the intact flock 2, birds fed for about an hour in a short-grass pasture each morning after leaving the roost then flew 600 m to an area where they remained most of the day. There were 13 ha of this route that lacked tall vegetation and was never used for feeding. Birds changed where they fed in agricultural fields over the season. During autumn migration, large flocks were usually widely dispersed in a harvested soybean field, often flying directly into its centre. In midwinter, birds fed mostly near trees at the field's edge, gradually moving into the centre of the field, possibly due to depletion of food near the edges. In the largest home range of 33 ha, only the 2 ends were used and the remainder was simply flown over. The second flock used most of its 17-ha range. The area actually used by both flocks was similar indicating that the needs of a flock of 11-13 birds could be provided by about 16 ha.

In Kansas, 57 males had an average distance of within-winter movement of 184 m, a home range of about 10.5 ha. Females moved an average of 132 m, a home range of about 5.3 ha. These calculations applied only to areas used for foraging and did not include nocturnal roost sites (Fitch 1958).

The Dark-eyed Junco occupies the same roost all winter. Roosts are often outside the diurnal home range. The same roost continues to be used even if the home range shifts. Flock members often roost near each other but do not huddle together. When it roosts in trees, the portions of trees

that have the densest vegetation are selected for roosting. In Illinois, the temperature within roosts was only 1°C warmer than outside the tree but the wind velocity was substantially reduced from 29 km per hour in the open to 1 km per hour in the roost. Conifers are highly selected for roosting where they are present, but there must be enough present to support the entire flock. In Illinois where conifers were scattered or absent, juncos roosted in tall grass or brush piles. In grass, it roosts on or near the ground, presumably to obtain maximum protection from the wind. It has roosted in red cedars, 82-142 cm above ground in jack pine plantations, in Osage orange thickets, in yews, 0.9-2.4 m from the ground in dense Norway spruce, and 0.6 m up in a hemlock hedge. Where there is no suitable vegetation, it may roost in crevices in road cuts and in protected niches beneath overhanging banks along ditches and gullies. In New Jersey, it roosted in old Barn Swallow nests on and in barns (Allen 2025; Eaton in Austin 1968; Fitch 1958; Gottfried and Franks 1975; Nolan et al. 2020b; Phelps in Austin 1968).

The need for territorial defence is avoided by establishing a winter dominance hierarchy. Males are dominant to females and adults are dominant to juveniles. Dominance is established by timing of arrival on the wintering grounds, with earlier birds being dominant. The need for conflict over food resources is further lessened by the sex and age classes wintering at different latitudes. Individuals that move to a different flock lose their dominance class and become subordinate. If they return to their original flock, they resume their original status, but only after 1-2 days of aggression. When a dominant bird moves to another flock, other birds that move with it retain their status relative to it and may have a higher rank in the new flock than in the one they left. Dominance interactions are infrequent in small dispersed groups of birds that are in inferior habitat. These birds may have better access to food resources than lower ranked birds in large flocks. Aggressive encounters are still frequent despite the dominance hierarchies, but losers simply move aside and resume feeding so that little energy is expended during conflicts. At feeders, males control the central portion of the feeding area and females are confined to the periphery. Dominant birds accumulate more fat and are in better shape than subdominant birds. Dominant birds may have a better chance of survival and arrive on the breeding grounds in better condition. Extremely hungry birds that are normally subdominant may become dominant for about a day, helping to alleviate the effects of food deprivation (Balph 1979; Balph et al. 1979; Cristol 1992, 1995a, 1995b; Fretwell 1969b; Ketterson 1979a, 1979b; Nolan and Ketterson 1990; Nolan et al. 2020b).

Winter site fidelity in migratory eastern populations is variable and highest in more southerly locations. In Ontario, approximately 66% of birds were encountered at the same location in a subsequent year (Brewer et al. 2018). Return rates were 6.3% in Michigan, 5.3% in Indiana, 9.4% in North Carolina, and 17.6% in Alabama, and the difference between the north and south was significant. Adult males returned significantly more frequently (10.7%) than juvenile males (5.6%). The rate of return of northern males (11.4%) greatly exceeded the rate of return of southern males (3.5%). In Michigan, female return rates were 2.3% for adults and 3.1% for juveniles. In Indiana, 0% of adult and 2.5% of juvenile females returned. In the north, 11.4% of males and 1.7% of females returned. Young birds of both sexes returned more frequently to the south than the north: 3.5% of males in the north and 17.4% of males in the south; 3.0% of females in the north and 13.8% of females in the south. Return rates of adults were 11.4% for males in the north, 8.5% for males in the south, 1.7% of females in the north, and 8.0% of females in the south. In cases when a bird returned

to a different location in a subsequent winter, it usually spent its first winter in the north and shifted further south (Ketterson and Nolan 1982). Nolan et al. (2020b) reported that site fidelity in Indiana was complex with a return rate of 20% at best. Once birds exhibited site fidelity, 50% returned in the third year, 50% in the fourth year, etc. This suggests that all surviving birds returned. In Kansas, Fitch (1958) documented 1 bird returning in 4 consecutive winters, but each winter most birds captured had not been present in previous years. Movements of 5 birds recaptured after an intervening summer averaged 262 m.

In Illinois, the Dark-eyed Junco fed on seeds on the ground except during periods of high snow accumulation. Then it fed on seeds that were still on the plants, either by pulling the seed head to the ground or pecking on the plant (Gottfried and Franks 1975). In North Carolina, foraging habitat use by the junco was 0% in bare fields, 9% in crabgrass, 14% in horseweed, 21% in fennel, 43% in asters, 10% in tall mixed weeds, 0% in pure broomsedge, 3% in broomsedge with pines, 0% in pines, and 0% in deciduous trees. Its overlap in habitat utilization was 73% with the cardinal, 67% with the Field Sparrow, 75% with the Song Sparrow, and 93% with the White-throated Sparrow. Seed sizes selected by the junco were: 0.5 mm, 45%; 1.5 mm, 40%; 2.5 mm, 10%; and 3.5 mm, 1-2%; mean size of seeds eaten was 2.4 mm. The seed size selected by the junco was the same as for the Field Sparrow but smaller than for the cardinal and Song and White-throated sparrows. Only the junco fed to a large extent on the ground: 35% of feeding was on bare ground, 8% by standing on the ground and feeding from a standing plant, and 57% perched on a plant. In late January, it fed mostly on lawns (Pulliam and Enders 1971). In Pennsylvania, Nastase and Linville (1995) provided a feeding station with food at heights of 0, 2, 4, and 6 m. Junco feeding heights were 24.5% on the ground, 38.3% at 2 m, 23.8% at 4 m, and 13.4% at 6 m. Foods consumed included 9.3% niger seed, 34.4% canary seed, 42.1% millet, 13.4% corn, and 0.8% sunflowers. In addition to the vegetative items consumed in the breeding season, the junco eats hemlock and yellow birch seeds in winter (Root 1988).

The junco is a very common visitor to bird feeders. Dunn and Tessaglia-Hymes (1999) reported that it visited 80% of feeders across North America, more than any other species. Despite this, it probably prefers natural foods to those presented at feeders. It is nearly twice as abundant at rural than urban feeders. Favourite feeder foods include mixed seeds, millet, hulled sunflowers, and cracked corn. It infrequently eats canary seed, striped or black-oil sunflowers, safflower, whole corn, milo, wheat, niger seed, hulled peanuts or hearts, oats, canola, peanut butter mixes, bird puddings, baked goods, and water. Horn et al. (2014) analyzed 27,502 junco feeding bouts. It preferred white proso millet and platform feeders.

During severe winter weather, the Dark-eyed Junco may move to different habitats and may suffer mortality. After a severe storm in Illinois, populations declined by more than 80% in bottomland and upland forests and increased 8.1% in urban habitat. Although some birds moved to urban areas, the overall population declined and several dead juncos were found (Graber and Graber 1979). Abundance of breeding juncos in New Hampshire northern hardwoods declined in years following severe winters in the northeast and southeast states (Holmes and Robinson 1988; Holmes and Sherry 2001).

James (1991) considered the Dark-eyed Junco a common winter resident in the south that was occasional and rare north to Thunder Bay and Moosonee. McIlwraith (1894) stated that only a few remained over winter in the Hamilton area; more recently, Curry (2006) considered it a very common winter resident. In the Kingston area, only a few overwinter annually, mostly at feeders and around white cedar stands (Weir 2008). In Simcoe County, it is fairly common, although most birds move further south to winter (Devitt 1967). On Manitoulin Island, it is rare and irregular in winter (Nicholson 1981). It is rare in Parry Sound and Muskoka districts and appears to reach the northern extent of its winter distribution at Magnetewan, Parry Sound, Baysville, Huntsville, Bracebridge, and Bala (Mills 1981). In Algonquin Park, it is irregular in winter, varying from absent to very common (Tozer 2012).

Freedman and Riley (1980) analyzed southern Ontario Christmas Bird Counts (CBC) for 1929-77. They noted an upward trend, with numbers doubling during that period. Population peaks were of low magnitude and did not correspond with those of other seed-eating birds. CBC trends for Ontario were annual increases of 4.69% 1970-2021 and 5.36% 2009-21 (National Audubon Society 2022).

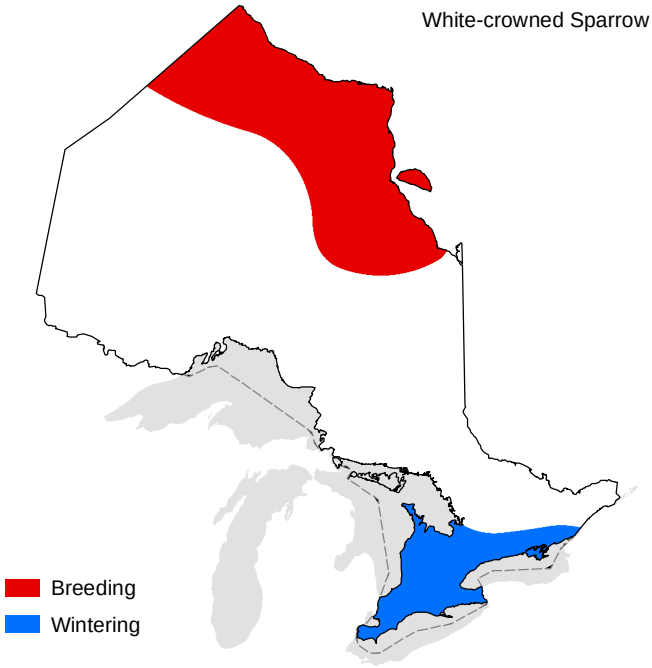
White-crowned Sparrow

Zonotrichia leucophrys

BREEDING SEASON

Habitat Requirements

In Ontario, the White-crowned Sparrow breeds in the Tundra Region and the Hudson Bay Lowland, with a few scattered records in the extreme northwestern portion of the Boreal Forest Region. It is characteristic of tundra and taiga habitats. Nests were in open stands of black spruce and tamarack in burns, bogs, and fens, often with associated stands of willow, poplar, and alder. In heath-lichen tundra, it nests both in the open and near growths of dwarf birch and willow (Peck and James 1987). At Moosonee, all occupied territories were in yards within the town (Wilson and McRae 1993). Three nests near the Hudson Bay coast were on raised tundra ridges covered with lichens, herbaceous plants, scattered shrubs, and small spruce. A nest on Akimiski Island was on a vegetated coastal ridge (Peck and James 1998b). On the Twin Islands in James Bay, it appeared to nest in willow thickets (Manning 1981). Along the Ontario Hudson and James bay coasts, Manning (1952) usually saw it among spruce trees.



In Quebec, the White-crowned Sparrow nests in taiga and tundra habitats, including in open lichen woodlands, lichen tundra, forest tundra, arctic tundra above the treeline, open spruce forests, and regenerating burns. In taiga, it occurs in thickets and scrub in open areas such as burns, open spruce woodlands, and clearings. Further north in the forest tundra, it inhabits alder, dwarf willow, and scrub birch along margins of rivers and streams, and peatlands. It also occurs in clumps of prostrate or stunted spruce on windswept coasts and in mountain-side shrubbery. In the Great Whale River region, it nests in a variety of habitats but is most abundant in recent burns and lichen heath. On the North Shore of the St. Lawrence River, stunted conifers are a typical habitat component (Breton in Gauthier and Aubry 1996). On the east coast of James Bay, it inhabited isolated scrubby spruce but was more common on barren peninsulas and islands where it frequented alder and scattered spruce (Manning and MacPherson 1952). At La Grande Reservoir, it was typical of shrub stands. It appeared in burns after the falling of dead trees about 15 years after fire and disappeared progressively as forests matured (Crête et al. 1995). In the western Ungava Peninsula, highest counts occurred in burned areas. It appears to do best where disturbance of the surface by fire or mechanical means has increased diversity and the shrub growth is still young. It is attracted by stunted tree growth and shrubs and is found in more southern areas only where summer conditions approximate those found in subarctic regions. In central Labrador, it breeds mostly in open lichen woodlands, the most extensive vegetation community. At Goose Bay, it nested only in the often-burned black spruce and dwarf birch on the high sandy delta of the airport. In more productive sites, it was replaced by the White-throated Sparrow (Clement in Austin 1968).

Erskine (1977) considered the White-crowned Sparrow characteristic of boreal forest ecotones with tundra and alpine habitats. In the interior of British Columbia, it occurs at lower densities in open woodlands and forest edges. Near Churchill, it was abundant along the treeline but also nested in small forest clearings; it is typically associated with small spruce in these habitats. It also nests in shrubby areas along roadsides and well above the treeline in isolated clumps of shrubs on the Hudson Bay shore (Jehl 2004; Jehl and Smith 1970). In northeastern Manitoba from the Hudson Bay Lowland north to the forest-tundra transition, it was most abundant in deciduous scrub followed by coniferous scrub, mixed scrub, coniferous forest with a shrub understorey, and heath. It was present in very low densities in coniferous forest without an understorey and tundra and absent in deciduous and mixed forests (McLaren and McLaren 1981). In the Churchill area, it was in the willow-nesting passerine guild (Sammler et al. 2008). In northern Manitoba, it nested in forests with

a mix of white spruce, black spruce, and tamarack as well as jack pine at 1 site. These were usually open stands with an understorey of dwarf birch and willow. Edges of these forests bordered tundra or rocky ridges. It also nested in riparian strips with very dense coverage by 2.3-m tall alder, birch, and willow (Gillespie and Kendeigh 1982). In the Northwest Territory, it nested in isolated spruce stands smaller than 0.01 ha to 12.3 ha with an understorey of mosses, dwarf birch, Labrador tea, willow, green alder, and bilberry. These stands were surrounded by shrub communities 0.3-1.5 m tall dominated by dwarf birch, willow, Labrador tea, bilberry, and green alder. The dwarf birch community was the principal nesting habitat, but it only nested near margins of isolated spruce stands (Norment 1992, 1995a). In the Yukon, it nests in a variety of habitats that usually have patches of shrubs, open grassy or tundra areas, river or lake shores, and occasionally scattered trees, open forest, or forest edge. It inhabits shrubby habitats from lowlands to subalpine areas and may be associated with tall shrubs (Sinclair et al. 2003). In Alaska, it was most abundant in subalpine habitats, followed by alpine habitats, hills or bluffs, floodplains and terraces, and lowlands. Subalpine habitat consisted of wet sedge meadows, low shrub thickets of willow and dwarf birch, spruce forests, and alder thickets. Alpine sites were covered with low or dwarf shrubs and contained some wet graminoid meadows. Hills and bluffs had gentle to moderately steep slopes with dry rocky soils covered with deciduous woods (Handel et al. 2009). In another Alaska study, it nested in a narrow strip along the Yukon River. Essential habitat components included bare ground, grass or grass mixed with short herbaceous plants, and extensive clumps of dense shrubbery. The bare ground was used for foraging and was not always incorporated into the territory. For some pairs, the nearest open ground was 1.6 km distant. These birds regularly flew unchallenged through other territories between the foraging and nesting areas (Oakeson 1954). DeWolfe (in Austin 1968) concluded that these 3 habitat features were characteristic of all western populations, and Chilton et al. (2020) concluded that they were essential range-wide for the White-crowned Sparrow. In at least the west, many territories have standing or running water in or near them with tall coniferous trees on their margins. Sites appear to be more favourable if bare ground, grass, and shrubs are patchily distributed. In central British Columbia, it nests along edges of deciduous woodlands in dense vegetation of young trembling aspen, willow, prickly rose, and fireweed. It also nests in sapling-stage trembling aspen clear-cuts, edges of coniferous woods, balsam poplar woods, riparian habitats, and pockets of dense shrubs in subalpine areas (Campbell et al. 2001).

In the Northwest Territories, Norment (1993) compared nest sites of White-crowned and Harris's sparrows. Within 1 m of the nest, nests of the 2 species differed significantly for 3 variables: shrub height was 62.1 cm at White-crowned Sparrow nests compared with 47.6 cm at Harris's Sparrow nests; the distance to the edge of the nearest stand of trees was 7.2 m for the White-crowned Sparrow compared with 27.9 m for the Harris's Sparrow; and vegetation density was almost 2 times greater at White-crowned Sparrow nests. At 1-10 m from the nest, significantly different parameters for the White-crowned and Harris's sparrows respectively were: shrub cover, 27.5% and 16.1%; average shrub height, 69.2 cm and 50.1 cm; ground cover, 98.7 and 88.6%; number of tree stems larger than 3 cm diameter at breast height, 12.7 and 5.7; foliage density within 5 m of the nest, 108.7 and 58.9 hits; foliage density within 10 m, 210.2 and 112.9 hits; and vertical vegetation density within 10 m, 0.64 and 0.31. Nonsignificant habitat variables for the White-crowned Sparrow that did not differ from those of the Harris's Sparrow included: within 1 m of the nest, 38.6 cm to the nearest

shrub, and orientation 106.5°; at 1-10 m from the nest, 21.8 hits for horizontal foliage diversity. A model that included percent shrub cover, foliage density within 10 m, horizontal foliage density, and percent ground cover significantly discriminated between nests of the 2 species. White-crowned Sparrow nests were closer to the edge of spruce stands in taller denser vegetation, with greater shrub and ground cover, and greater horizontal heterogeneity of cover than Harris's Sparrow nests.

Considerable information is available on the population of the White-crowned Sparrow that nests in alpine and subalpine areas in the Rocky Mountains in the western United States. In Oregon, it nested in alpine meadows in or near riparian vegetation at elevations as low as 800-1,500 m. It strongly preferred to nest near watercourses; 46 of 77 nests (59.7%) were 10 m or less from running water and 59 (76.6%) were within 30 m. The furthest a nest was from water was 175 m. When the population declined, all 12 nests were within 20 m of the creek and 10 were within 10 m. With a further population decline, all males occurred along creeks at elevations above 1,860 m (King and Mewaldt 1987). In Colorado, Glass and Floyd (2015) considered it a riparian species. It nested in aspen groves and meadows on slopes above and alongside streams. The stream banks were dominated by shrubby vegetation, especially willows growing in clumps ranging in size from 10 m^2 to more than 1 ha. Most willow clumps were surrounded by meadows bordered by aspen stands 5-600 m from the willow patches. In Arizona, it nested in alpine meadows with scattered clumps of currants and willows that gradually graded into meadows with low stunted trees near the timberline. The meadows were interspersed among coniferous forests and aspen groves. The nearest populations were 328 km distant, separated by unsuitable habitat (Balda et al. 1970). Another Oregon population nested in riparian strips dominated by trembling aspen or willows; 30 nests were in aspen habitat and 4 were in willow habitat (Heltzel and Earnst 2006). Populations in western and central United States reached their greatest abundance in montane sites. It occurred in alpine meadows and was positively correlated with the percent coverage by forbs. These meadows are often thickly carpeted with wildflowers in the spring. Birds may be responding to other features in the environment, but their association with the forbs was significant (Rotenberry and Wiens 1980). In western aspen forests, it occurred only in montane meadows and the foothills, with many pairs well within forests of large mature well-spaced trees (Flack 1976). At a Wyoming mountain, the White-crowned Sparrow was confined to subalpine habitats with dwarf shrub willow and boggy meadows. The habitat it selected differed significantly from random. It was positively correlated with shrub density and foliage density of the low understorey and was negatively correlated with high foliage at midcanopy or shrub-height. It used areas with fewer than 10 trees per 100 m^2, dense shrub cover less than 2.0 m tall, more than 70% coverage by willow, and high shrub foliage density (Finch 1989b, 1991a). Morton et al. (1972) reported that the meadows it used were typically wet with standing or running water. Habitats it used included grasses, bare ground, dense shrubs or scrub conifers, water, and tall conifers on the periphery. Suitable sites were often very small and widely separated; their suitability may change year to year.

In British Columbia, White-crowned Sparrows nested on Vancouver Island in all forest age classes except for old growth, but were consistently present only in stands that were 15-20 and 30-35 years old. Forty-one percent of nests were associated with human-altered habitats. Habitats associated with humans included rangeland, industrial sites, hydro transmission line corridors,

recreational areas, cultivated agricultural lands and pastures, and suburban, rural, and urban residential habitats. Twenty-seven percent of nests were in residential backyards and gardens, 24% in second-growth forest, 23% in forest edges, 11% in burns, and in open fields, roadsides, clear-cuts and early regenerating forests, riparian habitats, subalpine meadows, beach spits and jetties, orchards, and airports (Campbell et al. 2001). It has nested in margins of shopping centre parking lots, at ferry terminals, on university campuses, in villages, and in open grasslands with sparse shrub coverage. Nests may be placed in ornamental shrubs and vines along walls, fences, or buildings (Banks 1959; Blanchard 1936; Chilton et al. 2020; Ralph and Pearson 1971; Patterson and Petrinovich 1978; Pitelka 1942).

At night, males roost in dense vegetation (King 1986).

All Ontario nests were on the ground and most were at bases of small willows, black spruce, tamarack, and Labrador tea. Some were in dense grass or lichen in the open. They were in well-concealed and often deep depressions in mossy hummocks and in grass and lichen clumps. One nest was under a willow root and 1 nest depression was 15 cm deep in reindeer lichen (Peck and James 1987).

In Quebec and Labrador, most nests are on the ground, typically sunk into a moss-lichen or moss-crowberry mat and partly concealed by overhanging branches of dwarf birch or Labrador tea. Nests are commonly tucked into the lower side of a moss or crowberry mound. Much less frequently, they are built into moss hummocks on a string of heath shrubbery extending out into a sphagnum bog. A few nests are in small balsam firs and one was 0.9 m from the ground in brush thrown over a boat (Clement in Austin 1968). Most nests in the north and alpine areas are on the ground, but they may be elevated in shrubs and trees if snow cover and melting make suitable nesting sites scarce. At Churchill, nests were on the ground, always at the base of a small shrub or tree that offered protection. In the Northwest Territories, all nests were on the ground: 85.7% in dwarf birch habitat and 14.3% in open spruce forest. Of 14 nests, 64.3% were concealed by dwarf birch, 7.1% by spruce, and 21.4% by bog bilberry. In the Yukon, all 22 nests were on the ground. Fourteen were at the base of a shrub (mostly willow), with 1 nest each under alder, birch, and rose; 2 were in a tuft of grasses or sedges (Jehl and Hussell 1966a; Norment 1992; Sinclair et al. 2003). There is a greater tendency for nests to be elevated in alpine areas. In 2 years on a California mountain, more than 60% of nests were on the ground in 1 year but only 22% were on the ground in another year. This occurred because much of the ground was snow covered when nesting was initiated and grass was still not tall enough to conceal nests in thawed areas. Many birds placed their nests on the lowest suitable limbs in willow and scrub pine 21-40 cm above ground; there were few suitable nest sites below 20 cm. In 2 late springs, there was a greater tendency to build nests at heights above 60 cm, usually in pines at the periphery of meadows. The White-crowned Sparrow preferred to nest on the ground in thick grass clumps at the base of shrubs and in crowns of willows 41-60 cm from the ground, especially if they had leafed out. If insufficient sites are available, it will nest on fairly wet open ground in willow that is not leafed out and at the edge of preferred habitat in pines. In a dry year, 11% of nests were elevated compared with 72% in a year with deep snow pack. This adaptability allowed it to reduce delays in nesting due to heavy snow cover or inclement weather. Nests occurred at heights of 0-1.2 m with means over 3 years of 15.5, 38.4, and 18.2 cm. In alpine meadows in Oregon,

65 of 77 nests (84.4%) were on the ground in low grasses or beneath sagebrush and 12 (15.6%) were elevated in sagebrush or grass tufts. In other Oregon areas where the ground was too wet for nesting, nests were elevated 8-200 cm from the ground, with an average of 127 cm (King and Mewaldt 1987; Morton 1994; Morton et al. 1972). Sixty-six percent of British Columbia nests were on the ground; 20% were in shrubs such as rose, steeplebush, willows, and vines; and 14% were in living trees. One nest was in a garage. Seventy-two percent of ground nests were beneath a clump of vegetation or among ground cover, 27% were at the base of trees or among tree roots, and 1% were beside a log or rock (Campbell et al. 2001). Nests have been reported in a fencerow at a height of 1.27 m, in young pines and spruce, scrub oak, willow, alder, dwarf birch, rose, lupine, sagebrush, raspberries, ornamental exotic shrubs, bracken fern, and rarely in annual plants. Nests have been documented as high up as 10.7 m in a tree, in ivy growing on the side of a building, and in shrubs planted along walls, fences, and buildings (Banks 1959; DeWolfe in Austin 1968; Lewis 1973). Nests in subarctic and alpine areas are nonrandomly oriented so they face away from the prevailing wind. In the Northwest Territories, nest entrances were oriented at an average of 106.5° (south to southeast) and the mean wind vector was 329° (north to northeast). In California, northeastern sides of shrubs were selected and southwest orientations were avoided. Cold winds in early mornings and storms came from the south during the nesting season. Nest placement on the northeast side may provide shading and ameliorate heat stress during midday. Exposure of the nest interior to direct sun averaged only 58% at midday (Norment 1993; Zerba and Morton 1983). Females in colder areas locate nests such that solar heating is increased, but all nests are shaded more at noon than at any other time of the day. Nests are situated within natural windbreaks that significantly reduce wind velocity at the nest. In the warmest areas where it nests, some nests are depressed into cool, marshy ground (Clement in Austin 1968; Kern 1984; Morton et al. 1972; Webb and King 1984).

In California alpine meadows, females occasionally arrive before their mates. In these cases, the female takes up territorial residence and sings from elevated perches and flies at intruders to displace them. Upon spring arrival when much of the habitat may still be covered in snow, territorial defence may be weak. In Alaska, males often left their territories for hours, flying as far as 1.6 km. More traditional territorial defence occurred later when incubation began. In montane areas of California, males maintained singing perches in tall conifers bordering the meadows used for breeding until snow-free patches appeared. As soon as a patch of snow-free habitat appeared, a lone male or pair moved into it and defended it. The defended area tended to conform to the thawed area despite its fluctuating size and shape. At this time, adjacent pairs foraged for insects on snow patches between territories. Once the snow disappeared, an overlap in feeding areas continued with their extent depending upon the vegetation. In the Northwest Territories, territorial chases were infrequent and peaked during territory establishment and nest construction. Chases and singing decreased in late June when most pairs were feeding nestlings. Few chases or complete songs occurred after 7 July. In areas disturbed by fire or mechanical intrusions in Quebec and Labrador, territories were 0.36-0.75 ha. In large alpine meadows in California that had 70-80% open ground, there was little or no overlap in feeding areas. Pairs occupied 1.5-2.0 ha but actively defended only a radius of about 50 m (0.79 ha). Where only 20-30% of the meadow was open, territories were as small as 0.15 ha. In these cases, adjacent pairs commonly foraged in the same small grassy areas, with as many as 4 birds using the same 450 m^2 simultaneously. Nests were seldom

at the centre of territories; nests of adjacent pairs were as close as 13 m to each other (Chilton et al. 2020; Clement in Austin 1968; Morton 1992; Morton et al. 1972; Norment 1992; Oakeson 1954). Territories remain fairly constant throughout the breeding season and averaged 1,127 m^2 at 1 site. Another study determined that mean territory sizes were 3,460 m^2 for older males, 1,640 m^2 for yearling males, 2,520 m^2 for older females, and 2,220 m^2 for yearling females. Territory sizes of older males were significantly larger than those of yearling males but there were no differences in territory sizes of the female age classes. There was no difference in the territory sizes of successful (2,760 m^2) and unsuccessful pairs (1,770 m^2). Some aberrant territorial behaviour was observed in this population. Birds of 2 pairs frequently foraged together with no particular arrangement of individuals, and there was mutual use of approximately 80% of territories (Patterson and Petrinovich 1978; Petrinovich and Patterson 1982; Ralph and Pearson 1971).

Natal philopatry rates vary considerably across the White-crowned Sparrow's range. They appear to be very low in subarctic populations but high in western alpine habitats and along the Pacific coast. In the Northwest Territories, Norment (1992) reported that no fledglings returned. The most definitive studies on natal philopatry were conducted in alpine meadows in California. Because these habitats are isolated and separated by several kilometres of unsuitable habitat, they may function similar to islands which tend to have higher than average natal philopatry rates. During the postfledging period, there was an influx of juveniles later in the season from other locations. If males remained longer than 28 days, their return rates increased significantly from 11.1% to 28.5%. After more than 20 days, males became imprinted to the site but there was no difference in return rates of females that remained in the area for long or short periods. Local males returned at a significantly higher rate (18.3%) than females (11.4%) that were hatched on site. For nonlocal juveniles that entered the study area later, a significantly higher proportion of males (11.7%) than females (9.5%) returned to breed. Overall, 15.1% of local birds returned, significantly more than nonlocal birds (10.7%). Significantly more males (13.7%) than females (10.1%) returned. With the sexes combined, 188 of 1,555 birds (12.1%) returned including nonlocal birds. Seventy-three of 482 birds (15.1%) that hatched within the study area returned to breed. Local males that returned spent significantly more time on site as a fledgling (30.7 days) than males that did not return (22.3 days). The same was true for nonlocal males: 12.4 days for returning birds and 8.6 days for non-returning birds. There was no difference in duration of stay for returning and non-returning females: 23.2 days for returning local females, 23.7 days for non-returning local females, 9.6 days for returning nonlocal females, and 8.4 days for non-returning nonlocal females. There appeared to be 2 periods when final selection of breeding sites occurred: the postfledging period and the prebreeding season. The postfledging period was most important to males. It is possible that all surviving males that remained for more than 20 days returned. The prebreeding season could last a month depending upon the snowpack. This period was most important for yearling females in selecting a breeding site, and they moved greater distances than males. Some males dispersed during this period and selected their first breeding site. No individual bird bred in its natal territory. The mean distance of yearlings' first nest from their natal nest was 1,172 m for males (range 150-3,430 m) and 1,134 m for females (range 189-4,340 m). Young of both sexes that hatched in mid-July were more likely to return as yearlings than those hatched earlier or later. The later that young hatched after this, the less likely they were to return. Prior to mid-July, females were significantly less likely to return than males (Morton 1992,

1997; Morton et al. 1991). In the resident population in California, 55 of 706 nestlings (7.8%) returned to breed. There was no difference in return rates of the sexes. Of these, 73.7% entered the local breeding population as yearlings, 14.0% in their second year, 8.8% in their third year, 1.8% in their fourth year, and 1.8% in their fifth year. The median distance of their breeding territory from the natal territory was 110 m (range 0-586 m; Petrinovich 1988). In this population, some yearlings bred on their natal territory (Petrinovich and Patterson 1982).

Adult site fidelity rates are fairly consistent throughout the White-crowned Sparrow's range. In the Northwest Territories, 33% of adults returned (Norment 1992). In California alpine meadows, 22 of 43 males (51.2%) and 21 of 27 females (56.8%) returned to breed, with an overall return rate of 53.8%. Most birds moved a maximum of 2 or 3 territories between seasons. Females dispersed significantly greater distances (119.5 m) between seasons than males (72.5 m). Some riparian territories were long and narrow, so nests in the same or adjacent territory could be several hundred metres apart. The maximum distance between the first nests of subsequent years was 500 m. Breeding dispersal distances in both sexes was greatest between the first and second years, then decreased and remained stable thereafter. Almost all age-related movements occurred between the first and second breeding season, probably because yearlings may be forced to occupy territories of poorer quality. In their second year, they move in an attempt to occupy better habitat. Age effect was significant for females but not for males. Between their first and second years, some females made unusually long movements of 2.7-2.8 km to completely different meadows, something that males did not do. If a female switched mates between seasons, the median dispersal distance between nests in successive years increased significantly from 60.5 m to 119.5 m. Male dispersal distances increased nonsignificantly with a mate change from 60.0 m to 72.5 m. Nesting within 50 m of the previous year's nest was about 2 times more likely for males than females (Morton 1997; Morton et al. 1972). In a sedentary population in California, 105 of 211 males (49.8%) and 67 of 191 females (35.1%) returned; the difference between the sexes was significant. The overall return rate was 42.8%. Of returning birds, 84 of 105 males (80.0%) and 41 of 67 females (61.2%) remained on the same territory; the difference was significant. Overall, 72.7% of adults returned to the same breeding territory. Males remained on territory a mean of 1.7 years compared with 1.4 years for females (Petrinovich 1988; Petrinovich and Patterson 1982). In Oregon, 37% of adult males and 31% of females returned. Those that returned usually settled in their previous territory or nearby. Subsequent territories used by 71 males averaged 113 m apart compared with 160 m for 16 females. Both sexes strongly tended to nest in the same tenth of the creek's riparian strip that they had occupied the previous year (King and Mewaldt 1987).

Limiting Factors

Eggs have been found in Ontario nests from the second week of June until the third week of July, with most present in late June (Peck and James 1998b). In subarctic and alpine populations, the nesting period is compressed and nesting is highly synchronized. In Pacific Coast populations, the nesting period is extended and nesting is less synchronized. At 2 sites in California at approximately the same latitude, 43.4% of females were fertile at the same time at a high-elevation site compared with 17.1% of females at a coastal site. The nesting cycle took 38 days in Alaska, 90 days in Washington, and 116 days in California. In subarctic populations, time is saved by raising only a single brood and by the fact that both sexes are ready to mate as soon as they arrive. Judging by egg dates,

Ontario populations have a compressed nesting period and nesting is probably synchronous (Class et al. 2011; Oakeson 1954; Peck and James 1998b). In subarctic and alpine habitats, the onset of nesting may be delayed. In Oregon, where the snow melted in late April or early May, completion of initial clutches did not vary annually with only a 5-day difference over the years. In California alpine meadows, the chronology of egg laying differed every year due to the snow pack. Pairs occupied the territory for as long as 1 month before nest building when environmental conditions were unsuitable. Nest initiation dates varied by as much as 33 days in different years (King and Mewaldt 1987; Morton 1992, 1994; Morton et al. 1972). In the Northwest Territories, males began singing within 2 days of arrival, but in 1 year, a storm disrupted pair formation for 4 days, with all birds disappearing during this period. The average length of time between pair formation and nesting was 14 days. The nest is usually constructed in 2-4 days (average 2.7 days) in Alaska. Nest building took 7-8 days in Washington and 7-9 days in coastal California. The interval between nest completion and laying of the first egg was 0-3 days (average 1.2 days) in Alaska and 1-12 days (average 2.5 days) in California alpine areas. The 12-day interval was due to a snowstorm just after the nest was completed; the next longest interval was 5 days. Eggs are normally laid at the rate of 1 per day but occasionally a day is skipped. Incubation usually begins with the laying of the penultimate or last egg, but occasionally the day after the last egg is laid. The incubation period of 1 Ontario clutch was at least 10 days. In areas where snow cover and storms are a factor, the incubation period may vary considerably among individuals and year to year. The incubation period in the Northwest Territories was 12 days. In California alpine meadows, mean annual incubation periods were 10.9-13.4 days (range 9-15 days). Incubation periods from other areas include 13 days in coastal California, 11-13 days at Churchill, 11-12 days in British Columbia and Alaska, and 11-14 days in coastal California with most eggs hatching in 12-12.5 days. Hatching of eggs may be either synchronous or asynchronous. In the Northwest Territories, 80% of eggs hatched on the same day and the remainder hatched the following day. Hatching asynchrony in California increased as the season progressed, accounting for 24% of the variation in the time between hatching of the third and fourth eggs. The last chicks were smaller and died or disappeared with greater frequency when the food supply was artificially decreased. Selective starvation or brood reduction may occur in as many as 14% of successful nests. In the Northwest Territories, the nestling period averaged 9.08 days (range 8-10 days). The nestling period appears to decrease with increasing latitude and altitude. The nestling period was 8-11 days in Alaska with averages of 9.6 and 8.4 days at 2 different sites, 8.7 days at Churchill, 9-10 days in alpine areas of California, 9-12 days in coastal California, 9-11 days in British Columbia, and 7-9 days in the Yukon. Nestlings are capable of leaving the nest 1-2 days earlier than normal if they are disturbed (Campbell et al. 2001; Chilton et al. 2020; Clement in Austin 1968; DeWolfe in Austin 1968; Jehl 2004; King 1986; Mead and Morton 1985; Morton 1994; Morton et al. 1972, 1991; Norment 1992, 1995a, 2003; Oakeson 1954; Peck and James 1987; Petrinovich and Patterson 1982, 1983; Sinclair et al. 2003).

Egg dates indicate that only a single brood is raised in Ontario; single broods are also raised in the Northwest Territories and Alaska. A second brood was suspected at 1 nest in Quebec, but the evidence for this was not conclusive. In alpine areas of California, most birds raise a single brood but some raise 2 broods. Along the west coast, there is no evidence of double broods north of latitude 56°N. In coastal California, most birds attempt to raise 2 broods and a few successfully rear a third

brood. The female begins building a new nest a few days after the young of the previous brood fledge. Nearly all birds renest if the first nest is lost, but at northern latitudes renesting occurs only if the loss occurs early in the season. Nests of multiple broods and replacement nests are all in the original territory. Renesting occurs 4-7 days after the loss. In alpine areas of California, the median distance between subsequent nests of the same pair in the same year was 39.7 m (range 5-150 m). The mean interval between nest loss and the laying of the first egg in the next nest was 6.8 days with a range of 2-16 days (Campbell et al. 2001; Clement in Austin 1968; DeWolfe in Austin 1968; Jehl and Hussell 1966a; Mewaldt and King 1977; Morton 1994, 1997; Morton et al. 1972; Oakeson 1954; Peck and James 1998b; Pérez et al. 2016; Petrinovich and Patterson 1982, 1983). Ontario clutches contained 3-5 eggs, with 55% having 5 eggs (mean 4.50 eggs). The clutch size of the White-crowned Sparrow varies throughout its range depending upon latitude, altitude, time of season, and age of the female. Clutches tend to be largest at higher latitudes and altitudes, and with older females. Clutches of 3-6 eggs (mean 4.24 eggs) have been reported for the eastern subspecies, with 6 eggs rare. In the Northwest Territories, the mean clutch size was 4.50 eggs, with most clutches containing 5 eggs. In Alaska, clutch size was 3-6 eggs (mean 4.58 eggs); 3-6 eggs have been reported in the Yukon. In alpine areas of California, clutch size was 3-5 eggs with 80.4% of clutches containing 4 eggs (mean 3.93 eggs). There were no seasonal differences in clutch size. In British Columbia, most nests in the south have 4 eggs and most northern nests have 5 eggs. Overall, clutches of 3-7 eggs have been reported; 7-egg clutches are very rare and it has not been documented whether all eggs were laid by a single female (Baker et al. 1981; Campbell et al. 2001; Chilton et al. 2020; Clement in Austin 1968; DeWolfe in Austin 1968; Morton et al. 1972; Oakeson 1954; Peck and James 1998b; Petrinovich and Patterson 1983; Sinclair et al. 2003).

Both sexes are capable of breeding when they are 1 year old. In the western United States, some birds, including adults, do not breed. It is unknown if this is the case in northern populations. In alpine areas of California, 43.6% of yearling males and 62.1% of yearling females bred; the difference was significant. A significantly higher proportion of older birds nested: 59.8% of males and 75.3% of females. In an Oregon population, 36% of territorial males were unmated. In the resident California subspecies, 5-10% of males may not breed, including both yearlings and older birds. At another site, there was no difference in the proportion of the sexes that bred; 39.2% of birds entered the breeding population in the year they were banded, 37.4% entered the next year, and 22.0% did not become territory holders until 2-5 years after banding. Territory holders that disappeared were immediately replaced by floaters. Pairs containing a yearling male were significantly less successful in fledging young than pairs with older males. Pairs with yearling females tended to be slightly more successful than those with older females. There was a significant difference in the combined ages of the pairs, with successful pairs having a combined mean age of 3.0 years compared with 2.3 years for unsuccessful pairs (Chilton et al. 2020; Mewaldt and King 1977; Morton 1992; Petrinovich and Patterson 1982; Poesel et al. 2011; Ralph and Pearson 1971).

Most birds mate monogamously, but there are a few records of polygyny. One northern Quebec nest contained 8 eggs and was attended by 2 females and 1 male. In California, females that were mated polygynously subdivided the male's territory and defended their part against the other female by loud singing and fighting (Blanchard 1936; Clement in Austin 1968; DeWolfe in Austin 1968). Pairs remain mated throughout the breeding season, even after a nesting failure, but

individuals remate if their first mate dies. In California migratory populations, a mate change occurred in about two thirds of cases each year due to mortality or mate switching. In California resident populations, 27.4% of males and 53.7% of females that returned the following year to the same territory retained their previous mate. If there was a shift to a new territory, both sexes usually had new mates; only 2.9% of males and 3.4% of females that shifted territories had the same mate as previously. Of 36 possible cases of remating, 69.4% of pairs reunited and 30.6% divorced. Most divorced birds moved to an adjacent territory but 3 moved further. One mated pair moved together to a new territory 1.35 km from the original territory (Morton 1997; Morton et al. 1972; Petrinovich and Patterson 1982). Incestuous matings are rare. In a migratory California population over 13 years and in 473 pairs, there were no cases of parent-offspring mating and 1 case of siblings being mated. In a resident California population, there was 1 case of a father-daughter mating out of a possible 10 and no cases of siblings mating (Morton 1972; Petrinovich and Patterson 1982). Extra-pair fertilizations are common in 2 subspecies. In California, 34-38% of nestlings resulted from extra-pair copulations. Males whose nests contained at least 1 chick unrelated to them were significantly older than males with full paternity (Chilton et al. 2020). In an Oregon population, 38.5% of broods contained extra-pair young and 35.4% of young were extra-pair. Fifty percent of males that lost paternity did not father any young in their brood; the remaining males lost paternity of 25-75% of their offspring to extra-pair sires. Thirteen males that sired young with an extra-pair mate increased their reproductive success by an average of 2.5 offspring (range 1-5). For 8 unmated males and some males who lost their mates, this was the only reproductive success that they had. The sex ratio in this population was strongly male biased, which may have favoured extra-pair copulations (Poesel et al. 2011). Extra-pair copulations are unlikely to be common in northern and high-altitude populations where nesting is highly synchronized.

The White-crowned Sparrow forages predominantly on the ground where it scratches with both feet simultaneously to uncover food items. It often forages in bare or grassy ground, but may forage in spruce, tamarack, bog meadows, and tundra. It most often hops or runs along the ground, pecking or scratching at each stop. It often moves slowly over tops of boulders, gleaning from the surface, and moves through tops of shrubs and short trees when consuming buds. It may catch flying insects by leaping short distances into the air, but this is an incidental method of foraging typically conducted on warm sunny afternoons. It may capture insects from a perch similar to flycatchers. It may run through water up to its knees, raising its tail and flashing its wings to flush insects from moss in a bog (Chilton et al. 2020; Clement in Austin 1968; Morton 1967; Morton et al. 1972).

In Alaska under 24-hour daylight conditions, adults fed the brood more than 20 hours a day. In California, active feeding lasted 14.5 hours per day (King 1986; Laubach et al. 2015; Norment 2003; Petrinovich and Patterson 1982). Nestlings are fed mostly insects plus a few spiders. In the Northwest Territories, nestlings were fed a diet of 98.4% arthropods. They were also fed some bog bilberry flowers, but no fruit. On the California coast, young are also fed an introduced species of terrestrial amphipod and isopods. Young have been reported catching and consuming flies, mosquitoes, and spiders (Clement in Austin 1968; DeSante and Baptista 1989; Norment and Fuller 1997; Petrinovich and Patterson 1982).

Adults eat arthropods during the breeding season and vegetable matter the rest of the year. For birds nesting in subarctic and alpine areas, spring arrival on the breeding grounds is a critical period. At this time, arthropods may be scarce and seeds may be buried under snow. In Quebec and Labrador, the green capsules of the juniper haircap moss are an important food item early in the season. Birds may gorge on these and eat new catkins of willows and black flies, which emerge early in spring (Clement in Austin 1968). Near Kuujjuaq, Quebec, adults regularly fed on maggots on fish bodies (personal observation). In Alaska, it fed on moss capsules, willow catkins, poplar sap, tiny horsetail stalks, fresh blossoms and leaves, and mosquitoes at water's edge. It also ate bread scraps and seeds of thistles and knotweeds (DeWolfe in Austin 1968). Fruit was important in the spring diet in the Northwest Territories. Crowberry, mountain cranberry, alpine bearberry, and occasionally bog bilberry produced fleshy fruits that persisted over winter. Spring fruits of the first 3 species were still plump and juicy; those of bilberry were little more than shrivelled skins and seeds. The fleshy fruits were an important component of the diet in early spring throughout the prenesting and incubation periods. Fleshy fruits were an abundant, nutritious, and easily obtained food source that allowed it to remain in good physiological condition when other food items were scarce (Norment and Fuller 1997). The White-crowned Sparrow drinks frequently and dies within a week if fed a dry diet with no water (Chilton et al. 2020). Judd (1901) reported that stomachs collected in California in summer contained 43% animal matter and 57% vegetation. Animal matter included 23% parasitic wasps, 9% beetles (fireflies, weevils, and click, dung, and leaf beetles), 7% leafhoppers and other bugs, and 4% caterpillars. From October to February, the diet consisted of 90% grain and weed seeds, but no grass seeds. Thirty-five percent of food items were seeds of lamb's-quarters and amaranths; it also ate seeds of purslane and plants in the pink family. Grain comprised 39% of the diet during this period, predominantly oats, but also corn, wheat, and barley. Grain was taken from newly sown fields, from standing grain, and in stubble.

The White-crowned Sparrow is a host of the Brown-headed Cowbird only along the Pacific Coast from British Columbia southward. The ranges of the 2 species do not overlap elsewhere. It is only recently that parasitism has occurred on the west coast, but the incidence of it is increasing. In the San Francisco Bay area, 5% of nests were parasitized in 1978. At that time, it was concluded that parasitism did not affect desertion, predation, or fledging success rates. By 1993, 40-50% of nests were parasitized and it was concluded that the White-crowned Sparrow could not maintain its population when the parasitism rate exceeded 20%. In British Columbia, 9 of 469 nests (1.9%) were parasitized. Parasitism was documented in Washington and Oregon (6 of 42 nests, 14.3%) in the early 1970s and mid-1980s. Most records of parasitism come from urban habitats (Baptista 1972; Campbell et al. 2001; Chilton et al. 2020; Heltzel and Earnst 2006; Lavers 1974; Lewis 1973; King and Mewaldt 1987; Petrinovich and Patterson 1978; Trail and Baptista 1993).

In northern and alpine populations, severe weather during the breeding season is the greatest limiting factor. In years of deep snow pack, there is less suitable habitat available at the beginning of the breeding season. This may result in fewer pairs nesting or later initiation of nests which decreases opportunities for renesting. In an alpine population in California, fewer juveniles were captured during the postfledging season in a year preceded by a winter of heavy snows and a summer with storms that diminished fledging success. At an Oregon alpine site, snowstorms resulted in significant nest losses in 4 of 20 years. In 1 year, 95.5% of nests were destroyed and

renesting occurred; in another year, 85.7% of nests were lost and no renesting occurred. This population suffered a significant decline due to a combination of bad weather and high predation rates. Widespread nest losses may occur during hail storms and heavy rains accompanied by wind and cold temperatures. At Churchill, all nests containing young were lost during a rainstorm and no renesting occurred. In Alaska, nestling growth rates decreased with increasing precipitation and also with later nest initiation. During inclement weather, adults spent more time on self-maintenance and less time caring for nestlings (Jehl and Hussell 1966a; King and Mewaldt 1987; Morton 1992; Morton et al. 1972; Pérez et al. 2016).

Rivers et al. (2019) studied the effects of forest herbicides applied to clear-cuts on the White-crowned Sparrow. The herbicide reduced deciduous vegetation density and was applied at light, moderate, and intensive levels. Herbicide application had no influence on daily nest survival or postfledging survival. Although increased herbicide application intensity resulted in extensive reductions in vegetation cover at the stand and nest-patch scales, there was no difference in vegetative cover at nest sites among treatments and controls.

Dietz et al. (2013) studied the effects of a gravel road on the White-crowned Sparrow at an alpine site in Colorado. The road was 6.5 m wide and a mean of 35.5 vehicles used it daily in June and July. Nests were initiated before the road was opened to traffic. Nests were 1-223 m from the road (median distance 27.5 m). More nests than expected were within 10 m of the road and fewer than expected were at other distance categories from the road. Although areas near the road were selected, there was a significantly higher desertion rate at nests within 20 m of the road that was related to higher stress responses of males nesting in this area. The road was an ecological trap; the road and areas within 20 m of it were of reduced quality habitat.

Near Churchill, Sammler et al. (2008) studied the effects of intensive grazing by geese on other bird species. The White-crowned Sparrow was in the willow-nesting guild and this habitat was not affected by the geese. In western United States populations, livestock grazing reduces ground and shrub cover and is associated with lower populations of White-crowned Sparrows and higher rates of nest predation (Earnst et al. 2012; Heltzel and Earnst 2006).

The density of a California population declined over 30 years due to natural succession. Over this period, the vegetation changed from early successional scrub to later successional scrub and coniferous forest. The White-crowned Sparrow selected the earliest successional habitat and avoided later successional areas (Porzig et al. 2018).

DesGranges and LeBlanc (2012) reported that the White-crowned Sparrow occurred in stands with low summer temperatures and precipitation in central Quebec and Labrador. Consequently, it may be vulnerable to climate change in this area.

Status

The White-crowned Sparrow was first described as a species at Fort Severn (Forster 1772). Breeding was first documented for the province at this location in 1940 (Peck and James 1987). Baillie and Harrington (1937) stated that it was only known to breed along the Hudson Bay coast and along the James Bay coast north and west of the Albany River. During the first atlas, its breeding distribution included most of the Hudson Bay Lowland, although greatest abundance occurred within 100 km

of the coastlines with few records beyond 200 km. The transition area between tundra and boreal forest appeared to be its preferred habitat. It was uncommon along the James Bay coast and at Kerine Lake; fairly common at Fort Severn, Winisk, and Cape Henrietta Maria; and common at Hawley Lake. Highest abundance was on the tundra and along the treeline (Rising in Cadman et al. 1987). James (1991) considered it uncommon in the northern Hudson Bay Lowland south to Big Trout Lake and along the James Bay coast south to Moosonee. Wilson and McRae (1993) reported that it was most common along the north coast, becoming scarcer further south. It was common at Shagamu but considerably less abundant at Brant, possibly due to the scarcity of shrubs. It was uncommon at Ekwan and there was no evidence of breeding at Longridge. Several territorial birds were present within the Moosonee town limits.

The second atlas revealed a similar range for the White-crowned Sparrow as during the first atlas. It was somewhat more widespread throughout the Hudson Bay Lowland and breeding evidence was obtained in 4 squares in the northwest portion of the Boreal Forest Region. Its probability of observation increased significantly in the Hudson Bay Lowland. Highest densities occurred in the northern Hudson Bay Lowland from Fort Severn east into Polar Bear Provincial Park and inland from Peawanuk along the Winisk and Fawn rivers. Its abundance decreased with distance from the Hudson Bay coast (Rising in Cadman et al. 2007).

POSTFLEDGING PERIOD

Newly fledged young cannot fly or can fly weakly for short distances of 5-20 m. On the day of fledging or shortly thereafter, brood division occurs with each adult caring for 1 or 2 fledglings. They remain relatively sedentary, perched in dense vegetation near the nest and can fly 7-10 days after leaving the nest. Fledglings 9-10 days old averaged 20 m from the nest in California alpine meadows (range 0-50 m). This distance corresponded closely to the area that was defended as a territory. By day 30, they averaged 200 m from the nest. If a second brood is initiated, the male takes over feeding the first brood when they are about 20 days old, and the young begin to feed on their own when they are 16-20 days old. Family groups begin to dissolve once fledglings are about 25 days old; juveniles become independent when they are 28-35 days old (Chilton et al. 2020; DeWolfe in Austin 1968; Morton 1992, 1997; Morton et al. 1991; Petrinovich and Patterson 1983). Baker et al. (1982) studied movements of first-brood fledglings in California. For the first week after leaving the nest, they were extremely sedentary, perching cryptically in shrubs near the nest. The average length of stay in the natal area was 51 days (range 27-63 days). They remained within about 60 m of their first capture site for the first 10 days out of the nest, increasing to 110 m 14 days after fledging. Following that, there was a steady increase to 270 m followed by an apparent drop off in movement. The substantial increase in ranging distance occurred at about 35-40 days of age coincident with when tail growth ceases.

By age 40-60 days and beyond, some juveniles are highly mobile; others are sedentary. Many juveniles leave the natal area at age 30-70 days. Some make exploratory flights of 5 or more km. One female was captured 3.6 km from her natal nest at age 32 days. Fledglings from first broods tended to leave the natal area if second broods were raised. Fledglings of pairs that do not attempt a second brood and those of later broods may either leave or remain within the natal area. Some juveniles remain in the natal area for several weeks and even until autumn migration begins. Approximately

a month after local juveniles become independent, an influx of juveniles from other locations occurs; they outnumber local juveniles 2.5:1. These birds may stay a short period before moving on (with about 35% remaining only a single day) or remain for the remainder of the season. These latter birds may also return to breed (Morton 1992, 1997; Morton et al. 1991; Oakeson 1954; Petrinovich and Patterson 1982, 1983). In Alaska, there was an influx of adults that had not bred in the area in the third and fourth weeks of August indicating that some adults may move away from their breeding areas prior to autumn migration (Oakeson 1954).

Loose family groups were seen in August in an alder fringe along the George River in Quebec. By mid-September when they leave the region, they are usually restricted to dwarf birch thickets on slopes in timberline areas (Clement in Austin 1968).

MIGRATION

All subspecies except one in California are migratory. Birds banded in Ontario and Quebec overlap broadly in winter in an area extending from Missouri east to Kentucky and south to the Gulf Coast from Texas to Mississippi (Brewer et al. 2018). Migration is nocturnal and flocks forage together at stopover sites during the day. Flocks are not cohesive units. Each bird within a flock travels on its own schedule independent of the birds that it accompanies during the day. The rate of spring migration tends to increase with latitude. Spring migration is quick and compressed in time; autumn migration is prolonged. In Maine, the mean passage period was 18 days in spring and 42 days in autumn. Late snow and ice may delay arrival on the breeding grounds in northern Quebec and Labrador by as much as a week. Under these conditions, birds may stack up at Sept-Isles along the north shore of the St. Lawrence River. In Maine, the mean minimum stopover time was 4.5 days (range 1-20 days); there was little variation in stopover lengths between spring and autumn. In New Jersey, the mean autumn stopover period was 5.7 days (maximum 14 days). In the west, stopover times were 4.1 days at latitude 42°N, 2.5 days at latitude 60°N, and 2.1-3.8 days at 3 sites in the Yukon (Brewer et al. 2018; Campbell et al. 2001; Cherry 1982; Chilton et al. 2020; Clement in Austin 1968; DeWolfe et al. 1973; Heinemann 1981; King and Mewaldt 1981; Oakeson 1954; Seewagen and Newhouse 2018).

Males tend to arrive on the breeding grounds about a week before females (range 5-14 days). In Alaska near the Canadian border where the climate was less severe, females arrived about the same time as males. In California alpine meadows, the earliest cohort was predominantly males but a few females arrived with the males. Some females arrived before males and established territories until males were available. Older males arrived significantly earlier than females by 5.8 days; yearling males arrived an average of 5.3 days earlier than yearling females. Yearling males arrived 2.2 days later than adult males and this difference was significant. Yearling females arrived 1.6 days later than adult females, but this difference was not significant. Juveniles that were present in the area during their postfledging period arrived 2 days sooner than those that had not been present previously, but this difference was not significant (King 1986; King and Mewaldt 1987; Morton 1992; Norment 1992; Oakeson 1954; Poesel et al. 2011).

In southern and central Ontario, spring migrants usually arrive in late April or early May and leave by the end of May. The peak of migration is in the first half of May or mid-May in the southern Shield. Stragglers may persist into early June (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et

al. 2004; Mills 1981; Tozer 2012; Weir 2008). Wilson and McRae (1993) considered single birds seen on 6 and 9 June at Longridge to be migrants. The earliest observation on the Twin Islands was 9 May (Manning 1981).

In subalpine meadows in California, juveniles often migrated before adults in autumn (Morton 1992). On the Twin Islands, all birds left before 16 September (Manning 1981). At Longridge, migrants began to appear 4-13 September (Wilson and McRae 1993). In the southern Shield, most autumn migrants occur from mid-September to late October, but some may linger until late November (Mills 1981; Tozer 2012). In the south, migrants usually arrive in early to mid-September and leave by late November, but birds may be present from late August and remain into December (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

During migration, the White-crowned Sparrow prefers shrubby areas in open habitats. In the Yukon, these habitats may include wetlands and backyards (Sinclair et al. 2003). Along the British Columbia coast, it occurs in edge habitats, particularly areas of heavy shrub growth adjacent to more open areas. These may include transmission line and transportation corridors, beaches and spits, golf courses, city parks, airports, gardens, backyard feeding stations, shrub-dominated logged or burned areas, agricultural areas and road edges with short grasses and weed patches, edges of bogs, and riparian habitat adjacent to beaver ponds, sloughs, sewage lagoons, creeks, estuaries, and other wetlands. Similar areas are used in the interior, plus sagebrush grasslands, shrubby and weedy fencerows, avalanche chutes, subalpine areas, and grain elevators and sheds where spilled grain provides a food source (Campbell et al. 2001). In autumn in Ohio, it occurs in brushy areas, dense patches of tall weeds, and weedy uncut cornfields (Clement in Austin 1968). In Maine, Cherry (1982) trapped birds in a mixed wood and in an open field with a hedgerow. All White-crowned Sparrows were captured in the hedgerow. In Kansas, migrants occurred only in thickets, especially those at margins of weedy fields (Fitch 1958).

During spring migration in Algonquin Park, birds foraged mostly on the ground but occasionally went high in trembling aspens to feed on catkins. Birds lingering into November typically occurred at feeders (Tozer 2012). During autumn migration in Idaho, Carlisle et al. (2012) compared the White-crowned Sparrow's diet with food availability. Food items consumed in a greater proportion than their availability, in order of decreasing preference, included ants, other hymenopterans, beetles, lepidopterans, larvae, spittlebugs, and leafhoppers. Items that were eaten less than their availability, in order of decreasing avoidance, included jumping plant lice, hornets, spiders, flies, stink bugs, wasps, stilt bugs, and moths. It consumed a moderate amount of fruit but ate more seed matter. Caterpillars were consumed less than their availability, but were not abundant enough during autumn migration to be a major component of the diet.

Weir (2008) reported that only 1 White-crowned Sparrow was killed at the Lennox generating station chimneys and that 2 were killed by cars. It is occasionally killed by flying into windows during migration (DeWolfe in Austin 1968).

Clement (in Austin 1968) reported that juveniles of the eastern subspecies were often blown out over the Atlantic Ocean, where they presumably perished. Adults appeared to be capable of avoiding this.

James (1991) considered the White-crowned Sparrow a common migrant in Ontario. Spring flocks commonly number 50, with larger flocks of 250-500 in the Kingston area. Autumn flocks are larger and may contain 500-1,000 birds (Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

At Long Point Bird Observatory, Hussell et al. (1992) reported a nonsignificant decline of 1.0% per year in the number of White-crowned Sparrows banded 1961-88. Trends by period were: 1961-70, +3.8%; 1970-79, –4.5%; and 1978-88, +1.1%.

WINTER

The winter distribution of the White-crowned Sparrow is governed by temperature. It is mostly absent where the average minimum January temperature drops below –9°C. The eastern subspecies is the only one that regularly winters east of longitude 90°W, but it avoids the southeastern states. Dense wintering populations are all west of longitude 100°W; these are typically birds that breed west of Ontario. Highest abundance in these areas occurs along rivers (Clement in Austin 1968; Root 1988).

In winter, the White-crowned Sparrow uses habitats similar to those it frequents during migration: shrubby or weedy areas in open habitat. It seldom occurs much further than 2 m from vegetative cover. It may occur in grain fields, shrubby roadsides and hedgerows, scrub and steppe vegetation, abandoned farmland, riparian areas, grasslands, and anywhere there are clumps of tall weedy growth, shrubs, or saplings. It may occur at feeders in both urban and rural habitats. It is less reliant on water in winter than in the breeding season (Chilton et al. 2020; Clement in Austin 1968; DeWolfe in Austin 1968; Root 1988). In California, wintering White-crowned Sparrows were positively correlated with feeders and the presence of grass and negatively correlated with structures and roads (Kalinowski and Johnson 2010).

The White-crowned Sparrow roosts, often communally, in dense trees or shrubs in winter. It prefers to roost in woody vegetation that retains its leaves in winter. It avoids trees or shrubs that are sparsely foliaged or defoliated. Roosts are most frequently in open habitat and usually consist of isolated clumps of woody vegetation surrounded by open fields or other similar habitat (Barrentine 1991, 1992; DeWolfe in Austin 1968).

The White-crowned Sparrow avoids expending energy on intraspecific competition by each flock occupying an exclusive home range, sex ratios varying geographically thereby reducing intersexual competition, and establishing dominance hierarchies so birds do not have to assert dominance. In different study areas in California, winter flocks occupied areas of 6-8 ha and 20 ha. Flock sizes of 6-150 birds have been reported. Individual flocks consistently remain in the same location with approximately the same number of birds. Home ranges of flocks do not overlap and are frequently separated by unsuitable habitat. There is no evidence of interchange of birds between flocks, although daily movements of individuals may extend as far as 0.9 km. Within flock home ranges, each individual may have favourite foraging and roosting sites (Barrentine and McClure 1993; Chilton et al. 2020; Clement in Austin 1968; Dunn and Tessaglia-Hymes 1999; Morton 1967; Parsons and Baptista 1980; Ralph and Mewaldt 1975). Members of a pair may winter in separate flocks or at different altitudes and latitudes (DeWolfe in Austin 1968). Dominance is established by sex, age, and appearance. Some aggression occurs but subdominant individuals usually back down

without any conflict. Males dominate over females in each age class and adults are dominant over juveniles. When strange individuals meet, dominance is established by the brightness of the crown colours. In an artificial feeding study, adults fed closer to cover than juveniles and juveniles fed further from cover when adults were present than when they were absent (Parsons and Baptista 1980; Slotow and Rothstein 1995).

Most birds return to the same home range and roost in subsequent winters. Overwintering birds are rarely captured outside the 10-minute block where they were originally banded. Both adults and juveniles exhibit greater site tenacity to feeding sites than to roosts. Winter displacement studies indicate that adults have strong site fidelity and that juveniles develop site fidelity in mid-January. In California, birds of both age classes were displaced 4-160 km from the point of capture. No adults returned to where they were released in the subsequent year, but 65 of 384 (16.9%) returned to where they were captured. Twelve of 424 juveniles (2.8%) returned to the release station, but only those that were moved prior to mid-January. All returning juveniles were released less than 60 km from the point of capture. In another California study, birds were released at a roost 3.7 km from the roost where they were captured. Nineteen of 119 displaced birds (16.0%) were recaptured in the next 2 years; return rates were similar for juveniles and adults. One of 6 returning juveniles (16.7%) and 11 of 13 returning adults (84.6%) returned to the home roost; 5 of 6 juveniles (83.3%) and 2 of 13 adults (15.4%) returned to the roost where they had been released. One juvenile was recaptured 3 years after banding 145 km from the banding location. Delaying fixation on a site until midwinter may allow young birds to explore different areas prior to selecting a wintering area. One bird was captured in March 40 km from where it had been banded in January (Barrentine 1993; Barrentine and McClure 1993; Ralph and Mewaldt 1975). At a residential lot in California, 53 of 94 (56.3%) returned as adults; 51.1% of birds returned more than once. Seventy-four of 256 yearlings (28.9%) returned and 39 (52.7%) returned a second time. The lower return rate of yearlings may be due to late site fixation and higher mortality rates than adults (Mewaldt 1976). In California, Sandercock and Jaramillo (2002) banded 6,625 juveniles and 1,967 adults. The recapture rate was 59.7% for juveniles and 60.6% for adults.

In Washington State during high wind or heavy rain, the White-crowned Sparrow tended to avoid open ground and foraged almost exclusively in sheltered locations such as in and around weeds and brushy fencerows. Light rain and intermittent snow did not affect choice of foraging areas (Morton 1967). It seldom forages much more than 2-4 m from cover. Food was placed in bowls 0.3, 0.8, and 1.3 m from an artificial shrub. In 1 treatment, the shrub was removed and too few birds visited the food bowls to do any statistical analyses. More birds used the bowl closest to the shrub; 73-83% of birds were observed at this bowl but only 33.3% would be expected. Ninety-eight percent of birds went to the shrub before they went to the food. Few birds fed at the bowls when no cover was available despite the presence of dense cover 20 m away. It strongly preferred a nearby source of cover before it would feed (Slotow and Rothstein 1995). In an aviary, it handled seeds smaller than 0.74 mg more efficiently than finches; finches were more efficient in handling seeds larger than 1.44 mg. Based on its winter energy requirements, the White-crowned Sparrow must find and consume an average of 1 seed every 1-5 seconds throughout a 10-hour day. Therefore it must occupy habitats containing high densities of seeds to obtain adequate food. Because most of the day must be spent

foraging, it cannot exploit patchy food resources or make long flights in search of new patches (Benkman and Pulliam 1988).

In winter, the White-crowned Sparrow feeds predominantly on vegetable matter but also on arthropods when they are available. In Maryland and West Virginia, Llewellyn (1949) observed flocks feeding under smooth pigweed, presumably on its seeds. Morton (1967) collected 88 stomachs in Washington in winter and spring. Seeds, especially those of amaranths, were the predominant food item in January. In February, there was an increase in consumption of green plant material. Grass blades were ripped off and swallowed end-first. In late March and early April, there was a major shift in diet when the intake of grass decreased and it began to feed extensively on buds, particularly those of hackberry. With the onset of mild spring weather, there was a noticeable increase in invertebrates, especially flying insects. There was a 125% increase in the amount of animal material in stomachs and an increase in insect-chasing activities. Judd (1901) analyzed the contents of 217 stomachs from every month except August. Almost all were collected in the United States, so they represent either wintering birds or populations breeding near the Pacific Coast. Seventy percent of the diet consisted of insects, and it also ate spiders and amphipods. Half the insect diet was comprised of cutworms and other smooth caterpillars. The remainder of the insect diet included beetles (fireflies, weevils, and ground, leaf, and scarab beetles) and wasps. It did not eat grass seeds and only 1 bird had eaten grain. The primary seeds consumed were chickweeds, lamb′s-quarters, wild sunflowers, smartweeds, and docks. It also ate a few violet and mallow seeds. He examined 94 stomachs of the Eastern White-crowned Sparrow, all from central and eastern states from September to May. It subsisted almost entirely on seeds in winter but became somewhat insectivorous during warmer weather. In May and September, 11% of the food consisted of ants, caterpillars, weevils and other beetles, and spiders. Twelve percent of the diet consisted of grain, almost entirely oats but with some corn and wheat. In May, grain constituted 27% of the diet indicating that it was feeding in newly sown fields. It also ate small seeds including those of crabgrass, panic grasses, foxtails, and Johnson grass. Ragweed was important, comprising 20% of the diet; seeds of amaranths, lamb′s-quarters, chickweeds, gromwells, and wild sunflowers were important foods. Only 5 of 94 stomachs contained fruit, including those of elderberries and blackberries; it has been reported to eat grapes. In spring, it may consume blossoms of trees and shrubs. The entire sample of 217 stomachs contained 25% animal matter and 75% vegetation. Caterpillars formed 9% of the diet and a third of the animal food, a higher proportion than found in stomachs of other sparrows. Ants and parasitic wasps constituted 6% of the diet, which was also higher than average. Beetles comprised only 5% of the diet, below average for sparrows. Other animal matter included 1% grasshoppers, and 4% spiders, bugs, and miscellaneous insects. The vegetable matter consisted of 51% weed seeds, 15% grain, 4% grass seeds, and 5% fruit. It ate fewer grass seeds and more fruit than other sparrows. Beal and McAtee (1912) analyzed the contents of more than 600 stomachs collected predominantly in winter in the United States. It is probable that their results included the samples analyzed by Judd (1901). The stomachs contained 7.4% animal food and 92.6% vegetation. Beetles comprised 1.4% of the food, reaching a peak of almost 8% in June but they were insignificant in other months. Hymenopterans contributed 1.9% of the diet, reaching a peak of more than 16% in June but only about 1% in other months. Most were ants with fewer wasps, bees, and parasitic species. Caterpillars were the dominant animal food, comprising

3.5% of the annual diet and 37.5% of the July diet. Other minor animal foods included stink bugs, leafhoppers, and treehoppers. It subsisted predominantly on weed seeds which comprised 74% of the diet; over 90% of stomachs contained weed seeds. The favoured species was redroot amaranth. Grain constituted 8.6% of the diet and was consumed mostly in winter. Oats were the dominant grain in stomachs, but it also ate wheat, barley, and corn. Fruit represented 4.5% of the diet and included cherries in addition to the species mentioned by Judd (1901).

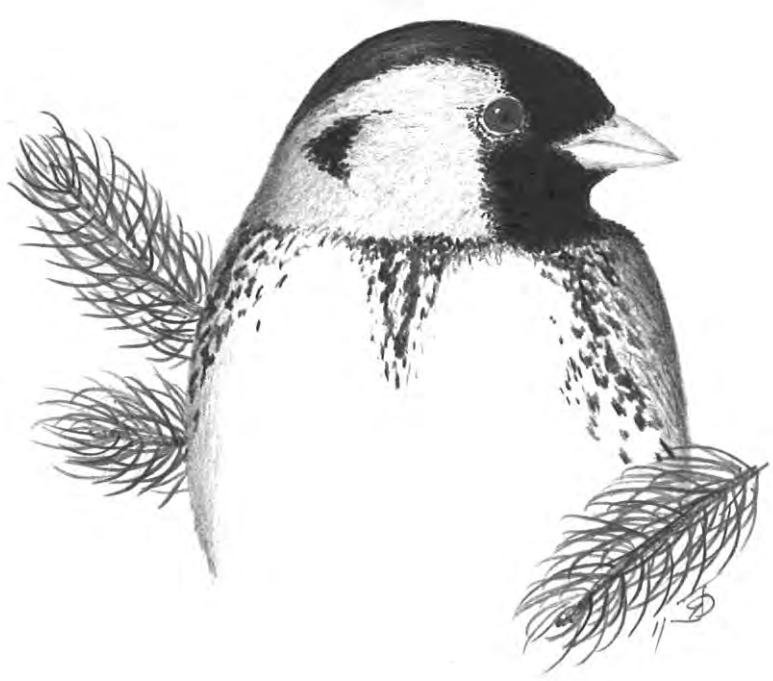
The White-crowned Sparrow is a regular visitor to winter bird feeders. The proportion of feeders visited is lowest in rural areas. Favourite feeder foods include mixed seeds, millet, and cracked corn, and it frequently eats milo, wheat, and hulled peanuts. Infrequently consumed foods include sunflowers, safflower, niger seeds, suet, peanut butter mixes, peanut hearts, baked goods, bird puddings, fresh fruit, and water (Dunn and Tessaglia-Hymes 1999).

James (1991) considered the White-crowned Sparrow a rare winter resident in southern Ontario north to Sudbury.

Clement (in Austin 1968) concluded that the White-crowned Sparrow had extended its winter range eastward and northward since approximately 1950. Possible reasons for its range expansion include climate amelioration, widespread planting of multiflora rose, and greater numbers of feeding stations. Christmas Bird Count data indicate that it increased in Ontario at annual rates of 1.99% 1970-2021 and 6.76% 2009-21 (National Audubon Society 2022).

Harris's Sparrow

Zonotrichia querula

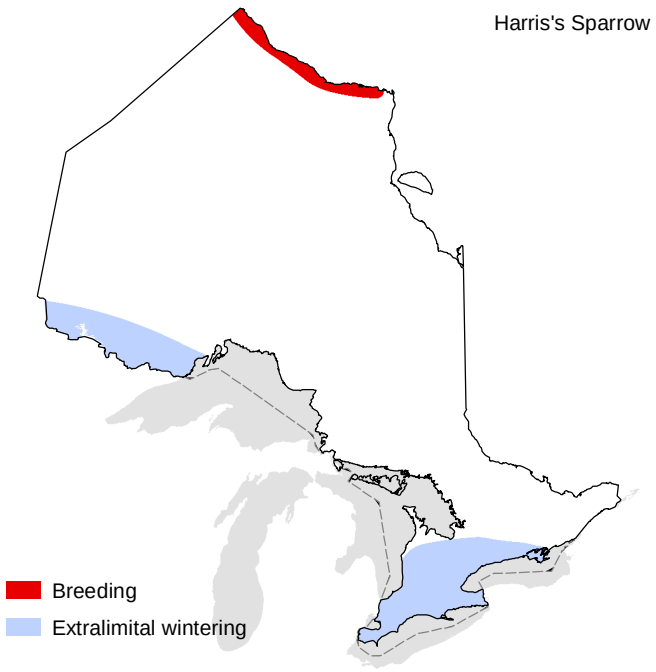


BREEDING SEASON

Habitat Requirements

The Harris's Sparrow is Canada's only endemic songbird. It breeds in the ecotone between tundra and boreal forest from the Northwest Territories to extreme northwestern Ontario.

The first and only Ontario nest was in a coastal fen supporting small tamaracks. The wetland was at a clearing near an airstrip (Peck and James 1987). The nest was in a patch of willow shrubs and stunted spruces in an area with a grassy substrate interspersed with sand and gravel associated with the Fort Severn airport runway. The habitat was predominantly open and the nest was about 10 m from the radio station. The antenna of the station was a favoured singing post (Cadman in Cadman et al. 1987). During the second atlas, birds were observed predominantly in willow thickets surrounding tundra lakes and ponds. Typical breeding habitat consists of patches of stunted conifers with a dense shrub understorey of birch, willow, and alder (Cadman in Cadman et al. 2007).



The breeding grounds of the Harris's Sparrow are confined to the strip of stunted timber along the northern edge of the Boreal Forest Region from Hudson Bay westward (Swenk and Stevens 1929). It prefers small pockets of coniferous trees surrounded by tundra and avoids contiguous boreal forest. The northern extent of its range is limited by the distribution of coniferous forest stands growing beyond the northern limit of the boreal forest. It occasionally nests in tundra. The southern extent of its range is limited by the Boreal Forest Region, which it avoids. Most territories include some coniferous trees. Densities are highest in forests dominated by spruce or tamarack with a shrubby understorey. Low densities may occur in jack pine or white birch with little understorey vegetation; it occasionally nests in areas without trees. Forest stands within territories are typically isolated and small (less than 0.01 ha to 12 ha) with trees less than 3-8 m tall. Most birds occur in areas with less than 30% canopy cover and where the maximum canopy height is 8 m (Norment et al. 2020).

In the Northwest Territories, breeding habitat consisted of a mosaic of small isolated spruce stands and extensive tundra habitat. The tree stands were typically surrounded by shrubby dwarf birch, willow, and green alder 0.3-1.5 m tall (Norment 1995a). Most forest stands had a dense understorey of mosses, dwarf birch, Labrador tea, willow, green alder, and bilberry. There were 4 tundra communities in the area: low sedge meadow, tussock meadow, dry heath, and rock field. Low sedge meadows were poorly drained and vegetated with sedges and cottongrass. Tussock meadows were characterized by cottongrass hummocks. Dry heath areas were dominated by lichens, scattered dwarf birch, and low evergreen shrubs such as alpine bearberry, marsh Labrador tea, mountain cranberry, and crowberry. Rock fields were dry rocky areas with less than 10% vegetation cover. Common plant species in rock fields included those found in dry heath along with prickly saxifrage and mountain avens. Dwarf birch habitat at or beyond the edge of spruce stands supported 89.2% of nests; 4.6% were in spruce stands including one in the interior of a 12.3-ha spruce stand, 3.1% were in tussock meadows, 1.5% were in dry heath, and 1.5% were in rock fields. In this area, the White-crowned Sparrow always nested in dense shrubby vegetation within 25 m of forest edge. The Harris's Sparrow used a wider variety of nesting habitats as far as 127 m from forest edge (Norment 1992).

North of Churchill, the Harris's Sparrow was most abundant in deciduous scrub followed by heath, coniferous and mixed scrub, and coniferous forest with an understorey. It was absent in deciduous and mixed forests, coniferous forest without an understorey, and tundra (McLaren and McLaren 1981). Near Churchill, it was most common at edges of woodlands, in clearings near railway

tracks, and in brushy areas of burned-over areas. It preferred a damp, rather sheltered woodland at the base of a rocky hill. Nests were also in mossy hummocky spruce-tamarack woods with an open canopy (Semple and Sutton 1932). In the same general area, it nested in forest-edge areas where the trees were mostly stunted, densely branched white and black spruce on the sheltered edge of a rocky ridge. The trees averaged 3 m in height with a diameter at breast height of 6.4 cm; tree density was 1,236 per ha. The ground was covered with moss and the shrub layer was comprised of Labrador tea, rhododendrons, blueberries, and bog rosemary (Gillespie and Kendeigh 1982). Also in the Churchill area, it nested mainly in shrubby clearings, old burned-over areas, bogs, and semiopen areas and boggy areas with large hummocks in spruce-tamarack woods (Jehl 2004; Jehl and Smith 1970).

Baumgartner (in Austin 1968) reported that the Harris's Sparrow invariably nested in open areas near Churchill, but always close enough to a spruce to use it as a singing perch. In the Northwest Territories, Norment (1993) characterized microhabitat conditions at nests and determined how they affected nest success and compared them with habitat characteristics of White-crowned Sparrows. Within 1-m of the nest, vegetation density was significantly greater at successful than unsuccessful nests. At 1-10 m from the nest, the amount of shrub cover was significantly greater at successful nests, ground cover was 94.2% at successful nests and 80.4% at unsuccessful nests, the number of hits by vegetation 5 and 10 m from the nest was significantly greater for successful nests, and horizontal vegetation heterogeneity was significantly lower for successful nests. The latter parameter suggested that more uniform distribution of vegetation interfered with the ability of predators to locate nests. Successful nests tended to be in areas with more cover and denser vegetation within 5 m of the nest than unsuccessful nests. The amount of shrub cover within 10 m of the nest was the most useful variable in discriminating between successful and unsuccessful nests. Nest sites of Harris's and White-crowned sparrows differed significantly for 10 of 13 variables tested. Harris's Sparrow nests were further from the edge of spruce stands, in shorter less dense vegetation, and in vegetation with less vertical complexity than White-crowned Sparrow nests. Significantly different parameters of nest sites of Harris's Sparrow and White-crowned Sparrow respectively included: shrub height, 47.6 cm and 62.1 cm; distance from nest to the nearest tree stand, 27.9 m and 7.2 m; ground cover, 88.6% and 98.7%; and vegetation hits, shrub hits, and vertical vegetation diversity significantly less for the Harris's Sparrow. Other Harris's Sparrow average nest-site characteristics included 35 cm from the nest to the nearest shrub and 16.5 cm vegetation height within 0.5 m of the nest (Norment et al. 2020).

All reported nests were on the ground. Most are at the base of a small shrub or tree and well concealed by overhanging vegetation or physical features; rarely nests are unconcealed from above. In the Northwest Territories, 67.7% of nests were concealed by dwarf birch, 7.7% by green alder, 7.7% by spruce, 7.7% by marsh Labrador tea, 3.1% by willow, 1.5% by bilberry, 1.5% by a rock overhang, and 1.5% by a turf overhang. The rim of the bulky nest is sunk into the ground and may be only a few centimetres above water in moss hummocks. In the Northwest Territories, nests were oriented nonrandomly at an average of 140.5°, or southeasterly. The average wind direction was 329°, so nests were oriented about 149° away from the direction of the prevailing wind. There are 2 records of old nest cups being used (Baumgartner in Austin 1968; Jehl and Hussell 1966a; Jehl and Smith 1970; Norment 1992, 1993; Norment et al. 2020; Semple and Sutton 1932).

Territorial chases are infrequent and most common during territory establishment and nest construction. Territorial activity wanes in late June when most pairs are feeding nestlings. Near Churchill, no evidence of territoriality was observed, with birds feeding together for long periods in the morning. The average territory size is approximately 2 ha but males may defend areas with maximum linear dimensions of 200-300 m, or about 6 ha. During the incubation and nestling periods, females remain near the nest but males may wander as far as 500 m from the territory. Females may wander widely during other phases of the nesting cycle (Norment 1992; Norment et al. 2020; Semple and Sutton 1932).

Only 1 study in the Northwest Territories examined natal philopatry. No philopatry was observed, with 0 of 62 nestlings returning (Norment 1994).

Return rates of adults in the Northwest Territories in 2 years were 38.5% and 38.9%. The first-year return rate was 34%; 4 adults (3 males and a female) returned 2 years after banding for a second-year return rate of 31%. Although a higher proportion of males (9 of 22, 40.9%) returned in the first year than females (6 of 22, 27.2%), the difference was not significant. Breeding success appeared to be the greatest factor in determining whether a bird returned. Six of 7 successful males (85.7%) returned compared with 2 of 5 unsuccessful males (40.0%). Two males returned to the same territory. In the following years, 4 of 6 males that had been successful the previous year occupied the same territory, including one that had occupied the same territory 2 years previously. The other 2 returning males established territories 150 m and 750 m from their previous territory. Six of 7 successful females (85.7%) returned the following year compared with 1 of 10 unsuccessful females (10.0%). No female returned to its same territory. The female that returned after nesting unsuccessfully nested 250 m from her original nest. She returned the following year after nesting successfully and again moved 250 m from the previous nest. Another female that had nested successfully nested 75 m from her previous nest (Norment 1994).

Limiting Factors

Peck and James (1987) reported that eggs were most likely to be in Ontario nests from mid-June to mid-July. Males begin singing within 2 days of their arrival. Pairs typically form 5-8 days after arrival, but pair formation may be delayed by adverse weather. During a late snowstorm in the Northwest Territories, all birds disappeared and pair formation was disrupted for 4 days. Both first and replacement nests may be built in about 2.5 days. An average of 3.5 days elapses between nest completion and clutch initiation. The earliest clutches are not initiated until at least 60% of the ground is snow-free. Eggs are laid at the rate of 1 a day. Incubation begins with the laying of the penultimate egg. The incubation period is typically 12.0-13.5 days; eggs at 1 Churchill nest took 15 days to hatch due to inclement weather. Mean incubation periods in the Northwest Territories in 3 years were 12.5, 12.7, and 12.9 days (average 12.8 days). In 61 clutches, 84.7% of eggs hatched synchronously, 14.8% hatched 1 day later than the rest, and 0.5% hatched 2 days later. The nestling period in the Northwest Territories averaged 9.26 days (range 8.5-10.0 days). At Churchill where the young were handled, the nestling period averaged 8.9 days. The nestling period appears to decrease with latitude. Nesting in populations is highly synchronized with all young fledging within 6-10 days in 3 years of study. Nesting phenology is related to food abundance. Hatching in the Northwest Territories began shortly after arthropod abundance began to increase in early and mid-June.

Fledging peaked in the second week of July just prior to the peak of arthropod abundance (Jehl 2004; Jehl and Hussell 1966b; Norment 1992, 1995a, 1995b, 2003; Norment et al. 2020; Semple and Sutton 1932).

A single brood is raised in a nesting season. If a nest is lost, a replacement nest may be initiated soon thereafter. Replacement clutches are laid only if the loss occurs prior to hatching and early in the season. Nests lost before 18 June may be replaced. If nests are lost later, they are not replaced and there is no resumption of territorial behaviour. One pair built a replacement nest 16 m from the original nest and laid the first egg 3 days after the loss. The Harris's Sparrow lays 3-5 eggs. Nests initiated early in spring may contain only 3 eggs, possibly due to lower food availability at this time. Clutch sizes are smaller in years when nest initiation is late due to delayed snow melt. Four eggs is the most frequent clutch size. Clutch sizes increase with latitude with a higher proportion of clutches containing 5 eggs in the Northwest Territories than at Churchill. Mean clutch sizes include 4.26 eggs in the Northwest Territories, 3.88 eggs at Churchill, and 3.50 eggs at Herchmer, Manitoba (Baumgartner in Austin 1968; Jehl 2004; Jehl and Hussell 1966a; Norment 1992, 1995a, 1995b; Norment et al. 2020; Semple and Sutton 1932).

The age at first breeding is unknown but is probably 1 year similar to other sparrows in this genus. The mating system appears to be monogamous. The highly synchronized nesting reduces the possibility of extra-pair copulations. In the Northwest Territories, both members of 3 pairs returned the following year but none retained the same mate. There is no evidence of intraspecific egg parasitism (Norment 1994; Norment et al. 2020).

At Churchill, the Harris's Sparrow was predominantly a ground feeder. It kicked and scratched with both feet simultaneously among fallen leaves and dry herbaceous stalks. It worked its way through grass and moss searching for seeds and insects. It frequently fed in tamarack where it appeared to be feeding on buds, insects, or insect eggs in leaf clusters (Semple and Sutton 1932). In the Northwest Territories, 85% of foraging was by ground gleaning. It plucked food from vegetation or the bare ground, sometimes after kicking the litter away. It also gleaned for arthropods less than 3 m from the ground in trees and shrubs, plucked fresh spruce needles from trees, and pursued flying arthropods by either chasing them along the ground or sallying into the air from the ground. Eighty-three percent of the foraging substrate was the ground, but it also obtained food from snow and the air (Norment et al. 2020). It foraged in more open habitats and further from cover than the White-crowned Sparrow (Norment 1993).

A ligature study determined that the nestling diet was comprised of 15.3% flies other than crane flies, 13.7% caterpillars, 13.1% adult beetles, 12.6% crane flies, 12.6% bilberry flowers, 9.0% adult hymenopterans, 7.4% spiders, and 5.8% seeds (Norment et al. 2020). Of 190 food items that were observed being fed to nestlings, 81.6% were arthropods. They were also fed some bilberry flowers but not fruit (Norment and Fuller 1997).

Six adult stomachs at Churchill contained 66% vegetable matter and 34% animal matter. Vegetable matter included seeds of grasses, sedges, and bulrushes; seeds or fruit pulp of crowberry, cranberry, and blueberry; seeds of birch, amaranths, and lamb's-quarters; and a considerable amount of oats that was gleaned along railway tracks. The Harris's Sparrow ate both larval and adult insects including ground beetles, leaf beetles, wood borers, click beetles, leaf-miner flies, stink bugs, small

moths, horse flies, ants, ichneumonid wasps, and crickets. It also consumed small spiders and fragments of small snails and other molluscs. Miscellaneous foods included short-horned grasshoppers, caterpillars, crowberry seeds, heath seeds, bearberry seeds, fly eggs, and flatsedge seeds (Semple and Sutton 1932). Norment and Fuller (1997) determined that fruit was important in the diet early in spring. Birds arrived almost a month before arthropods became abundant. Crowberry, mountain cranberry, alpine bearberry, and occasionally bog bilberry produced fleshy fruits that persisted over winter. Bilberry seeds were little more than shrivelled skins and seeds by spring but fruits of the other 3 species were still plump and juicy. They made 510 foraging observations of approximately 100 Harris's Sparrows. Fruits, primarily crowberry and mountain cranberry were the most frequently observed food items during the prenesting period (82% of all items) and constituted 66% of food items during the incubation period. Arthropod use increased from 9.4% in the prenesting period to 73.4% in the nestling period. Flowers, mostly of bilberry, were consumed most often during the nestling period. It also plucked and ate spruce needles and buds during the prenesting period. They collected 6 stomachs during each of the prenesting, incubation, and nestling periods. Average mass of food items during the prenesting period was 31 mg fruit seeds, 7.5 mg arthropods, 8.0 mg other seeds, and 0 mg flowers. During the incubation period, averages were 17.5 mg fruit seeds, 10 mg arthropods, 2 mg other seeds, and 0 mg flowers. During the nestling period, averages were 11 mg fruit seeds, 16 mg arthropods, 1 mg other seeds, and 2.5 mg flowers. It consumed bearberry fruit more frequently than its abundance and mountain cranberry less than its abundance. The tendency to eat bearberry fruit more than its availability may have been due to the relatively large mass of this fruit.

One of the greatest limiting factors during the breeding season is the limited range and habitat niche of the Harris's Sparrow. It is confined to a short narrow band along the transition area between boreal forest and tundra, although it occasionally nests in open tundra. It is uncertain how this habitat will respond to climate change. Its habitat in some areas may be adversely affected by forest clearing, mining, and exploration and development for the oil and gas industry (Erskine 1977; Norment et al. 2020; Wells 2007).

Nest loss due to cold rainy or snowy weather occurs frequently. If this occurs early in the season before the eggs have hatched, the adults may initiate replacement nests. If nest loss occurs during the nestling period, renesting does not occur and no young are raised in that year (Jehl and Hussell 1966b; Semple and Sutton 1932).

Status

The first Ontario nest was found at Fort Severn in July 1983. The Harris's Sparrow may have moved into Ontario recently as a breeding species. In 1940, only a single bird was found at Fort Severn with no evidence of nesting. The 1983 record at Fort Severn was the only breeding evidence during the first atlas. The area around Winisk was well covered during this atlas and no Harris's Sparrows were observed. It was concluded that it did not nest as far east as Winisk (Austen et al. 1994; Cadman in Cadman et al. 1987).

During the second atlas, breeding evidence for the Harris's Sparrow was obtained in 4 squares along the Hudson Bay coast. This extended the breeding range eastward to about 120 km west of Cape Henrietta Maria. In all cases, only possible breeding evidence was obtained and none of the birds remained until later in the season (Cadman in Cadman et al. 2007). The Harris's Sparrow wanders

widely during migration and summer and does not reach the breeding grounds until late May (Norment et al. 2020). Some birds detected during the second atlas may still have been migrating or been wanderers rather than breeders.

The Harris's Sparrow has been designated special concern in Canada.

POSTFLEDGING PERIOD

Young are incapable of flight when they leave the nest. By about 4 days after fledging, they can fly short distances of less than 10 m. Young move as far as 100 m from the nest within 5 days of fledging and may be 300 m from the nest after 10 days. Young may be separated by 30-40 m after fledging and appear to be fed by different parents. The adults continue to feed the young for at least 2 weeks after they fledge. The Harris's Sparrow forms flocks in late summer prior to migration, sometimes with other species (Norment et al. 2020).

MIGRATION

Ontario is outside the Harris's Sparrow migration route, except for the Lake of the Woods area which is on its extreme eastern edge. It wanders considerably during migration, so strays have been reported in most provinces and states. In spring, it migrates in flocks, sometimes foraging with American Tree Sparrows and White-throated Sparrows. Inclement spring weather may temporarily halt migration. In North Dakota, southward flights appeared to be driven by the calendar and were not well correlated with weather fluctuations. Southward departures commonly coincided with a temperature increase and a south wind; continued warm weather did not delay departures. The average autumn stopover time over 14 years ranged from 4.3 to 7.6 days with most birds remaining about a week. Spring migrants move faster than autumn migrants. During spring migration, stopover times were 1-5 days (average 1.5 days) (Baumgartner in Austin 1968; Brewer et al. 2018; Norment et al. 2020; Stevens 1957; Swenk and Stevens 1929).

At Churchill and in the Northwest Territories, males and females arrived at the breeding grounds at the same time (Norment 1992; Semple and Sutton 1932). Because the Harris's Sparrow is a rare and irregular migrant in Ontario, limited information is available on the timing of spring migration. This is further confounded by the fact that some early-spring migrants may be birds that overwintered. Southern Ontario spring records range from 10 April to 24 May; northern Ontario records range from 4 to 27 May (Curry 2006; Speirs 1985). At Atikokan, Peruniak (1971) reported that it was fairly common 6-23 May.

At Shagamu, Wilson and McRae (1993) saw single birds on 21 and 25 August and considered these autumn migrants at the eastern extent of their range. Migrants were present at Atikokan 13 September to 23 October and at Hornepayne 22 September to 5 October (Peruniak 1971). In southern Ontario, records range from mid-September until the end of November (Curry 2006; Speirs 1985; Weir 2008). In North Dakota, adults moved southward more promptly than juveniles (Swenk and Stevens 1929).

In northern Manitoba, spring migrants were abundant along the wooded shore of a small lake near a town and in open spruce forest. First arrivals at Churchill occurred mostly in open tundra but they also flocked in areas where they did not breed, including on a ridge near the coast (Jehl 2004; Semple and Sutton 1932).

In autumn, the Harris's Sparrow has been documented taking corn from fallen ears (Baumgartner in Austin 1968).

Storms during migration that result in food supplies being covered by snow or ice probably account for numerous fatalities. The Harris's Sparrow been killed at a television tower in Nebraska during autumn migration, but no information was provided on the number of birds involved or the frequency of kills (Baumgartner in Austin 1968; Norment et al. 2020).

James (1991) considered the Harris's Sparrow a rare migrant in the eastern part of the province and uncommon in the west. Peruniak (1971) considered it a fairly common migrant at Atikokan. Swenk and Stevens (1929) considered it an uncommon to rare irregular migrant in northwestern Ontario. In eastern Ontario, particularly south of the Canadian Shield, it is rare and irregular and is a vagrant outside its normal range. The number of records for the area south of the Shield is low even when wintering birds are included: 3 records from the Kingston area (Weir 2008), 15 from the Hamilton area (Curry 2006), 5 from Niagara Region (Black and Roy 2010), and 5 in Elgin County (Lancaster et al. 2004).

WINTER

The Harris's Sparrow has an unusual restricted winter range of only about 464,000 km^2 that extends from northern Nebraska and central Iowa to central Texas. The winter range is almost entirely south of latitude 41°N and mostly south of 40°N. Highest winter concentrations occur in Kansas, Nebraska, Oklahoma, and Texas. Small numbers occur in South Dakota and throughout the western United States into southern British Columbia and southeastern Alaska. Its prime winter habitat consists of landscapes dominated by tall grasses, oak-hickory woods, and tree and shrub savannahs. It tends to avoid short-grass prairies and areas of dense woods (Norment et al. 2020; Root 1988; Swenk and Stevens 1929).

Where it is common in winter, the Harris's Sparrow may occur in flocks. It is often in the company of other sparrows, American Goldfinches, and Northern Cardinals. During migration and winter, the Harris's Sparrow frequents brushy areas, thickets, edges of woodlots, and weed patches (Baumgartner in Austin 1968; Judd 1901; Swenk and Stevens 1929). One bird in Niagara Region spent 10 weeks in a ditch with some running water where there was dense shrubbery and numerous trees (Black and Roy 2010). In Oklahoma, where it is an abundant wintering species, it occurs in underbrush such as dense shrubbery along creeks and at edges of woods, and particularly favours vine-covered trees. It may also occur in gardens in towns, but only in years when it is particularly abundant (Nice 1929). Typical winter habitat includes shrubby hedgerows, brush piles, thickets bordering watercourses, shrubby ravines, shelterbelts, agricultural fields with weedy patches, pastures undergoing secondary succession, dense shrubs adjoining open land where weeds or cultivated crops provide a food source, patches of sunflowers, shrubby roadsides, raspberry thickets, thistle patches, ornamental hedges in residential areas, and overgrown clearings near grain elevators (Campbell et al. 2001; Fitch 1958; Leighton et al. 2002; Norment et al. 2020; Swenk and Stevens 1929).

In North Dakota, wintering birds congregated in spruces, hedges, and shrub thickets to roost for the night (Swenk and Stevens 1929).

The Harris's Sparrow does not defend a territory in winter but maintains linear dominance within flocks. The dark throat is a sign of dominance and the status of individuals can be changed by altering the throat pattern. Many birds remain within a small home range for 1-2 weeks, then leave and return 1 month or later. Oklahoma birds mostly stayed within an area of 8.1 ha, but also made regular movements as far as 1 km. Birds displaced as far as 3.2 km returned to their usual home range (Baumgartner in Austin 1968; Norment et al. 2020).

Some birds exhibit winter site fidelity and have been detected in as many as 5 consecutive years. In Oklahoma, 121 of 1,361 birds (8.9%) returned in 1 or more years. In Kansas, 2 of 71 birds (2.8%) were recaptured in a subsequent year: one the year after banding and the other 2 years after banding. Other return rates include 8.5% in Kansas and 3.6% in Oklahoma (Baumgartner in Austin 1968; Norment et al. 2020; Swenk and Stevens 1929).

Judd (1901) examined 100 stomachs taken from October to May, mostly in Saskatchewan, Kansas, and Texas. The analysis covered the migration periods and winter. Stomachs contained 92% vegetable matter and 8% animal matter. Vegetable matter included 42% seeds of ragweeds and smartweeds, 25% seeds of wild fruits and miscellaneous plants, 10% grain (more corn than wheat and oats and chiefly waste grain), 9% grass seeds (mainly foxtails, crabgrasses, June grass, paspalum, and Johnson grass), and 6% seeds of amaranths, lamb's-quarters, wild sunflowers, and gromwell. Animal food consisted of insects, spiders, and snails, including an unusual amount (2%) of leafhoppers. Tame birds in Texas ate grasshoppers, moths, beetles, millet, corn, and canary seed. In Oklahoma, it ate poison ivy berries and elm seeds in addition to weed seeds (Nice 1929). One Nebraska bird ate 14 grasshoppers, 5 beetles, and other larvae and seeds. A Wisconsin bird consumed numerous ants, 2 wireworms, moths, spiders, and a small snail (Swenk and Stevens 1929).

The Harris's Sparrow is readily attracted to feeding stations. It prefers more wooded and brushy areas but will come to residential feeders during severe weather. It feeds predominantly on the ground but prefers to be near tall trees where it can rest and take shelter. It is one of few species that readily eats milo. Its favourite feeder foods were mixed seeds, water, and probably striped sunflower seeds. It infrequently consumed black oil sunflower seeds, millet, and cracked corn (Dunn and Tessaglia-Hymes 1999). In Oklahoma, it was particularly fond of canary seeds and sunflower seeds. Other feeder foods it has eaten include hemp seeds, suet, finely chopped meat, and breakfast cereal (Baumgartner in Austin 1968; Nice 1929; Swenk and Stevens 1929).

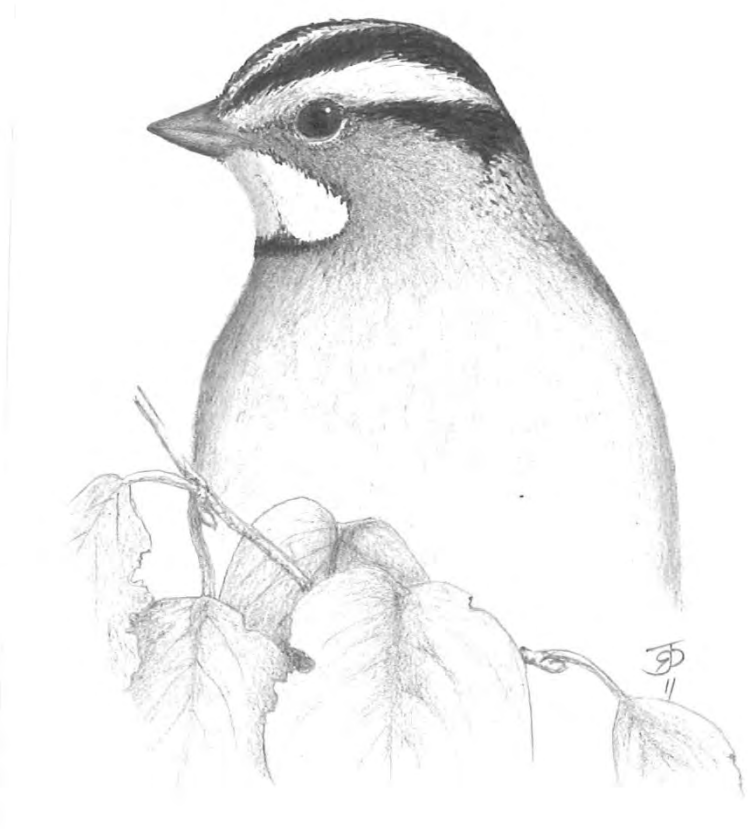
The greatest limiting factor to wintering Harris's Sparrow and probably overall is loss, fragmentation, and degradation of scrub habitats within its United States wintering range. These changes are due to intensification of agriculture (Norment et al. 2020; Wells 2007).

James (1991) considered the Harris's Sparrow a rare winter resident in the south north to Peterborough and in the west at Atikokan and Thunder Bay. In addition to being rare in winter, it is irregular, with Ontario well outside its normal wintering range. Black and Roy (2010) reported 5 winter records for Niagara Region, Curry (2006) reported 4 records for Hamilton, Lancaster et al. (2004) reported 1 record for Elgin County, and Weir (2008) reported 1 record for Kingston.

Christmas Bird Count results from 1965 to 2002 indicated that the Harris's Sparrow declined significantly range-wide at a rate of 1.8% per year (Norment et al. 2020).

White-throated Sparrow

Zonotrichia albicollis



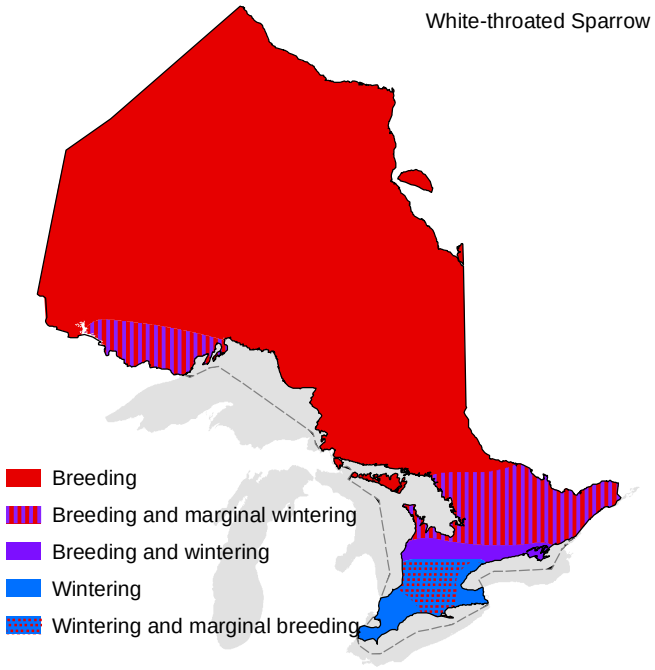
BREEDING SEASON

Habitat Requirements

The White-throated Sparrow has 2 colour morphs of the crown stripe, the white-striped and tan-striped morphs. Birds preferentially mate with birds of the opposite morph. Whether a bird has a white-striped or tan-striped crown affects many aspects of its biology. These may include its aggression and dominance, breeding habitat, contribution to care of young, participation in extra-pair copulations, and timing of spring migration (Falls and Kopachena 2020; Knapton and Falls 1982, 1983; Knapton et al. 1984; Kopachena and Falls 1993a; Lowther 1961).

Most Ontario nests (73.7%) were in woodlands, including 26.6% in coniferous, 20.8% in mixed, 6.9% in deciduous, and 19.3% in unspecified forests. Other nesting habitats included 11.2% in muskeg areas, 5.4% in overgrown fields and shrubby areas, 3.5% in clear-cut and burned forests, 2.7% in swamps and beaver meadows, 2.3% on bedrock outcrops, and 1.2% in bracken fern–

blueberry barrens. The White-throated Sparrow preferred open second-growth woodlands over mature and dense stands. Nests in woodlands were most often at edges, clearings, lake and river shorelines, and along roadsides and survey cuts. It selected dry as well as damp or wet habitats without any clear preference (Peck and James 1987).



In the Hudson Bay Lowland, the White-throated Sparrow nested close to the northern extent of forest along the Hudson and James bay coasts, but was probably more numerous inland. Most observed on Sandy Island in the Moose River were in tall willows and poplars close to the river. Those at the Raft River were among spruce (Manning 1952).

In the Boreal Forest Region, the White-throated Sparrow was associated with open mixed woods with high edge density. In these studies, interfaces between different forest types were considered edge. It was significantly associated with higher amounts of edge and older than average stands. It was also associated with higher levels of disturbance and higher levels of age-class interspersion. It tended to be associated more with conifers than hardwoods and with more intact mature forests (Rempel 2007; Rempel et al. 2007). From Pickle Lake northward, McLaren and McLaren (1981) observed it in all available habitats. It was most abundant in deciduous scrub followed by mixed scrub, coniferous forest with an understorey, heath, deciduous forest, coniferous scrub, mixed forest, coniferous forest without an understorey, and tundra. Near Pickle Lake, James (1980) observed it in open or disturbed woods, bog edges, and about the town. North of Lake Nipigon, it preferred semi-openings and dry alder thickets, but also occurred in dense forest. It used shrubs for refuge and singing, but preferred to sing from trees if they were available, often from the top of 9-m spruce, white birch, or dead trees (Kendeigh 1947). In the same area, it was one of the more common species in immature spruce–balsam fir stands. It frequented the lower crown of the canopy and thickets (Sanders 1970). Near Hearst, Welsh and Fillman (1980) observed it in both uncut and clear-cut upland mixed and lowland coniferous forests. It occurred in all ages of clear-cuts studied, from 3-24 years old. In older clear-cuts, it tended to be more abundant in lowland stands. In young cuts it was equally or more abundant in deciduous stands. In jack pine stands at White River, it was significantly correlated with the earliest stage of succession 3-5 years after clear-cutting. It was a significant indicator of this age class. It was not significantly correlated with any habitat variables that were examined (Venier and Pearce 2005). Welsh (1993) considered it an early successional species throughout the Boreal Forest. Although it occurred in stands 1-200 years old, peak abundance occurred in stands 14 years or less in age. In the Clay Belt, Welsh and Lougheed (1996) found it in all 23 stands they surveyed. These spanned the entire continuums for moisture

regime and nutrient richness. It was most abundant in jack pine stands followed by those dominated by black spruce, trembling aspen, white birch–white spruce, tamarack, balsam poplar, and white cedar.

In white pine forests in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, the White-throated Sparrow was equally abundant in mature and old-growth forests older than 130 years. It occurred in about 20% of both age classes of forest (Kirk et al. 2012). In Quetico Park, it occurred in stands 1-370 years old but was most abundant in those 1-23 years old (Apfelbaum and Haney 1985). In jack pine stands near Gogama, it was one of the most ubiquitous species in both pine and mixed forests. Peck and James (1995a) considered it a species of shrub growth in early regeneration or at edges or in openings of older forests. It moved into areas once deciduous shrubs reached a height of 1 m provided that they covered at least 50% of the ground. It was abundant where the pines were less than 10 years old and decreased in successively older stands as the canopy closed. In jack pine stands near Parry Sound, James (1979a) recorded it on all transects. The habitat was open-canopied jack pine mixed with a variety of deciduous species with openings due to wetlands and bedrock outcrops. MacLulich (1938) considered the White-throated Sparrow the most abundant sparrow in Algonquin Park where it was commonly and evenly distributed. It occurred in and near shrubs and was often found far into forest interior. It was more abundant in mixed and coniferous woods than in sugar maple forests. Tozer (2012) reported that it bred in the park in open coniferous and mixed woods, old burns and cutovers, brushy clearings, and borders of bogs, beaver meadows, and old fields. It preferred edges of second-growth coniferous forests with an understorey and an open canopy. In shelterwood cuts in white pine stands in the park, it was observed in 91.7% of 2-9-year-old cuts, 70-83.3% of 10-16-year-old cuts, and 35.7-53.3% of cuts older than 24 years. It was significantly more abundant in young than old cuts. Its abundance was negatively correlated with the deciduous component of the forest, canopy cover, and the extent of herbaceous cover (Kingsley and Nol 1999). In Algonquin Park, Martin (1960) did not find it in bogs or forests dominated by black spruce, black spruce–white cedar, or tolerant hardwoods. In white birch–poplar stands, its activities extended from the ground upward to the lower tree branches above the shrub layer to a height of 4.5 m. It was fourth in abundance in white birch–poplar stands containing balsam fir and spruce. In balsam fir–spruce forests, it was among the most abundant species; it occupied the shrub and lower tree foliage layers. In hemlock stands, it ranged to a height of 6 m, 1 m below the top of the canopy. Lowther and Falls (in Austin 1968) stated that it nested in Algonquin Park most frequently in semiopen stands of balsam fir and spruce and, to a lesser extent, semiopen mixed stands of white birch, poplar, balsam fir, and spruce. It nested in both wet and dry thickets and occurred everywhere except dense spruce forests. Falls and Kopachena (2020) concluded that it was abundant in the park in successional coniferous and mixed forests with openings carpeted with blueberries, but it declined as the forest canopy closed. Males sang mainly from 2-4 song posts that were usually 6-12 m above ground in the outer branches of a spruce. White pines were occasionally used for singing but birches and aspens were avoided. It occasionally sang from a stump or small tree, but never from the ground (Lowther and Falls in Austin 1968). Knapton and Falls (1982) compared the vegetation in territories of pairs of white-morph males and tan-morph females to that of pairs of tan-morph males and white-morph females. In territories of white-morph males, trees were further apart (478 cm compared with 354 cm), there was less wild

sarsaparilla (3.5% compared with 7.0%), less beaked hazel (8.9% compared with 11.3%), less bracken fern (11.2% compared with 13.0%), and more blueberries (12.7% compared with 9.3%). Characteristics that were similar in white- and tan-morph males' territories included: reindeer lichen, 2.1% and 1.4%; grasses, 8.1% and 5.8%; orange hawkweed, 1.2% and 1.6%; American fly honeysuckle, 8.3% and 6.4%; and Canada mayflower, 1.2% and 1.6%. Territories of white-morph males were predominantly in open habitat. Tan-morph males occupied a broader range of habitat from the open habitats occupied by white-morph males to dense habitats not used by white-morph males. Only 3 of 37 plant species differed in their abundance within 30 cm of nests of white- and tan-morph males, respectively: large-leaved aster, 17% compared with 44%; American fly honeysuckle, 25% compared with 48%; and raspberries, 33% compared with 12%. Tree size, distance between trees, and coverage by trees and shrubs near the nest did not differ for the morphs. Trembling aspen occurred more often than expected near nests of tan-morph females, but it was considered unlikely that females chose nest sites based on the species of the nearby trees. Results indicated a greater proportion of tan males inhabiting dense habitat but there was no simple habitat division by the morphs. The morphs foraged in similar manners within and around their territories and did not behave as though they were separate species. The plants that occurred most frequently and with the greatest cover values did not differ between the morphs, and the structural habitat of the morphs was similar. Tan morphs nesting in dense habitat were equally successful as those nesting in more open habitat. Tan morphs may be better adapted to nesting in denser habitat because they are smaller and have shorter wings. They may select dense habitat rather than being excluded from open habitat by white morphs. In Muskoka District and Haliburton County, the White-throated Sparrow was negatively correlated with increasing canopy volume and tree density. It was positively associated with shrubby areas, lawns in highly developed cottage areas, high coniferous composition, and dense understorey. Its preference for an open canopy with a well-developed understorey made it well suited for inhabiting cottage lots in coniferous woods where most of the tree layer had been removed (Clark et al. 1983).

South of the Canadian Shield, the White-throated Sparrow was positively correlated with the amount of forest 100 m or more distant from an edge, woodlot size, amount of forest cover within 2 km, and the amount of regional forest cover. The relationship with the amount of forest core area was the only one that was significant (Austen et al. 2001). In Durham Region in the Great Lakes–St. Lawrence Forest Region, Speirs and Orenstein (1975) observed it in wet forests with open canopies and in a black spruce bog surrounded by a red maple–poplar swamp. They considered it associated with white cedar and mid-succession forests.

In the Carolinian Forest Region, the White-throated Sparrow is confined to isolated patches of conifers, especially white cedar swamps and spruce bogs (Lowther and Falls in Austin 1968). Near Cambridge, McIlwraith (1894) found it breeding in tamaracks surrounding a pond. In Halton Region and the Flamborough area of Hamilton, it nests in white cedar swamps (Curry 2006). It is a rare breeder in Elgin County swamps (Lancaster et al. 2004).

Throughout its range, the White-throated Sparrow nests in a variety of treed and shrubby habitats. Lowther and Falls (in Austin 1968) stated that it normally nests in coniferous forests in the east, preferring spruce and balsam fir, but that it often breeds in clear-cuts. In western Canada, it

breeds in aspen parkland and the Boreal Forest Region, in areas dominated by mature trembling aspen growing in semiopen stands with occasional dense groves of smaller trembling aspen and scattered white spruce and white birch, and groves of willows along seepages and watercourses. In Newfoundland and Labrador, it nests in high rock barrens with clumps of dwarf spruce and tamarack, in black spruce around borders of open sphagnum bogs, in clear-cuts, second growth, open woods, and hillsides. At Churchill, maximum density occurred where spruce forest reached its maximum density and a height of 10.7 m, but only where openings were present such as roadsides and railways. In Maine, highest densities occurred at high elevations on mountains where thin soils supported only stunted and widely spaced trees. Falls and Kopachena (2020) considered it a habitat generalist and an edge species. It breeds in coniferous, mixed, and deciduous forests, especially those having numerous openings with dense low shrubby ground cover. It is abundant in second growth after logging, fires, and insect damage; around margins of ponds, lakes, rivers, bogs, and beaver meadows; in and around clumps of trees near the treeline; where rock outcroppings create openings in the forest canopy; in clearings around cottages and along roads, railways, and utility rights-of-way; and in shrubby field edges and overgrown pastures. It avoids very dense spruce forest. In the east and north, it occurs mostly in coniferous forests of spruce, balsam fir, hemlock, white cedar, tamarack, and pine, often mixed with poplars, white birch, and alder. In the Boreal Forest Region, Erskine (1977) considered it typical of black spruce forest and one of the most characteristic species of the boreal forest. It is common in spruce and balsam fir stands, found in most jack pine stands, and also occurs in tamarack and bog forests. It is more common in young than mature stands and is one of the most regular species in young deciduous stands. Within poplar–white birch stands, it is associated with scattered spruce and balsam fir with an open canopy or small trees. It inhabits both coniferous and deciduous stands, particularly at edges or in or near openings. It is common in burns and clear-cuts where there is nearby shrubbery and a litter layer on the soil that has survived burning. It occurs in bogs where there are more or taller trees rather than open bogs. In Quebec, it was especially common in coniferous and mixed forests, but also abundant in deciduous forests and in urban and agricultural landscapes where small mixed and deciduous woodlots are common and provide suitable habitat. Near the northern extent of its distribution, it frequents shoreline scrub, burns, and black spruce–moss stands. In the Nottaway, Broadback, and Rupert watersheds of Quebec, it was more abundant in old and recent burns than in any other habitat. Shoreline scrub was favoured in the Eastmain River watershed (Spencer et al. in Gauthier and Aubry 1996). In black spruce forest in Quebec, it was associated with younger forest stages. It was most abundant in recent burns and cuts where shrubs were 2-5 m tall, and significantly less abundant in burns and cuts with saplings 5-11 m tall and in forests 120 and 200 years old. Open habitats were dominated by the White-throated Sparrow, with it representing 37% of all birds in young burns and cuts (Imbeau et al. 1999). Also in Quebec, it was abundant in strip-cuts, especially final cuts, and in clear-cuts. It was much more abundant in newly created strips than in older strips where vegetation regrowth created a closed canopy (Falardeau et al. 1999). In New Brunswick, it was one of the dominant species in spruce plantations 20 years or less in age and was uncommon to absent in natural spruce forests. In Nova Scotia clear-cuts in northern hardwoods, it was one of the dominant species. It was characteristic of stands 12 years old and younger, although it occurred in the oldest stand examined (74 years) at very low density. It was significantly correlated with high coverage by slash, abundant ground cover, and high shrub stem density (Freedman and Johnson 1999; Morgan

and Freedman 1986). In the Prairie Provinces, it demonstrated a pronounced increase in abundance from coniferous to deciduous sites. It was associated mostly with mixed or deciduous forests, but also occurred in black spruce and species-poor jack pine stands. Its habitat averaged moderate on the nutrient and wetness scales (Kirk et al. 1996). In boreal areas of British Columbia, it nests in a variety of shrub-dominated habitats. These include mature deciduous, mixed, and floodplain forests with dense shrub growth; recent burns and clear-cuts; and forest edge habitats around beaver ponds, wetlands, and bogs. It prefers trembling aspen stands with dense shrub undergrowth. Along rivers, it is most common in mature deciduous riparian forests dominated by trembling aspen or balsam poplar and birch, followed by mature coniferous riparian forests. Preferred balsam poplar stands often have a dense undergrowth of red-osier dogwood (Campbell et al. 2001). In the Yukon, it is abundant in shrubby old-growth white spruce and mixed forests, shrubby balsam poplar and riparian forests, and shrubby clear-cuts and burns (Sinclair et al. 2003). In the northeast, Taylor and Taylor (1979) considered the White-throated Sparrow a species of small forest openings, edges, and forest edge, but not of large openings. In New Hampshire, Wasserman (1980) reported densest populations in semiopen fields where the dominant vegetation was common juniper approximately 1 m tall and often several metres in diameter. In Indiana, Grundel and Pavlovic (2007b) did not consider it characteristic of any habitat. It nested in open prairie remnants with little overhead canopy or subcanopy, savannahs, scrub, woodlands, and forest. It was most abundant in woodlands that were open forests with more canopy cover than savannahs. The White-throated Sparrow rarely nests in urban habitat. What was possibly the same pair nested in 4 years in the business section of Buffalo in an intensively developed area. The area was completely dominated by buildings, streets, and other paved structures. The birds nested in ornamental plantings along the foundation of a church (Andrle 1974; Andrle and Rew 1971). In Saskatchewan, 1 pair raised young in a Saskatoon yard (Leighton et al. 2002).

Three studies examined habitat preferences of the White-throated Sparrow at the landscape level. In Minnesota, it was positively correlated with the interspersion of habitat types within 1 km^2 (Crozier and Niemi 2003). In Saskatchewan, it was more common in large forest fragments or in areas with high local forest cover within 5 km. It was randomly distributed among fragmented and intact landscapes (Hobson and Bayne 2000). In Newfoundland, it occurred in 83% of landscapes containing some clear-cuts, 76% of natural landscapes, and 79% overall. It declined as the amount of woodland increased in both landscape types, from almost 100% occupancy at 10% forest cover, dropping to 65% at 95% forest cover (Taylor and Krawchuk 2005).

The White-throated Sparrow nests in all age classes of forests, but is most abundant in early successional and old stands; reproductive success is also greatest in these stands (Falls and Kopachena 2020). It is probable that stand structure is more important than its age. It prefers forests with an open canopy and a shrubby understorey. The earliest stages of succession provide this structure as do older forests where treefalls create gaps in the canopy. In Quebec, Rousseau et al. (2012) concluded that it could be considered a generalist because it nested in forest habitats from 1 month-old clear-cuts to mature stands. It was unknown if females preferred mature forests; it might be a generalist species with specialist individuals. In New York, it increased over 35 years in an open agricultural field that became a second-growth forest, but there was no change over 33 years in a mixed forest (Brooks and Bonter 2010). In northeastern northern hardwoods, it occurred on 8%

of plots in mature undisturbed habitats and 23% of plots in disturbed and early successional habitats (Noon et al. 1979). Temple et al. (1979) did not consider it characteristic of any forest age class in northeastern mixed forests. Niemi and Pfannmuller (1979) considered it ubiquitous in early successional habitats in the northeast. Kirk et al. (1996) considered it a very early successional species in forests in the Prairie Provinces. In Newfoundland balsam fir stands, it was most abundant in old stands. These were somewhat more open, had larger dead standing trees, more shrub coverage, and the most large woody debris on the ground (Thompson et al. 1999). In Vermont, it was associated with low successional age (Lent and Capen 1995). In trembling aspen stands in Alberta, it was significantly more abundant in forests older than 120 years than in forests 51-63 and 23-26 years old. It was more abundant in the young stands than in intermediate-aged stands, but not significantly. Old stands had significantly fewer trees per ha than other age classes (Schieck et al. 1995). In British Columbia trembling aspen stands, it was common in mature forests and in clear-cuts 5-20 years after cutting (Campbell et al. 2001).

Several studies examined microhabitat preferences of the White-throated Sparrow. In Minnesota, its abundance was positively correlated with the density of dead trees but was unrelated to habitat complexity (Niemi and Hanowski 1984a). In New Hampshire and Maine, it was associated mostly with poplar followed in decreasing order by white pine, spruce–balsam fir, balsam fir, northern hardwoods, hemlock, and hardwood swamp stands. It was absent in white birch stands. It was positively correlated with coniferous trees larger than 10 cm diameter at breast height (DBH) and number of woody stems per ha. It was negatively correlated with foliage volume of both coniferous and deciduous trees larger than 10 cm DBH and foliage volume of deciduous stems smaller than 2 cm DBH (DeGraaf et al. 1998). In northeastern mixed forests, it was associated with increasing abundance of trembling aspen (Temple et al. 1979). In Saskatchewan, it was more common than expected in trembling aspen stands (Hobson and Bayne 2000). In Newfoundland balsam fir stands, it was significantly more abundant in sites that were nutrient-rich than nutrient-poor (Thompson et al. 1999). In Newfoundland, nests were in areas that were more characteristic of open and harvested areas. There was more downed wood and less tall vegetative ground cover within a 1-m radius of nests than in random areas. Within a 5-m radius, nest-site characteristics did not differ from random sites. Successful nests had a more open canopy and less downed small wood than unsuccessful nests at both the 1-m and 5-m scales. Successful nests had more coarse woody debris than unsuccessful nests at the 1-m scale but there was no significant difference at the 5-m scale. Tall vegetation occurred within the territory and was characteristic of the nest site at a larger scale, but was not selected for at the nest microsite. It did not nest in more open canopy, but success was associated with less canopy cover (Dalley et al. 2008). Lowther and Falls (in Austin 1968) described microhabitat within the vicinity of nest sites. Within 15 m of the nest, there was usually 1 large object or group of objects such as a tree, stump, shrub, or log. There was a positive correlation between the height of the object and its distance from the nest. These objects may provide a lookout prior to flying down to the nest. The amount of cover within 3 m of the nest was similar to the general nesting habitat but there was much less variation within 3 m. It selected nest sites in relation to the amount and dispersion of the nearby cover. The nesting habitat could be described as forest edge. In subalpine areas of New Hampshire, it nested predominantly in high-elevation mixed and coniferous stands, but extended upwards into the tundra zone. Mean habitat

characteristics included exposed upper slope to upper mid-slope, no water or slight wet depressions present, canopy height 5.0 m, 45% canopy coverage, 75% conifer foliage volume, 41% conifer foliage volume at 0-2 m, 12% deciduous foliage volume at 0-5 m, and 8 cm DBH live trees (Sabo 1980). On Wisconsin islands, it was significantly correlated with aspen and preferred pioneer forests of aspen and pine forests. It was the most abundant species in young aspen stands (Beals 1960). In Vermont, it exhibited strong clumping of territories in logged patches and was absent in undisturbed forest. It was associated with low successional age, increasing coverage by conifers, and moderate amounts of dead trees. It was also associated with low coverage by hophornbeam, red oak, sugar maple, and beech; decreasing coverage of red maple; and moderate amounts of poplars and white pine. Its habitat was ephemeral so it may adapt a fugitive strategy as it seeks nesting habitat in the shifting mosaic of habitat patches in spring. Lent and Capen (1995) considered it a gap-specialist species. In Maine spruce–balsam fir stands, it was positively correlated with raspberries, woody stems less than 10 cm DBH and 2.1-4.5 m tall, and slash 0-1.0 m from the ground. It was negatively correlated with woody stems greater than 10 cm DBH and more than 4.5 m tall, slash higher than 1 m, deciduous trees 15-20 cm DBH, and conifers larger than 20 cm DBH (Titterington et al. 1979). In clear-cuts in northern hardwoods in Vermont, mean habitat characteristics were 84.7% green ground cover, 9.1% ground cover slash, 32.0% canopy closure, 9.4 m canopy height, 6.5 m canopy depth, 4.2 m^2 basal area of deciduous trees, 1.0 m^2 basal area of conifers, 7.0 cm DBH for deciduous trees, and 8.5 cm DBH for conifers. It occurred in habitats with dense vegetation less than 3 m tall and no overhead canopy such as clear-cuts with dense hardwood saplings (Thompson and Capen 1986). In Minnesota, it was negatively correlated with tree size and density and the number of different habitats present in the landscape (Crozier and Niemi 2003).

In Alberta, both white- and tan-morph males occurred in forest interior, edges, and clear-cuts but white morphs were most abundant in edge and tan morphs were most abundant in forest interior. In New York, white morphs tended to cluster in contiguous suitable habitat. Tan morphs occurred in more isolated patches. Territories sometimes supported the opposite-coloured morph in different years (Falls and Kopachena 2020).

In subalpine habitat in New Hampshire, the White-throated Sparrow used clearing edges with a lookout for nesting. The Dark-eyed Junco used dense shrub clumps with a rock outcrop or exposed bank. The 5 forest-floor species were separated by the Winter Wren's speciality for fallen logs, the junco's use of twig pecks while foraging and use of the understorey, the White-throated Sparrow using both twig and litter pecks, and the Swainson's and Gray-cheeked thrushes pecking and gleaning in the litter and also feeding in the understorey (Sabo 1980).

The White-throated Sparrow nests in clear-cuts, forest edges, and forest interior, but is commonly termed an edge species because it is often more abundant in this habitat (Freemark and Collins 1992; Taylor and Krawchuk 2005). Along an interstate highway in Maine, it was most abundant within 100 m of the highway (Ferris 1979). In Newfoundland, it was significantly more abundant at clear-cut and access road edges than in forest interior; abundance at riparian edges was intermediate. Whitaker and Montevecchi (1997) considered it an open or edge species associated with early successional openings and edges. In balsam fir–white cedar stands in

Newfoundland, there was no significant difference in its abundance in riparian stands with a narrow strip of alder-grass wetland and in nonriparian stands (Whitaker and Montevecchi 1995). In Alberta stands of trembling aspen, balsam poplar, white spruce, and white birch, density was highest in edge and lowest in clear-cuts. There were no significant differences in settlement dates, but it was slightly earlier in edges and forest interior than in clear-cuts. Fewer territories were abandoned after unsuccessful reproduction in forest interior (5.4%) than in edge (17.2%) and clear-cuts (65.8%). The proportion of territories fledging young was significantly lower in clear-cuts (19-23%) than in edge (32-35%) and forest interior (35-55%) in 2 years. Pairing success was significantly higher in forest edge and forest interior than in clear-cuts; habitat was a significant predictor of pairing success. Territory density was not a useful indicator of habitat quality. Edges had the highest density but were not the highest quality for pairing success, nesting success, or fledgling production. Clear-cuts represented lower-quality habitat and forest interior was higher-quality habitat. Individuals did not select the highest-quality territories first in spring. Body condition indices were higher in edge habitats suggesting that they provided greater food availability. Differences in nesting success may have reflected pairing success because predation and parasitism rates were not significantly different among habitats. Females may opt to mate with males in more intact habitat such as forest interior and edge. Individuals in clear-cuts were apparently unable to effectively evaluate habitat quality during territory establishment and suffered reduced reproductive success (Hannah et al. 2008). In another Alberta study, Villard et al. (2007) predicted that the White-throated Sparrow would be attracted to edges created by clear-cuts, but its response was neutral and nonsignificant. The mean distance to edge averaged 40 m 1 and 2 years after clear-cutting.

The White-throated Sparrow is not an area-sensitive species and may occupy very small habitat patches. Morse (1977) studied the distribution of birds on small islands (0.1-0.4 ha) in Maine. The White-throated Sparrow occurred only on islands that were as large as its mean territory size. The smallest island it occurred on was 0.49 ha, the same size as the mean territory size. The size of the next smallest island was 0.39 ha. Islands with the highest densities of Song Sparrows did not support White-throated Sparrows. In downtown Buffalo, the White-throated Sparrow occupied a small triangle of habitat that was a maximum of 0.18 ha (Andrle and Kew 1971).

Ninety percent of Ontario nests were on or near the ground and the others were elevated in shrubs, trees, brush, or fallen trees. Most ground nests (53.7%) were under low shrubs (commonly blueberries) and trees, and were usually well concealed by grasses, bracken ferns, and other plants; 21.5% were in grass clumps; 14.8% were in mosses with grasses and sedges; 8.1% were in weedy plants and ferns; 0.7% were in leaf litter; 0.7% were under logs; and 0.4% were under roots. Some ground nests were somewhat sunken into the substrate. Approximately equal numbers of elevated nests were in deciduous shrubs and small conifers. Nest heights were 0.2-0.9 m, mostly 0.2-0.5 m. One nest was 2.4 m from the ground in a fallen cedar supported by another cedar (Peck and James 1987). In Algonquin Park, the White-throated Sparrow preferred to nest in clearings large enough to allow direct sunlight to strike the ground vegetation at some time of the day. Of 42 nests, 36 were under blueberries and the remainder were under sweet fern, beaked hazel, hair-cap moss, or mountain-rice grass. Of the 36 under blueberries, 28 were under plants 15-30 cm tall. Two nests were under cover less than 15 cm tall and 13 were under cover taller than 30 cm. Thirty-six nests were on level ground and 2 of the 6 nests on sloping ground were in the middle of 3-m

embankments. Canopies were present over 34 of the 42 nests. Twenty-nine nests were under a mat of dead bracken fern from the previous year, 4 were under clumps of dried mountain-rice grass, and 1 was under the tip of a lower branch of a spruce. The 8 nests without overhead cover were either in vegetation taller than 30 cm or built later in the season in cover lacking an overstorey of live bracken fern. The White-throated Sparrow usually nested on the ground in areas of small trees between which there were clumps of beaked hazel and a ground flora of blueberries and various grasses and forbs. Six replacement nests were all within 33 m of the first nest. Of 197 nests in Algonquin Park, 6 (4.7%) were above ground: 23 cm up on the lower bough of a white spruce, 1 on the bough of a fallen white spruce, 15 cm up in a blueberry, 5 cm up among blueberry and sweet fern stems, 53 cm up in sweet gale, and 76 cm up in bracken fern. Of 54 nests initiated after 15 June, 11.1% were elevated. It was not known to reuse nests (Falls and Kopachena 2020; Lowther and Falls in Austin 1968). In the Hudson Bay Lowland, all nests were on the ground in mixed spruce–deciduous growth (Schueler et al. 1974).

All 34 British Columbia nests were on the ground except for one in a pile of river debris. They were usually well concealed beneath the shrub layer in grass clumps or under other low vegetation. Several were at the base of a deciduous shrub or sapling and one was underneath an upturned root. Most were in or near natural forest openings or human-made clearings such as road or hydro corridors, seismic cuts, clear-cuts, footpaths, and fields. Several were among or near deadfalls or other natural accumulations of woody debris, or near human-created brush piles. The single elevated nest was 1 m from the ground (Campbell et al. 2001). A New Hampshire nest was on the ground under a common juniper. When it failed, the replacement nest was built 15 cm from the ground in a juniper 35 m from the first nest. The first nest was within 10 m of the male's centre of activity. The second one was between the activity centres of 2 adjacent pairs in an area that was infrequently used (Wasserman 1980). An Ohio nest was 0.9 m from the ground well hidden among the branches of a fallen spruce (Davis 1973). In Newfoundland, 32 nests were on the ground and one was 0.5 m from the ground in a balsam fir. Twenty-five nests (75.8%) were in moss (Dalley et al. 2008). In New Brunswick, Philipp and Bowdish (1917) found 2 nests, both of which were elevated in small spruce; 1 was 101.6 cm from the ground. In New York, nests were at the base of a clump of grass or a small shrub. Tan-morph females nested closer to the ground and in brighter light than white-morph females. There was no significant difference in the placement of nests of the morphs for these characteristics in Algonquin Park (Falls and Kopachena 2020).

Territorial activity is greatest in spring and involves singing and chasing of intruders to just beyond the territory boundaries. Interactions with neighbours decrease with time but responses to strangers remain strong. Males establish territories as soon as spring flocks break up. Singing is greatly reduced in early June when nesting is underway but resumes in July for second nestings. Territories are maintained until the last brood fledges. Fledglings that leave the territory are accompanied by only the female. The male remains on the territory but no longer defends it. Singing is concentrated at a few song posts which may influence the territory location and results in uneven usage of the territory by the male. White-morph males are more responsive to other males' songs than tan morphs and are more aggressive in defending their territories. White-morph females may participate in territorial defence but tan morphs do not. In Algonquin Park, females may nest anywhere within the territory or rarely in areas defended by neighbours. In these cases, either the

territory boundaries are shifted or the nest is abandoned. Females in New Hampshire nested predominantly in the centre of the territory and males concentrated their activities within 15 m of the nest site. The area in which males sang ranged from 1,200 to 7,200 m^2 with the least area used during the incubation and nestling periods and the most during the fledgling period. The male spent more than 50% of his time in the same 100 m^2 quadrant as the female when she arrived. The amount of time spent together decreased during incubation, increased during mating activities for replacement or second nests, then decreased. Males appear to conduct all their activities in the territory but females may leave the territory to forage. North of Lake Nipigon, there was no overlap in territories. Territories in clear-cuts were frequently contiguous but those in forest cover were often isolated. One case of polyterritoriality has been documented with the 2 territories 300 m apart (Falls 1988; Falls and Kopachena 2020; Kendeigh 1947; Kopachena and Falls 1993a; Lowther and Falls in Austin 1968; Wasserman 1980, 1982, 1986). There is no significant difference in the size of territories of white- and tan-morph males. In Algonquin Park, 90 territories averaged 0.99 ha (range 0.22-3.26 ha). Territory sizes tended to decrease from the time that females arrived until the young fledged. An earlier study at Algonquin Park determined that average territory sizes were 0.77 ha (range 0.36-1.29 ha) for 20 mated males and 1.01 ha (range 0.61-1.13 ha) for 3 unmated males (Falls and Kopachena 2020; Lowther and Falls in Austin 1968). Another Algonquin Park study determined the average size of 110 territories to be 0.21 ha (range 0.02-1.09 ha; Martin 1960). North of Lake Nipigon, 20 territories averaged 0.47 ha (range 0.20-0.97 ha). Fourteen forested territories averaged 0.49 ha and 6 territories in clear-cuts averaged 0.36 ha (Kendeigh 1947). In Algonquin Park, nonterritorial males wandered through territories quietly and covered areas that averaged 3.6 times the home range of territorial birds (Falls and Kopachena 2020). In Maine, mean territory sizes in mainland spruce forests were 0.35 ha in damaged spruce stands, 0.49 ha in edges of spruce forests, and 1.67 ha in white spruce forests. Mean territory size in white spruce stands on small islands was 0.49 ha (Morse 1977). In subalpine forests in New Hampshire, territories averaged 0.6 ha (Sabo 1980). In Quebec, mean territory size was 0.79 ha in balsam fir forest with scattered white spruce, black spruce, and white birch (Rousseau et al. 2012).

Natal philopatry rates are very low, but few young have been banded. In Algonquin Park, 0 of 65 nestlings returned (Knapton et al. 1984) and 0 of 21 nestlings returned in Alberta (Hannah et al. 2008).

In Algonquin Park, 19 of 47 males (40.4%) and 3 of 30 females (10.0%) were retrapped on the same territory in the following year (Lowther and Falls in Austin 1968). In another Algonquin Park study, the percentage of returning males over 2 years was 50.0% and 47.6% for white-morph and 52.4% and 39.1% for tan-morph males; the differences were not significant (Knapton et al. 1984). The return rate estimates may have been low because a male that returned to an area just outside the study area would not have been detected. In 1 year, 3 of 55 females (5.5%) returned and all were white morphs. Two returned to the same territory but to a different mate. The following year, 4 of 43 females (9.3%) returned. These included 3 white morphs and 1 tan morph, with 2 returning to the same territory. Forty percent of successful males and 54.5% of unsuccessful males returned the following year; the difference was not significant. In New York, 60% of males and 46% of females returned in a subsequent year. Sixty percent of white-morph males and 40% of white-morph females returned compared with 66% of tan-morph males and 50% of tan-morph females. Most

birds reoccupy the same territory but some birds of both sexes move so the estimated return rates are probably low (Falls and Kopachena 2020). In Alberta, 29 of 73 adult males (39.7%) returned: 41.9% in 1 year and 36.7% in another year. In forest interior, the return rate was 44.4% compared with 41.2% in forest edge habitat, and 25.0% in clear-cuts (Hannah et al. 2008). In Quebec, Rousseau et al. (2012) reported adult male return rates of 35% in mature forests and 50% in recent clear-cuts, 90% territory fidelity in forest interior and 100% in clear-cuts, and 33 m median dispersal distance in forest interior and 46 m in clear-cuts. Treatment plots were partially clear-cut in winter after breeding birds had been banded. Return rates were similar between control (35%) and treatment plots (41%). Territory fidelity was significantly higher for control (90%) than treatment (50%) plots. The mean dispersal distance of treatment males (86 m) was significantly greater than for control males (33 m). The higher the proportion of the original territory that was clear-cut, the further the male dispersed. Two males dispersed more than 700 m.

Limiting Factors

Eggs have been reported in Ontario nests from mid-May until mid-August, with most present in June (Peck and James 1987). Almost all information on nesting phenology is from Algonquin Park. Nests are under construction there from mid-May to late July, eggs are present mid-May to early August, nestlings are present from late May to mid-August, and fledglings have been observed from late May to mid-August (Tozer 2012). Pair formation begins immediately upon the female's arrival in tan-morph male–white-morph female pairs and within a few days for pairs comprised of white-morph males and tan-morph females. Most birds are paired before the end of the third week of May in the park. Nest building starts in the third and fourth weeks of May, as much as 2 weeks after pair formation for pairs with tan-morph males and within a few days for pairs with white-morph males. Nest building takes 4-6 days early in the season and 2 days for later nests. Laying usually starts 1-2 days after nest completion. In 1 year in the park, pairs with tan-morph males initiated egg laying significantly earlier by 5 days than pairs with white-morph males but there was no significant difference the next year when all clutches were initiated approximately 9 days later. Most first eggs were laid 21-27 May between 1986 and 1990, with the earliest egg laid on 15 May. First clutches are highly synchronized but synchrony declines with season. One egg is laid per day. Incubation usually starts with the laying of the last egg in clutches of 4 or fewer eggs. Incubation starts with the penultimate egg in 5-egg clutches. The incubation period in Algonquin Park and the remainder of Ontario is 11-13 days, with 12-14 days reported elsewhere. In smaller clutches, the eggs all hatch on the same day but in 5-egg clutches the last egg hatches a day later. The nestling period in the park is 7-12 days, but mostly 8 or 9 days, particularly in the morning of the ninth day (Falls and Kopachena 2020; Knapton et al. 1984; Kopachena and Falls 1991, 1993a; Lowther and Falls in Austin 1968; Peck and James 1987).

The White-throated Sparrow may raise either 1 or 2 broods in a season. Double broods have been confirmed in Ontario at Rutherglen and Algonquin Park. In the park, pairs fledging young before the end of June may attempt a second brood but it is unlikely that a second brood will be attempted after the first week of July. Of 11 pairs that fledged young before 7 July in the park, 6 (54.5%) attempted second broods. Double broods have been attributed to high abundance of food during spruce budworm outbreaks, but budworm populations were not particularly high when this study was completed. It is probably frequently double brooded provided that the first brood fledges

early enough. It is possible that double broods occur only in the more southern portions of its range. In 2 cases in Algonquin Park, females laid the first egg of the second clutch 4 days after the first brood fledged. There was an average of 8.5 days between fledging and incubation of the second clutch. In New York, almost all females have 2 broods. In Quebec, egg dates suggest double broods but this has not been confirmed. Only single broods have been reported in British Columbia (Campbell et al. 2001; Falls and Kopachena 2020; Knapton et al. 1984; Kopachena and Falls 1993a; Lowther and Falls in Austin 1968; Spencer et al. in Gauthier and Aubry 1996). In 1971 and 1972 in Algonquin Park, 24 pairs were double brooded and 1 pair attempted a third brood in 1972. The first brood of 4 fledged on 14 June and both adults were observed tending fledglings on 27 July that appeared to have been out of the nest for about 2 weeks. On the same day, the female was flushed from a nest that contained 3 eggs. The eggs hatched on 31 July but all young perished by 4 August. Poor survival in August is normal due to depletion of food resources and a decline in parental attention. This pair successfully raised 2 broods and hatched a third in 70 days (Loncke and Falls 1973). The White-throated Sparrow commonly renests if the previous nest is unsuccessful. In Algonquin Park, 16 of 50 pairs (32.0%) that lost their nest initiated a replacement nest and 1 pair renested after 2 failures. For 6 pairs, there was an average of 8.7 days between nest loss and incubation of the replacement clutch (Falls and Kopachena 2020; Knapton et al. 1984; Kopachena and Falls 1993a; Lowther and Falls in Austin 1968). Clutches of 2-5 eggs have been reported in Ontario with 4- and 5-egg clutches most frequent; 63.3% of clutches contained 4 eggs. The average clutch size was 4.00 eggs (Peck and James 1987). In Algonquin Park, 41 clutches had an average of 4.1 eggs (range 3-5 eggs). In 2 years in another Algonquin Park study, clutch sizes for tan-morph females were 4.19 and 4.27 eggs compared with 4.50 and 4.11 eggs for white-morph females. There was no significant difference in clutch size of the morphs in either year or any evidence that clutch size declined with season (Knapton et al. 1984; Lowther and Falls in Austin 1968). Clutches typically contain 3-5 eggs with 1 record of a 7-egg clutch from Saskatchewan. It is possible that the large clutch was due to intraspecific parasitism. Mean clutch size throughout the range of the White-throated Sparrow, excluding Ontario, is 4.3 eggs. In Maine, mean clutch sizes were 3.81 for white-morph females and 3.78 for tan-morph females. Mean clutch size in Newfoundland was 3.85; 50% of British Columbia clutches contained 4 eggs (Campbell et al. 2001; Dalley et al. 2009; Falls and Kopachena 2020; Lowther and Falls in Austin 1968).

Both sexes of both morphs are capable of breeding when they are 1 year old. Populations often contain nonterritorial floaters and unmated males, suggesting that some yearling males are unsuccessful in attracting a mate (Falls and Kopachena 2020; Lowther 1961). The assortative mating, whereby a bird of 1 morph typically mates with a bird of the opposite morph, appears to be unique among birds. The differences in plumage are independent of both sex and age. White morphs have a single M chromosome that is lacking in the tan morphs. Because of the assortative mating, neither morph is selected for genetically. Of 110 pairs in Algonquin Park, 79 were white-morph males x tan-morph females (60 expected), 27 were tan-morph x white-morph females (8 expected), 4 were tan-morph males x tan-morph females (23 expected), and 0 were white-morph males x white-morph females. The number of all pair-type combinations was significantly different from random. In Algonquin Park, over 90% of the breeding population consists of 2 pair types: white-morph males x tan-morph females and tan-morph males x white-morph females. In another sample of 180 pairs in

Algonquin Park, 65% were white-morph males x tan-morph females, 33.3% were tan-morph males x white-morph females, 1.6% were white-morph males x white-morph females, and 0% were tan-morph males x tan-morph females. When a bird loses a mate, its replacement mate is usually the same morph as the original mate. There is no difference in the reproductive success of the 2 morphs (Falls and Kopachena 2020; Knapton and Falls 1983; Knapton et al. 1984; Kopachena and Falls 1993a; Kuenzel and Helms 1974; Lowther 1961).

The White-throated Sparrow is typically monogamous, but polygyny occasionally occurs. In Alberta, polygynous matings occurred in forest interior and edge, but not in clear-cuts. Polygynous matings typically consist of 1 white-morph male mated with 2 tan-morph females. One case of polyterritorial polygyny has been reported (Falls and Kopachena 2020; Hannah et al. 2008). Pairs usually remain together for the entire breeding season but not between breeding seasons. If a mate is lost, it is usually replaced until incubation begins and infrequently thereafter. Extra-pair copulations are a common breeding strategy. Tan-morph males spend 67% of their time mate guarding when the female is fertile. White-morph males spend more time seeking extra-pair copulations. In New York, 18 of 89 nestlings (20.2%) were a result of either extra-pair copulations or intraspecific parasitism. Both common pair types are recipients of extra-pair copulations. Seventy-nine percent of intrusions were by white-morph males and 21% were by tan-morph males; 75% of observed extra-pair copulation attempts were by neighbours. In Algonquin Park, there were 2 cases of white-morph nestlings in tan x tan-morph matings, indicating either extra-pair copulation or intraspecific parasitism. Two cases of intraspecific brood parasitism have been confirmed and a clutch of 7 eggs suggests another (Falls and Kopachena 2020). In New York, 31.8% of nestlings were extra-pair and 56.3% of broods from white-morph males and tan-morph females contained extra-pair offspring. These numbers were only 4.4% and 6.3% respectively for tan-morph male and white-morph female pairs. In another New York study, 182 of 1,183 nestlings (15.4%) were extra-pair and 26.6% of nests contained extra-pair young. Extra-pair young were present in 41.7% of nests with white-morph males compared with 8.7% of nests with tan-morph males. The relationship between breeding synchrony and extra-pair paternity was highly significant in nests of white-morph males, but highly nonsignificant in nests of tan-morph males. Neighbours constituted 29.5% of the extra-pair sires, significantly more than the expected 4%. White-morph males are responsible for most extra-pair paternity, but also lose more paternity (Grunst et al. 2017).

The White-throated Sparrow forages on the ground and vegetation, and frequently on small shrubs or lower portions of coniferous trees on the upper surfaces of horizontal branches. Males may forage near treetops between singing bouts. It clears away leaf litter by kicking with both legs simultaneously. It is able to find deeply buried seeds and is adapted to foraging near woody vegetation where the litter is deep. It also flips leaves side to side with its bill. In vegetation, it gleans along stems and through leaves or needles, especially near branch nodes or tips. It pounces on active insects, eats the pulpy part of fruits, and flycatches. It eats only the pulpy parts of fruits and does not eat skins or large seeds. In Algonquin Park, it has been observed chasing and catching dragonflies and may forage aerially on spruce budworm moths during outbreaks. In downtown Buffalo, the male occasionally sallied for insects in ivy growing on a church (Andrle 1974; Falls and Kopachena 2020; Lowther and Falls in Austin 1968). In subalpine areas of New Hampshire, 9.2% of foraging was by leaf gleaning, 0% by flycatching, 0.7% by leaf hawking, 0.2% by leaf hovering, 19.2%

by twig perching, 21.3% by twig gleaning, 2.0% by twig hawking and hovering, 1.4% by branch pecking, 1.8% by branch gleaning, 0.4% by bole pecking, 0% by bole gleaning, 36.3% by litter pecking, 6.2% by litter gleaning, and 1.4% by fallen log manoeuvres. In relation to tree trunks, 18.8% of foraging was distal and 34.9% was proximal. Foraging substrates included 37.2% in coniferous foliage, 16.4% in deciduous tree foliage, 2.4% in forb foliage, 42.7% on the forest floor, 9.4% 0.1-2 m from the ground, 34.2% 2-5 m from the ground, 13.4% 5-8 m from the ground, and 0.3% in the upper canopy above 8 m. It was a high-elevation ground forager (Sabo 1980). In Vermont, 78% of foraging was by gleaning and 22% was by aerial flights. Foraging substrates included 70% foliage, 15% air, 8% ground, and 7% tree trunks (Lent and Capen 1995). In New Hampshire, males foraged mostly on the ground but occasionally jumped from the ground to capture flying insects. Females fed exclusively on the ground. The area where males foraged was significantly larger than where they sang, and significantly larger than the areas where females foraged. Females foraged closer to the nest thereby reducing the amount of time spent off the nest. In 1 pair, the female's foraging areas were initially 5,500-7,000 m^2, 2,200-2,500 m^2 during the incubation and nestling periods, 6,000 m^2 during mating, 3,000 m^2 during incubation, 5,200 m^2 during the nestling period, and 8,000 m^2 during the fledgling period. The male's foraging areas were 6,000-6,500 m^2 during the first mating period, 8,000 m^2 during nest building, 5,200 m^2 during incubation, 4,500 m^2 during the nestling period, 6,500 m^2 during the second mating period, 3,000 m^2 during nest building, 4,000 m^2 during incubation, 5,200 m^2 during the nestling period, and 8,500 m^2 during the fledgling period (Wasserman 1980, 1982, 1986).

The median length of food items brought to Algonquin Park nestlings was 1.34-1.59 cm (range 0.90-2.59 cm), the median width was 0.30-0.45 cm (range 0.23-0.51 cm), and the median proportion of food items that were caterpillars was 54-62% (range 20-98%). The nestling diet consisted of 60.9% caterpillars, 5.1% adult lepidopterans, 3.4% fly larvae, 2.3% adult crane flies, 2.3% odonates, 2.2% beetles, 3.5% orthopterans, 0.6% mayflies, 2.0% winged insects, 1.6% pupae, 1.1% spiders, and 12.6% unidentified animal material. Food provided to fledglings is similar in composition. After the young become independent, their diet is similar to the adults and is dominated by vegetable matter (Knapton and Falls 1983; Kopachena and Falls 1993b; Lowther and Falls in Austin 1968).

In summer, the adult diet is predominantly insects supplemented with fruits and seeds later in summer and autumn. Stomachs collected in Algonquin Park in early May contained about 60% vegetable matter but by late May the diet consisted of 90% insects. In early May, the White-throated Sparrow ate young catkins of birch and beaked hazel. The most important insects in the breeding season diet were adult odonates, hymenopterans, bugs, adult and larval beetles, flies, and lepidopterans. It also eats spiders, millipedes, centipedes, and snails. Fruits important in late summer and fall included those of sumac, grape, highbush cranberry, mountain-ash, rose hips, blueberries, raspberries, bunchberries, and berries of red-osier and silky dogwoods. Other fruits it has consumed elsewhere include those of greenbriers, elderberries, black cherry, and strawberries. Coarse husks of grain are not eaten and chitinous parts of some insects such as wings of beetles and dragonflies are also rejected (Falls and Kopachena 2020; Lowther and Falls in Austin 1968). Judd (1901) analyzed the contents of 217 stomachs collected every month except June. The annual diet consisted of 19% animal matter and 81% vegetation. The animal food was comprised of 5% beetles, 3% bugs and flies, 3% lepidopterans, 6% hymenopterans, and 2% spiders, millipedes, and snails. The most

frequently eaten beetles were weevils and ground, leaf, click, scarab, and clown beetles. The hymenopterans consisted of 2% parasitic wasps, 3% ants, and 1% miscellaneous. Only 2 birds had consumed grasshoppers. Another study reported that White-throated Sparrows had each eaten an average of 18 Rocky Mountain locusts. The vegetable matter consisted of 3% grain, 50% weed seeds, and 28% wild fruits. Its fondness for berries was striking and 25% of its diet from July to November consisted of fruit of blueberries, black cherry, mountain-ash, greenbriers, strawberries, spicebush, wild sarsaparilla, common elderberry, blackberry, and guelder-rose. In July, fruit comprised 44% of the diet. In addition to eating berries, it picks up their dry seeds and cracks them to obtain the inside meat long after the fruit pulp has disappeared. From January to May, it fed on seeds of fruits such as blueberries, blackberries, elderberries, and grapes. Nearly a third of the January and February diet in Texas consisted of bits of seeds or drupes of wild berries. It may consume berry seeds that have been previously eaten by birds whose digestive systems are not strong enough to crush the seeds. It eats grass seeds such as those of foxtails, Johnson grass, crabgrass, panic grasses (approximately 5% of the entire diet), mainly in September when they constitute 25% of the diet. It eats lesser amounts of seeds of amaranths, lamb's-quarters, gromwells, chickweeds, wood-sorrel, sedges, violets, and sheep sorrel, but predominantly ragweeds and smartweeds. Ragweed constituted 9% of the annual diet and smartweeds constituted 25%; in October, 45% of the diet consisted of ragweed seeds.

The White-throated Sparrow usually increases during spruce budworm outbreaks (Falls and Kopachena 2020). Near Manitouwadge, it increased significantly with increasing budworm numbers in stands 1-21 and 24-36 years old but declined slightly in older stands; overall, it increased significantly (Venier et al. 2009). In New Hampshire and Maine, White-throated Sparrow stomachs contained an average of 11.9 spruce budworms, the highest of any species. It consumed significantly more as their density increased but had no discernible numerical response to budworm abundance. Its density was higher than in previous studies so numbers could have increased gradually over several years (Crawford and Jennings 1989). In Maine spruce-fir forests over 2 years, spruce budworm larvae and pupae constituted 18.9% and 16.5% of the invertebrates consumed (Mitchell 1952). In New Brunswick, Morris et al. (1958) observed no response to spruce budworm numbers. In the same province, it increased with increasing populations of the black-headed budworm. It consumed an average of 31 budworms per day, second only to the Dark-eyed Junco. Consumption rate was 0 when budworms were small and in their first instar even though they were most abundant at this time. Consumption increased to its maximum as prey size increased even though prey density was lower and gradually decreased to 0 as prey density declined (Gage et al. 1970).

The White-throated Sparrow is an infrequent host of the Brown-headed Cowbird, probably because the 2 species have different habitat preferences. It accepts parasitic eggs and has not been documented deserting parasitized nests. The effects of parasitism on the White-throated Sparrow are unknown, but it typically fledges both its own and cowbird young from nests. In Ontario, 24 of 449 nests (5.3%) were parasitized; only 1 of 192 Algonquin Park nests (0.5%) was parasitized. In southern Quebec, 20 of 507 nests (3.9%) were parasitized. In British Columbia, 6 of 34 nests (17.6%) were parasitized (Campbell et al. 2001; Falls and Kopachena 2020; Peck and James 1998b; Spencer et al. in Gauthier and Aubry 1996).

Spencer et al. (in Gauthier and Aubry 1996) concluded that the White-throated Sparrow probably expanded its range in southern Quebec in response to forest clearing by settlers. It has declined there since the beginning of the 20th century due to clear-cutting of woodlots for urban development or agriculture. In Ontario, it is uncertain if forest clearing had any positive effects. It has retracted from much of its range south of the Canadian Shield due to agricultural intensification and urbanization. Habitat loss and degradation is not significant for this species in the Shield and northward, although concerns have been raised about the effects of clear-cutting in some areas.

Most researchers concluded that the White-throated Sparrow benefits from clear-cutting and other forest management practices that open up the canopy. Falls and Kopachena (2020) concluded that it was little affected by logging or forest fragmentation. It tends to increase as the forest canopy opens and decrease as the canopy closes. Habitat may potentially be improved by forestry, insect outbreaks, and fire. It demonstrated a positive response to partial harvest of forests in the Boreal Forest Region of Ontario. It was expected to increase by 50% when 100% of the forest was retained, indicating that minor thinning would result in increases. It apparently responds to the short-term availability of suitable habitat within small gaps created by harvesting (Vanderwel et al. 2007). Rempel et al. (2007) predicted that its population would be maintained in Ontario for the next 100 years under natural conditions and forest management under guidelines such as silvicultural guidance for replanting, tending, and harvest objectives. It was expected to increase if timber management guidelines for marten, moose, caribou, and fish were applied. In Ontario in the Canadian Shield, there was no difference in its abundance in early and mid-successional clear-cuts compared with similarly aged stands after fire. Compared with mature stands, it was significantly more abundant in early successional stands and significantly less abundant in mid-successional stands (Zimmerling et al. 2017). At Sault Ste. Marie, it increased in selectively harvested blocks 1-2 years after harvesting; abundance in control forests did not change. In 1 cut, its abundance declined to levels in control forests by 5 years after cutting but it continued to increase 6-7 years after cutting on the other 2 plots. Based on the number of juveniles captured in mist nets, productivity increased on 2 of the 3 harvested areas. It was associated with small deciduous shrubs rather than sugar maple regeneration (Holmes and Pitt 2007). In Algonquin Park, it was significantly more abundant in stands that had been selectively harvested within 1-5 years than in stands harvested 15-20 years previously. Harvesting reduced canopy cover and allowed sunlight penetration to the forest floor, resulting in the establishment of a dense shrub layer of red raspberries and seedlings of sugar maple, beech, and striped maple (Jobes et al. 2004). In Algonquin Park, Tozer et al. (2010) studied the effects of typical and intensive group-selection harvesting that removed 5% and 20% of the tree cover respectively. It increased in both treatments 1 and 2 years after harvest but the positive response was short lived. In Alberta deciduous forests, it increased when 100%, 90%, 80%, and 25% of the forest was harvested but declined when 50% was removed; the increase was significant only when 90% of the forest was harvested. In deciduous forests with an understorey, mixed forests, and coniferous forests, it increased when 25-100% of the forest cover was removed; the only other significant increase was associated with a 90% cut in mixed forests (Harrison et al. 2005). In hardwoods in New York, it increased in abundance with increased intensity of logging, but there was little increase until 75-100% of the merchantable timber was removed (Webb et al. 1977). In Minnesota, it responded more favourably than any other species to harvesting in riparian buffers

(Hanowski et al. 2003, 2005). In Newfoundland, it was significantly more abundant in 30-m buffers to water bodies where the area beyond the buffer was clear-cut; it was only more abundant when birds within the clear-cut were counted (Whitaker and Montevecchi 1999). In New York, Keller et al. (2003) studied the response of the White-throated Sparrow to clear-cutting. The sparrow guild declined significantly as leaf area increased and the shrub-opening edges that they preferred disappeared with time. This guild represented 37% of the total avian population on 2-year-old cuts but only 9% on 6-year-old cuts. The White-throated Sparrow attained its maximum density 2 years after cutting. Its density on 6-year-old cuts was low and was only 13.5% of the density on 2-year-old cuts. In Alberta, Tittler et al. (2001) studied the effects of clear-cutting and of retaining 10%, 30%, and 40% of the tree cover. The White-throated Sparrow declined in the first year after cutting but the population rebounded by the third year to be as common as in uncut stands. It responded negatively to harvesting. The researchers considered it a generalist species that was unaffected by the amount of retained forest. In Maine spruce–balsam fir forests, it was absent in forests with a dense overstorey and an open forest floor, but occurred in clear-cuts from the time of cutting until trees reached a DBH of 10-15 cm and were taller than 4.5 m. Greatest abundance occurred 3-12 years after cutting when regenerating hardwoods were less than 2-4.5 m tall, with a residual raspberry layer and slow-growing softwood regeneration (Titterington et al. 1979). Two Newfoundland studies examined the effects of harvesting at the landscape level on productivity and survival of the White-throated Sparrow. Dalley et al. (2009) determined that nest survival and fledgling production was negatively affected by the amount of harvested area at the 20- and 115-m scales, but positively correlated with the proportion of harvested area at the 1,250-m scale. They found no compelling evidence for negative effects of harvesting but concluded that habitat fragmentation coupled with weather factors could cause dramatic differences in breeding success. Whitaker et al. (2008) found no difference in its survival rates in natural landscapes, where openings were mostly wetlands and water bodies, and landscapes where clear-cutting had occurred. It was resilient to a moderate amount of clear-cutting. In this study area, only about 5% of the landscape was clear-cut.

Two studies cautioned that clear-cutting may be detrimental to the White-throated Sparrow, and these are reinforced by the study by Tittler et al. (2001) in Alberta. In the same province, numbers were lower in clear-cuts than in forest edge and interior, and those nesting in clear-cuts had low productivity and site fidelity. This suggested that populations nesting in clear-cuts were not sustainable and had to be maintained by immigration. Harvesting could reduce habitat quality for decades. In landscapes heavily fragmented by forestry and other disturbances, the remaining habitat may reach a threshold where rates of recruitment, immigration, and site fidelity are reduced to a point that regional population declines occur (Hannah et al. 2008). In Quebec, Rousseau et al. (2012) experimentally clear-cut portions of breeding territories after the breeding season. Treatment males had an average of 69% of their territory clear-cut (range 9-100%). Males that experienced a clear-cut were less faithful to their territories and dispersed 2.6 times further than control birds. Although clear-cuts are a readily used habitat, they were not suitable for most individuals with previous experience breeding in mature forest stands.

Some studies examined the effects of creating gaps in forest habitat on the White-throated Sparrow. In Quebec, Rail et al. (1977) used playback to test the widths of forest gaps that it would

cross. They tested 19 different widths of gaps from 5-95 m at 5-m intervals. A 65-70 m threshold response was apparent, with it reluctant to cross wider gaps. The response was similar among gap types including power lines, roads, ski trails, and clear-cuts. The response at 65-70 m might be an expression of its territory size rather than a gap effect. In British Columbia, seismic lines 8-10 m wide provide edge habitat where it nests among piles of woody debris and in shrubby areas (Campbell et al. 2001). Bayne et al. (2016) determined that it was more abundant at seismic lines and pipelines than in forest interior adjacent to these features. There was no significant difference in its abundance at well pads and in adjacent forest interior.

DesGranges et al. (1987) studied the effects of sugar maple decline in Quebec on the White-throated Sparrow. As a result of tree die-back, the canopy became more open with more growth of shrubs and herbaceous species. It was 4 times as abundant in die-back-affected stands as in healthy stands, a significant difference.

Chemicals associated with forest management may have detrimental effects. Spraying of fenitrothian to control spruce budworms reduced adult populations through mortality and territory abandonment, disrupted normal incubation behaviour, and reduced fledgling success (Falls and Kopachena 2020; Forsyth and Martin 1993). In Nova Scotia, there was a 55% decline in numbers in the second year following treatment of clear-cuts with glyphosate; numbers recovered in the fourth year (Freedman and Johnson 1999). It was not affected by application of this herbicide in Maine. It was second in abundance in untreated clear-cuts, representing 26% of all birds. On treated clear-cuts, it was the most abundant species, comprising 35.7% of the entire bird population. In this area, it was not significantly related to any habitat parameters and did not decline when vegetation complexity decreased (Santillo et al. 1989).

On Anticosti Island, the White-throated Sparrow was unaffected by high deer densities and browsing (Cardinal et al. 2012).

In Alberta, the White-throated Sparrow was 2-4 times more abundant at quiet well edges than at noisy compressor station edges. Bayne et al. (2008) concluded that it was adversely affected by noise from energy sector facilities. Its abundance was not significantly related to noise in Edmonton. Noise in that study was related to urban activities such as traffic. Its focal song is at frequencies of 2.8-4.5 kHz and it is most likely to be affected by noise in this range (Proppe et al. 2013).

Price (2004) concluded that the White-throated Sparrow might no longer breed in southern Ontario if the average summer temperature increased by 2°C. In central Quebec and Labrador, it was associated with warmer summer temperatures and drier stands. At this more northern latitude, it might benefit from climate change (DesGranges and LeBlanc 2012).

Status

McIlwraith (1894) had breeding records for the White-throated Sparrow from the Cambridge and Milton areas but concluded that it did not commonly nest in this portion of the province. Curry (2006) stated that there had been little change in its status in the Hamilton area since that time and that it was absent as a breeder south of Hamilton. Baillie and Harrington (1937) considered it one of the most common and characteristic summer residents, breeding throughout the province but more rarely along the southern boundary. The first atlas confirmed that it bred throughout the Great

Lakes–St. Lawrence Forest Region, except in the urbanized area of Toronto, northward to the Hudson Bay coast. It was uncommon and sparsely distributed in the Carolinian Forest Region and in intensively farmed areas in Huron and southern Bruce counties. In the extreme south, it was confined to isolated coniferous swamps or plantations. Highest populations occurred in the northern part of the province (Falls in Cadman et al. 1987). James (1991) considered it an abundant summer resident throughout most of the province, but rare in the agricultural south and almost completely absent in the Carolinian Forest Region. In the Hudson Bay Lowland, Wilson and McRae (1993) observed that its abundance changed substantially away from the Hudson Bay coast, with the transition area near Ekwan. It was uncommon near the coast and common to abundant further south.

The second atlas demonstrated that there had been no change in the range of the White-throated Sparrow since the first atlas. There was no significant change in its probability of observation province-wide or in any region except the Great Lakes–St. Lawrence Forest Region south of the Shield. It declined significantly there, but the reasons for this were uncertain. Declines may have been related to loss of early successional habitat due to agricultural intensification, urbanization, and natural succession. It was most abundant in the Boreal Forest Region between latitudes 47°N and 51°N. This is where intensive commercial logging occurs. It was considerably more abundant in the Shield and the Hudson Bay Lowland than south of the Shield (McLaren in Cadman et al. 2007).

Breeding Bird Survey data indicate that the White-throated Sparrow decreased at an annual rate of 0.451% in Canada and 1.32% in Ontario 1970-2021. For 2011-21, it experienced annual decreases of 3.09% in Canada and 3.7% in Ontario. All results were of medium reliability (A.C. Smith et al. 2023). Tozer (2012) reported that numbers had declined in Algonquin Park over the past 40 years due to forest succession and the absence of any major spruce budworm outbreaks.

POSTFLEDGING PERIOD

Fledglings cannot fly until 2-3 days after they leave the nest but are strong fliers a week after leaving the nest. As soon as they leave the nest, fledglings move into dense cover. One remained in the lower boughs of a large white spruce 10 m from the nest for 3 days. Young are fed by the adults for at least 2 weeks after they fledge (Falls and Kopachena 2020; Kopachena and Falls 1993b; Lowther and Falls in Austin 1968).

In Algonquin Park, Kopachena and Falls (1991) examined whether brood division occurred. They placed individual fledglings in enclosures that were open at the top so adults could access the young. Brood division occurred, but was characterized by overlapping patterns of parental feeding rather than each parent feeding certain young exclusively. In only 1 of 16 pairs (6.3%) did both parents fail to show preferences for individuals within the brood. In the remaining 15 pairs, there were 2 cases (13.3%) in which 1 parent failed to exhibit preference for individual fledglings. Ten of 27 adults (37.0%) cared for fledglings that were fed only by that parent. In these broods, the remaining offspring was fed by both adults. Of 13 broods in which adults showed preferences for individuals, 84.6% of the fledglings that received the most male feeding trips received the fewest female trips; 76.9% of the fledglings that received the most female feeding trips received the fewest male trips. When fledglings were moved by the researchers, 50% of adults were able to recognize

individual brood members and altered their provisioning behaviour appropriately. Twenty-five percent failed to respond and had therefore keyed in on the location to identify young. The remaining 25% altered their behaviour but failed to match their previous preference for individuals. Most adults started to show preferences for individual fledglings within a few hours of their leaving the nest, but some adults did not establish a pattern until a day after young had fledged.

In Quebec clear-cuts, the White-throated Sparrow was the most abundant species caught by Major and Desrochers (2012). It was more abundant where the researchers had not removed elderberry fruits and results were almost significant. Frugivory contributed to its abundance. It was not entirely dependent upon frugivory because it also occurred in experimental plots where there was no fruit. It was found throughout clear-cuts and did not restrict its movements to edges. In Minnesota, Streby et al. (2011b) captured 81 adults and 87 juveniles in regenerating clear-cuts over 4 years during the postfledging period. During 1 breeding season, they caught 9 adults. The youngest clear-cuts were dominated by red raspberry and aspen saplings 1-2 m tall; older cuts were dominated by aspens 4-6 m tall interspersed with red maple, hazel, and pussy willow. In addition to clear-cuts, many other habitats with dense shrub growth or short deciduous saplings may provide suitable habitat for the White-throated Sparrow during the postfledging period.

In Michigan, Piper (1995) investigated the onset of social dominance in juveniles. Nestling mass was unrelated to their final dominance status and the number of dominance interactions in flocks of brood-mates was not related to dominance status. Social conditions appeared to strongly influence dominance. Birds artificially placed in a flock of 6 for 17 weeks were all of low social dominance, those placed in isolation achieved the top rank, and wild-caught birds were intermediate in dominance. Social conditions experienced by juveniles before they leave the breeding grounds and during autumn migration might have a lasting effect on their dominance status and therefore their winter survival.

MIGRATION

The entire population of White-throated Sparrows migrates. Breeding and wintering ranges overlap in some areas, but different birds are present in different seasons. Although the breeding range extends from British Columbia to Newfoundland, migrants converge to winter in the southeastern United States. Spring migrants arrive when snow melt exposes portions of the forest floor. Timing of arrival in Manitoba was strongly correlated with the mean April temperature. Spring activity increases with high or increasing temperatures, falling barometric pressure, and southern winds. In autumn, birds show random patterns with respect to weather. Latest autumn departures occur prior to the first permanent snowfall. This suggests that it is a weather-dependent migrant, relying on changes in temperature and food supplies to initiate migration instead of endogeneous rhythms and photoperiod cues. Autumn migration is more leisurely than spring migration, with spring migration about a week shorter than autumn migration in Michigan. During both periods, the peak of migration averaged 33 days, but numbers dropped off more quickly after the peak in spring than in autumn. In autumn, there is differential migration with females wintering further south than males, and larger males wintering further north than smaller males. Birds with larger bodies are more likely to survive cold weather and dominant birds force subdominant birds to migrate further from the breeding grounds. There is no evidence that wintering latitudes differ between the 2 colour

morphs (Falls and Kopachena 2020; Fischer and Gill 1946; Jenkins and Cristol 2000; Mazerolle and Hobson 2007; Stack and Harned 1944).

White-throated Sparrows breeding in southern Ontario wintered from Texas east to Georgia and South Carolina. Northern Ontario birds appeared to travel almost directly north-south. Some birds banded in southern Ontario moved strongly in a northeast-southwest direction and probably bred in Quebec. Some birds that breed in Quebec winter in southern Ontario. One bird banded at Mitchell's Bay was recovered in New York the next day, having travelled 673 km overnight (Brewer et al. 2018). Gesicki et al. (2016) concluded that the central basin of Lake Erie was a partial barrier to spring migrants. In the western basin of the lake, more were recorded at West Sister Island than on the Ohio mainland suggesting that it was attracted to the islands when crossing the lake. In the central basin, fewest birds were detected offshore at Cleveland. A higher proportion migrates through the western basin and those in the central basin are less likely to cross the lake.

The White-throated Sparrow migrates at night in loose flocks and forages in flocks during daily stopovers (Falls and Kopachena 2020). Gaymer (1962) observed the initiation of migratory flights in Toronto. In the first half of October, birds moved progressively higher from the ground after sunset, gathering at the top of 25-m tall trees. When it was almost dark, individuals flew straight upwards from an exposed branch to a height of 10-20 m above the trees, circled 2 or 3 times then flew off in a southerly direction. In spring, the northward flight began with many individuals leaving simultaneously and continued with a steady stream of sparrows rather than the entire flock leaving at once. In spring, birds left in a normal flight pattern without the perpendicular upward flight.

In Manitoba, males arrived in spring 4.8 days before females and white-morph birds arrived 4.8 days before tan-morph birds. In New Hampshire, females arrive approximately 2 weeks later than males. At Long Point, the midpoint of migration was 2 May 1977-2000, with males arriving significantly earlier (10.4 days) than females. Males arrived earlier than females north of Lake Nipigon and in Algonquin Park. Most females arrive there between the first and third weeks of May, 1-2 weeks after the first males arrive. White-morph males tended to arrive earlier than tan-morph males in Algonquin Park, but not significantly. White-morph females arrived significantly earlier than tan-morph females but it is possible that the more cryptic tan-morph females were overlooked. At Long Point, white-morph birds arrived significantly earlier (2-15 days) than tan-morph birds when all birds were considered. When sex was taken into account, white-morph females arrived significantly earlier (1.3 days) than tan-morph females, but there was no significant difference in the migration timing of male morphs. Tan-morph females took 7% longer than white-morph females to complete their migration. Tan-morph males took 2.6% longer than white-morph males. Older birds of both sexes arrive in spring earlier than yearlings. At Long Point in autumn, adults of both sexes and juveniles migrate at the same time, but juveniles arrive later in North Carolina (Caldwell and Mills 2006; Falls and Kopachena 2020; Kendeigh 1947; Knapton et al. 1984; Mazerolle and Hobson 2007; Mills 2005b; Wasserman 1980). In Michigan, the average stopover period was 4.5 days in spring and 10.67 days in autumn (Stack and Harned 1944). In Ohio, there was no significant difference in the duration of spring and autumn stopovers by adults and juveniles. In spring, the average stopover period was 5.3 days (5.4 days for adults and 5.1 days for juveniles). Autumn stopovers were significantly longer than in spring, averaging 8.7 days, with means of 8.5 days for adults and 9.1 days

for juveniles (Borror 1948). During spring migration south of Lake Erie in Ohio, birds in good condition began their flight across the lake directly from inland areas. Those in poorer condition staged south of the lake before crossing. There was no difference in body condition between the morphs (Hoh et al. 2018). On islands in the Gulf of Maine, autumn stopover times were 5.6 days on a shrubby island and 3.7 days on a treed island (Suomala et al. 2012). Autumn stopovers could range from 1 day to more than a week (Fischer and Gill 1946).

In southern and central Ontario, migrants move through from mid-April to mid-May, with most passing through by the third week of May (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). In Thunder Bay, average arrival during 1938-52 was 27 April with extreme dates of 17 April and 6 May. Most White-throated Sparrows leave the Thunder Bay area by early October (Allin 1952). Autumn migration begins in earnest in September in the southern Shield, peaking at the end of the month. Most leave by mid-October, but some remain into late November or December (Mills 1981; Tozer 2012). In southern Ontario, it arrives in mid- to late September, with peak numbers from late September until the second to fourth weeks of October (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

Mills (2005a) analyzed banding data for the White-throated Sparrow from Long Point Bird Observatory for 1975-2000. There was no significant change in the date of first arrivals or in spring quartiles and no significant difference for either sex in spring over time. There were no significant differences in the timing of autumn migration. The midpoint of autumn migration was 20 September.

During migration, the White-throated Sparrow seldom occurs far from dense shrub or herbaceous cover. In the Kingston area, it was most abundant in poorly drained areas dominated by dense willows, dogwoods, and buttonbush 1.5 m tall. Similar shrubby habitat is used in other areas but species composition may vary. It also occurs in towns and urban areas where only patches of cover are available (Falls and Kopachena 2020). Most birds seen in November in Algonquin Park are at feeders (Tozer 2012). In southern Ontario, flocks are common in shrubby hedgerows, roadsides, and edges of forests (personal observation). In British Columbia, it is most common during migration in deciduous forests with a dense shrub understorey, but it also occurs in mixed forests and young successional forests such as burns and clear-cuts. It particularly favours forest edges and natural forest openings, as well as shrubby perimeters of lakes, beaver ponds, wetlands, muskegs, and watercourses. In all cases, it exhibits a strong affinity for low dense shrubby vegetation (Campbell et al. 2001). In Kansas, migrants occurred mostly in woodland edge thickets; in spring, this habitat type was used around a pond. Autumn migrants congregated in flocks in woodland edge thickets, brush piles, and weedy margins of a pond (Fitch 1958). During spring migration in Pennsylvania, it was significantly more abundant in shrubs than forest. Detections per 100 m of transect were 0.03 in forest and 0.16 in shrubs; captures per 1,000 mist-net hours were 0.6 in forest and 13.8 in shrubs (Smith and Hatch 2008). During spring migration in Wisconsin and Minnesota, it was equally abundant in upland and floodplain deciduous forests (Kirsch et al. 2013). During autumn migration in New York, it used mature shrublands more than early successional forests (Mudrzynski and Norment 2013).

In both spring and autumn in Pennsylvania, the White-throated Sparrow was significantly more abundant in fragmented than forested landscapes. Fragmented landscapes were 15% forested; forested landscapes supported 40% forest cover. Its abundance was correlated with patch size (Keller and Yahner 2007).

In Ohio, most migrants had home ranges of less than 3.2-4.0 ha, but confined most of their activities to 0.4-0.8 ha. Some moved as far as 400 m during their stopover (Borror 1948).

In many areas, spring migrants may arrive while birds that have overwintered are still present. Winter birds were significantly more dominant than expected based on interactions and the proportion of winter residents and spring migrants that were present. Migrants were significantly less dominant than expected. White-morph birds chased other birds 2 times more than they were chased and tan-morph birds chased half as frequently as they were chased; these differences were significant (Hailman 1975; Harrington 1973).

Based on banding data, Fischer and Gill (1946) concluded that the White-throated Sparrow seldom used the same stopover sites on subsequent migration flights.

In early spring, the White-throated Sparrow moves to the tops of the tallest deciduous trees where it feeds on buds and blossoms of white and red elms, silver and red maples, oaks, beech, and apples (Fitch 1958; Judd 1901; Lowther and Falls in Austin 1968). In downtown Toronto, Lang (1994) observed one feeding on the carcass of another White-throated Sparrow. Food resources may have been depleted forcing it to search for alternative food sources. In Alabama, it eats mulberries during spring migration (Holt 1918). On the Ohio Lake Erie shoreline, MacDade et al. (2011) used stable isotopes to analyze breath samples of White-throated Sparrows to determine their diet. There was a large emergence of midges during the peak of migration. Associations between midge biomass and refuelling performance were not strong. They had breath values consistent with consumption of both aquatic and terrestrial arthropods. There was no significant difference in dietary composition between shoreline and inland sites, possibly due to little difference in midge biomass. Even small shoreline sites of 1.18-2.86 ha often supported high densities of migrants that received energetic benefits from their use. The autumn diet is comprised mostly of grass and weed seeds and fruit. In New York, 19.0% of fecal matter contained evidence of fruit consumption. It ate fruits of Bella honeysuckle and buckthorn but not those of gray or red-osier dogwoods. In Rhode Island, the autumn diet was dominated by fruit which comprised 60% of food items (Fitch 1958; Langlois and McWilliams 2010; Mudrzynski and Norment 2013). In Oxford County, Dance et al. (2012) observed it feeding on giant ragweed seeds.

The White-throated Sparrow commonly collides with buildings and other tall structures during migration. In Toronto, it is among the top 3 of 164 species found killed by striking windows and buildings, and it has a similar rank in other cities (Falls and Kopachena 2020). Weir (2008) reported that 42 were killed at the Lennox generating station chimneys 1972-79.

James (1991) considered the White-throated Sparrow an abundant migrant in Ontario. At Long Point, it is the number 1 banded species, with over 66,000 banded 1960-2010 (Anonymous 2010a). Fischer and Gill (1946) reported that it was the second most abundant species banded in the Atlantic Coast and Mississippi flyways to the Dark-eyed Junco. High spring daily counts in southern Ontario

range from 250 to 2,000. In autumn, flocks may number 1,000-5,000. During a grounding, 10,000 were seen at Prince Edward Point on 2 May (Curry 2006; LaForest 1993; Mills 1981; Weir 2008).

The number of White-throated Sparrows banded at Long Point Bird Observatory declined significantly at a rate of 2.6% per year 1961-83. Trends by period were: –4.0% 1961-70, –2.7% 1970-79, and –2.7% 1979-88 (Hussell et al. 1992). Falls and Kopachena (2020) reported that numbers banded at Long Point 1963-2005 were stable in spring and increased significantly in autumn; since 1987 in autumn and 1991 in spring, the trend was positive.

WINTER

Root (1988) stated that the entire winter distribution of the White-throated Sparrow was limited to areas that receive 102 cm or more of precipitation annually. The western edge of its range stops abruptly where the annual precipitation rate drops below 81 cm. It most often frequents areas with an average minimum January temperature above –1°C. Individual abundance peaks are strongly associated with open water. It avoids snow cover; the longer the snow season length, the less likely it is to be present (Keyser et al. 2023). The bulk of eastern populations winter in North and South Carolina, with its abundance progressively decreasing north and south of these states (Fischer and Gill 1946).

In Pennsylvania, the White-throated Sparrow was equally abundant in winter in landscapes with 15% and 40% forest cover (Keller and Yahner 2007). It inhabits dense shrubby areas similar to what it uses during migration. Birds rarely venture out into the open. Within dense habitats, it seeks areas with minimal snow cover to facilitate its ground foraging. Where snow is deep, it is highly reliant on feeders for winter survival. Winter habitats include edges of woodlots, hedgerows, sheltered ravines with shrubby cover, and dense vegetation adjacent to watercourses, swamps, and cattail marshes. Within thickets, it frequents small openings where leaf litter covers the ground. In Ontario, it winters singly or in small flocks, often with Song Sparrows and other sparrows (Curry 2006; Falls and Kopachena 2020; Fitch 1958; LaForest 1993; Lancaster et al. 2004; Lowther and Falls in Austin 1968; Root 1988; Tozer 2012; Weir 2008). In British Columbia, wintering White-throated Sparrows were found mostly at feeders but also in other anthropogenic habitats such as shrubby edges of fields, utility corridors, foot paths, roads, city parking lots, and in low dense vegetation in city parks and golf courses. It also occurs in shrub thickets along lakeshores and creeks and edges of weedy fields and pastures (Campbell et al. 2001). In Maryland, Blank et al. (2011) investigated the effects of autumn mowing of vegetated buffers between row-crop fields and forested wetlands on wintering White-throated Sparrows. Some buffers were mowed to a height of 10-15 cm; others were not mowed. It was the sixth most abundant species and was significantly more abundant in unmowed than mowed buffers. Densities per km^2 were 16 in mowed and 159 in unmowed buffers. Vertical vegetation density and height and percent coverage by grasses and forbs were significantly greater in unmowed buffers. In Arkansas, Kentucky, and Mississippi, Evans et al. (2015) compared its abundance in fields with and without vegetated buffers. Fields were planted with row crops and buffers were planted to a mix of native grasses and forbs. The White-throated Sparrow was equally abundant in fields with and without buffers and in buffers less than and greater than 23 m in width.

In Arkansas, all roosting habitats were composed of dense stems, vines, or branches and 82% of roosts were 1-5 m from the ground. The species with the most roosts were blackberry and

greenbrier thickets (33% of roosts), autumn olive (28%), red cedar (20%), and privet and Japanese honeysuckle (12%). White-throated Sparrows exhibited strong roosting site fidelity. Habitat at foraging and roosting sites, respectively, was 3.99 cm and 2.74 cm leaf litter depth, 26.21% and 64.4% understorey vegetation density, and 17.74 hits and 17.18 hits horizontal vegetation density. Nocturnal roosting areas and diurnal foraging areas were spatially disjunct and varied significantly in vegetation habitat metrics. Foraging locations had greater leaf litter depth and were concentrated near the forest edge of a hydro right-of-way. Roosts were more dispersed and associated with increased understorey vegetation density (Gonzáles et al. 2023). In Arkansas, a male used the same roosting area in 2 consecutive winters. Its core roost home range in the second year overlapped 100% with its previous year's core roost home range. It roosted in the exact same roost site as it did in the previous year, spending 37 nights in a Japanese honeysuckle shrub (Gonzáles and Ruhl 2025).

In winter, the White-throated Sparrow establishes a small foraging range and may return to it in subsequent years. Home ranges often overlap broadly and individuals frequently join loose flocks when foraging. In Kansas, 1 wintering bird remained within an area of 0.98 ha. Winter home ranges of 0.1-0.4 ha have been reported elsewhere (Dunn and Tessaglia-Hymes 1999; Falls and Kopachena 2020; Fitch 1958).

The dominance hierarchy is established in winter. Dominant birds sing more frequently, feed closer to protective cover, get to access food first regardless of who found it, spend more time foraging, experience fewer interruptions while foraging, accumulate greater stores of subcutaneous fat, and use smaller home ranges than subordinate birds. Dominant birds tend to remain within their home ranges when food levels decline in midwinter; 45-50% of dominant birds return to the same wintering area compared with 30-39% of subordinate birds (Dunn and Tessaglia-Hymes 1999; Falls and Kopachena 2020; Wiley 1991). In New York, Schwabl et al. (1988) concluded that sex and age were important in predicting dominance, but morph colour was not. Adult males held the 2 highest ranks significantly more often than females. Rank was correlated with age in males but not in females. Adult males, but not yearling males, were dominant in more relationships with members of other age or sex classes than expected. All females won fewer contests than expected. Dominance by the 2 morphs varied with season, with white-morph birds dominating in spring and tan-morph birds dominating in autumn. In winter, males were observed in aggressive encounters more frequently than expected and females were in aggressive encounters less frequently than expected (Watt et al. 1984). Ficken et al. (1978) determined that white-morph birds were more frequently the aggressor in interactions during spring migration.

When foraging, the White-throated Sparrow stays within or near cover even if food is more abundant in the open (Dunn and Tessaglia-Hymes 1999; Pearson 1991). As food near cover becomes depleted, birds move increasingly further from cover, but staying within or near cover takes precedence over high food density distant from cover (Schneider 1984). In North Carolina, the main habitats used for foraging were areas of crabgrass, horseweed, asters, mixed tall weeds, and shrubs, with greatest numbers in asters and mixed tall weeds. Fifty-nine percent of foraging occurred while perched on a plant, 41% while standing on the ground but feeding on a standing plant, and 0% on bare ground. Its abundance was not related to food abundance. It ate mostly seeds 0.5-2.5 mm in length but some as large as 6.5 mm. All foods smaller than 3.5 mm were hard seeds (grains, achenes,

and nutlets) and larger ones were soft fruits. Approximately 90% of the diet between October and March consisted of vegetable matter; 13% of the diet consisted of fruit. In Algonquin Park, all birds that survived winter had food provided to them. One subsisted on food pellets given to captive moose (Tozer 2012). In Maryland, Petrides (1942) observed it eating holly berries. Falls and Kopachena (2020) reported that the winter diet included seeds of grasses (including wiregrass), ragweeds, and smartweeds, plus fruits of sumac, grape, highbush cranberry, mountain-ash, and rose hips.

The White-throated Sparrow is one of the more widespread species at winter feeders. Unlike most ground-feeding birds, it is willing to visit raised-platform feeders. Its favourite feeder foods are mixed seeds and millet. It infrequently eats all types of sunflowers, safflower, whole or cracked corn, milo, hulled peanuts or hearts, peanut butter mixes, baked goods, water, and canary seed (Dunn and Tessaglia-Hymes 1999).

During a prolonged period of heavy snow and extremely cold weather in Illinois, Graber and Graber (1979) observed a 99.7% decline in the number of White-throated Sparrows. Densities per km^2 were 249 before the storm and 0.75 after the storm. They found some carcasses and concluded that the decline was due to very high mortality. Falls and Kopachena (2020) reported that populations may decrease after cold weather. Even under normal conditions, birds wintering in Ontario may not survive if they do not have access to a feeder. One that was at a Huntsville feeder until February did not survive until spring (Mills 1981). At Presqu'ile, it was very difficult to find in late February and early March, suggesting that few overwintered successfully (LaForest 1993).

James (1991) considered the White-throated Sparrow a rare but regular winter resident in the south, and occasional and rare in the north to Atikokan, Thunder Bay, and Moosonee. In the Hamilton area, Curry (2006) reported small winter flocks of as many as 10 birds, with 15 birds the most observed. He concluded that more overwintered now than previously.

Freedman and Riley (1980) summarized the results of Christmas Bird Counts (CBC) for southern Ontario for 1929-77. It was recorded in low numbers, but there was a trend to irregular but increasing abundance since approximately 1958. CBC results for 1965-2005 indicated a nonsignificant decrease rangewide of 0.25% per year (Falls and Kopachena 2020). Lepage and Francis (2002) examined CBC and Project FeederWatch data for Ontario. It had low but significant annual variations in population numbers and apparent small peaks every 3-4 years. CBC results for Ontario indicate that it increased at annual rates of 2.15% 1970-2021 and 4.6% 2009-21 (National Audubon Society 2022).

Vesper Sparrow

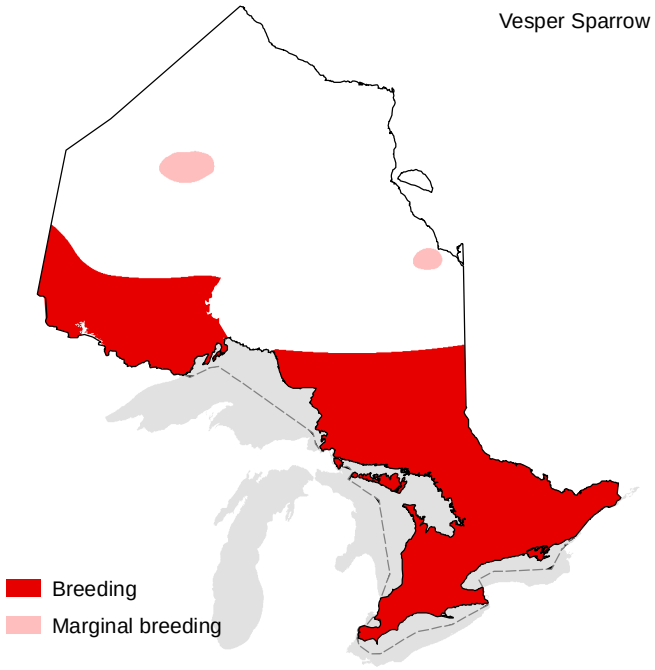
Pooecetes gramineus

BREEDING SEASON

Habitat Requirements

Ontario Vesper Sparrow nests were in grassy fields and pastures that were usually open (62.6% of nests) but 9 (5.7%) were in overgrown fields and pastures; in cultivated grain, vegetable, and berry fields (17.3%); in young open conifer plantations (8.3%); along road and railway rights-of-way (7.1%); in gravel pits (2.0%); in very open woodlands and recent burns (2.0%); in orchards (0.4%); and on golf courses (0.4%). One nest was on soil dug from a pond. Most were in dry locations but 3 were in marshy areas and 5 were in wet areas. Breeding habitats were mostly flat with sparse ground cover; short grass was preferred to long grass for nesting (Peck and James 1987).

The Vesper Sparrow previously nested in the Hudson Bay Lowland area near Moosonee (Manning 1952; Wilson and McRae 1993), but no habitat description was provided. In the Boreal Forest Region, it is restricted mostly to large burns and clear-cuts. It may also occur near settlements and other anthropogenic openings in forests (Rising in Cadman et al. 2007). Near the northeastern



shore of Lake Superior, it was common in large areas of dry open country (Baillie and Hope 1943). Smith (1957) reported that it occurred in agricultural fields in the Clay Belt.

Near Gogama in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, the Vesper Sparrow bred where there was a ground cover of grasses or sedges among well-spaced regenerating jack pines. There were few or no tall pines that shaded the ground in inhabited areas. Once pine trees reached 10 years of age, the habitat was no longer suitable (James and Peck 1995a). In the Sudbury area, it was well distributed along the railway right-of-way and in clearings (Baillie and Hope 1947). In Muskoka and Parry Sound districts, it breeds mostly in open scrubby areas and dry pastures (Mills 1981). In Algonquin Park, it was restricted to open areas around old camps and settlements; there were a few birds in barren burns (MacLulich 1938). Tozer (2012) reported that the only recent record in the park was in a burn.

In the Carolinian Forest Region, Sheppard et al. (1936) considered the Vesper Sparrow a very common bird of roadsides and pastures. It now appears to prefer recently fallow fields with hedgerows containing small trees (Black and Roy 2010).

In southern Ontario agricultural fields, the Vesper Sparrow was positively correlated with spring grain, hedgerows, hay, fences, and row crops, but the relationship was significant only for hedgerows. It was significantly negatively correlated with pasture, wooded areas, and road, railway, and hydro corridors. There was no significant difference in its abundance on conventional and organic farms, even though conventional farms had larger fields (Kirk et al. 2011). Dechant et al. (2002a) reported that it was more common on organic than conventional farms and minimal tillage farms, possibly because of greater retained crop residue for nesting.

Throughout its range, the Vesper Sparrow is an open-country bird. It prefers dry areas with sparse, short patchy vegetation, low to moderate shrub coverage, and areas of bare soil. In Ontario, it is 1 of only 3 species that regularly nests in corn and soybean fields along with the Killdeer and Horned Lark. Agricultural fields are widely used for nesting in the Midwestern United States but are rarely used in the Prairie Provinces. Habitats it has nested in include roadsides, grassy fields, abandoned fields, short-grass and mixed-grass prairie, sagebrush and shrubsteppe habitats, hayfields, shrubby grasslands, woodland edges, woodlands with sparse canopy cover and understorey, orchards, shelterbelts, jack pine barrens, fencerows, recent burns and clear-cuts, grazed and ungrazed pastures, grassed waterways in agricultural fields, young Christmas tree farms and coniferous plantations, oak savannahs, shorelines with beach grass, blueberry fields, montane

meadows, airports, and reclaimed strip mines. It often occurs at ecotones between forested or shrubby habitat and open areas such as grasslands and agricultural crops (Askins et al. 2007; Berger in Austin 1968; Beauchesne et al. 2007; Best and Rodenhouse 1984; Camp and Best 1994; Campbell et al. 2001; Dechant et al. 2002a; Faanes and Andrew 1983; Graber and Graber 1963; Graham and Cotter in Gauthier and Aubry 1996; Jones and Cornely 2020; Judd 1901; Leighton et al. 2002; Mossman et al. 1991; Mousley 1916a; Rodenhouse and Best 1983; Rotenberry and Wiens 1980; Swanson 1996; Vickery et al. 1994; Wiens 1969; Wray et al. 1982).

Presence of suitable perches is a critical habitat component and their absence can be a significant limiting factor. In agricultural areas, territories usually extend along the length of a hedgerow or fence. In Iowa, areas in croplands further than 80-110 m from a hedgerow were not used by the Vesper Sparrow. In grasslands, it uses shrubs most frequently as perches. Grasslands without shrubs may be unoccupied. In addition to shrubs, woodland edges and herbaceous vegetation taller than the dominant cover type may be used as perches. In Iowa, birds with territories along hedgerows in cropland used elevated perches heavily. During the preincubation period, males sang primarily from hedgerows, with fence wires, fence posts, or shrubs used most frequently. During incubation, 72% of singing occurred in the field. Song perches used at this time consisted mainly of clods of soil and tall crop residue. Later in the season, 71% of singing occurred in the crops. In soybean fields, males sang from tall weeds and in cornfields they sang from the rows of corn closest to the fencerow; the corn was taller than fence posts and many shrubs. Only 1 of 51 Iowa territories (2.0%) did not include a fencerow. Only fencerows that were entirely herbaceous were unoccupied. In 1 year, the only unpaired male was along a herbaceous-shrubby fencerow and in another year all 4 unpaired males had territories on herbaceous fencerows. Densities along shrubby fencerows were 20% higher than those along herbaceous-shrubby fencerows. The Vesper Sparrow used artificial perches 1.5-2.0 m tall in Michigan, exhibiting no preference for height. The structural diversity of vegetation is important: taller vegetation, such as scattered shrubs or trees, is used for cover and singing perches and areas with shorter sparse vegetation are used for foraging and nesting. Vegetation structure probably is more important than plant species in habitat selection (Beauchesne et al. 2007; Best and Rodenhouse 1984; Dechant et al. 2002a; Harrison 1977; Jones and Cornely 2020; Perritt and Best 1989; Rodenhouse and Best 1983).

At the landscape level, abundance of the Vesper Sparrow is correlated with agricultural land. In Quebec, its distribution corresponded with that of cropland (Graham and Cotter in Gauthier and Aubry 1996). Although it occurs in forested landscapes in Ontario, highest densities occur in agricultural landscapes (Rising in Cadman et al. 2007). In seeded, highly erodible land, its frequency of occurrence was higher in sites surrounded by grassland than sites surrounded by cropland, wetland, woodland, or human settlement (Dechant et al. 2002a). In extensive mixed-grass prairie in North Dakota, it was positively correlated with the amount of aspen woodland within 500 m. It increased as the amount of aspen increased at the landscape level but was unaffected by the amount of aspen at the territory level (Grant et al. 2004). Berger (in Austin 1968) concluded that it appeared to avoid heavy clays and concentrated in areas of lighter soils that contained considerable sand and gravel. This does not appear to be true in Ontario because the heavy clay soils of Essex Counties support high densities of the Vesper Sparrow (Rising in Cadman et al. 2007). In Alberta, its presence was negatively correlated with the number of wetlands within 2.8 km^2 around point

counts (Dechant et al. 2002a). In Colorado, it was more frequent in mixed-grass prairies distant from urban edges (Jones and Bock 2002). In North Dakota, it responded positively to increasing tree cover within a 100-m radius in 400-m landscapes with less than 30% forest cover, but negatively in wooded landscapes. In open habitat, its probability of occurrence was 5% at 0% tree cover, 15% at 20% tree cover, and 20% at 40-70% tree cover. In wooded landscapes, its probability of occurrence was 25% at 0% tree cover, 18% at 40% tree cover, and 10% at 60-80% tree cover. It preferred landscapes with 20-52% tree cover (Cunningham and Johnson 2016, 2019). In the Prairie Pothole Region of Canada, it was positively associated with the amount of cropland within 400 m and the amount of grasslands within 3,200 m. It was negatively associated with the amount of tree and shrub cover within 800 m (Fedy et al. 2018).

The Vesper Sparrow prefers some shrub coverage, short sparse vegetation to tall dense vegetation, and areas that have some bare soil. In Alberta, its presence was positively correlated with woody vegetation around pond margins (Dechant et al. 2002a). In Washington State, it used sites with an average of 32% bare ground with the remaining area covered by grasses and forbs. Beauchesne et al. (2007) concluded that it required some shrub coverage in open habitat. In Washington State, it was most abundant in shrubsteppe habitat followed by Conservation Reserve Program (CRP) fields. It preferred sites with more than 5% shrub cover. Cover of perennial grasses at the site level was positively associated with daily nest survival (Vander Haegen et al. 2015). In South Dakota and Wyoming, it was one of the most abundant species in grass-sagebrush habitat on mines reclaimed 3-10 years previously. Lower densities occurred where sagebrush was absent. In Iowa cropland, pairing success was significantly related to the number of shrub groups and amount of crop residue in territories and almost significantly related to coverage by non-productive areas other than fencerows, such as washes and uncultivated field corners (Best and Rodenhouse 1984). In North Dakota, shrubby plots that were 30-80% covered with shrubs (wolfberry and silverberry) supported 3.5 pairs per km^2 (range 0-17.5). It was absent on plots with less than 10% shrub coverage (Arnold and Higgins 1986). In North Dakota, there was more cover by aspens within 500 m, more shrubs taller than 1 m, and less litter cover where it was present than where it was absent. Invasion by woody vegetation was beneficial (Grant et al. 2004). In Wisconsin, it declined significantly when shrub coverage decreased from 19-24% to 4-12%. Fairly tall woody vegetation was required for singing and perching (Swanson 1996). In Wyoming, Montana, and South Dakota, it was more abundant where black-tailed prairie dogs were absent. Areas without prairie dogs had less shrub cover but more bare ground, less visual obstruction, and low grass cover, conditions favourable for the Vesper Sparrow. Vegetation height and density and availability of bare ground may be more important than shrub density, provided that at least some shrubs are present to provide singing perches (Augustine and Baker 2013). In North Dakota, its probability of occurrence was 70% where there were no woodlands within 500 m and 90% where the area within 500 m consisted of 70% woodland. Probability of occurrence was 50% with no tall shrubs within 100 m and 85% with 35% shrub coverage. Probability of occurrence was 55% with no brush coverage within 100 m and 65% with 50% brush coverage (Grant et al. 2006). In Montana, the Vesper Sparrow occurred where the vegetation was short and dense with a high percentage of ground cover. It was absent where the vegetation was tall and patchy. High amounts of ground cover may be needed for nest concealment and it may be easier for birds to forage in short vegetation (Reed 1986). In Maine, its abundance was

significantly correlated with habitat patchiness and the amount of bare ground (Vickery et al. 1994). In Saskatchewan, its density increased with greater amounts of bare ground (Ludlow et al. 2015). In Wisconsin, it preferred the most xeric, sparsely vegetated sites; its habitat was characterized by the sparseness of vegetation. Unoccupied areas had similar grass and forb coverage but forbs averaged significantly taller in unoccupied areas. Vertical vegetation density and mean effective height were significantly greater in unoccupied sites and light penetration was somewhat reduced. Coverage of low vegetation was greater in unoccupied areas. Litter cover and composition were similar in occupied and unoccupied areas, but litter was significantly deeper in unoccupied areas (Wiens 1969). Rotenberry and Wiens (1980) reported that it reached its maximum density in montane meadows where it was highly correlated with forb cover. These meadows were thickly carpeted with wildflowers early in the season. In Wisconsin, mean vegetation characteristics included 4% woody cover, 68% herbaceous cover, 17% litter cover, 13% bare ground, 62 cm maximum vegetation height, and 21 cm vegetation height density. A significant increase occurred as grass cover increased from 1-4% to 10-57%; densities were positively correlated with percent forb coverage (Swanson 1996).

Comparisons have been made between Vesper Sparrow usage of native grasslands and prairies with planted nonnative, or tame, grasses. In Manitoba, its abundance was negatively correlated with native grasses and positively correlated with nonnative grasses (Wilson and Belcher 1989). In Colorado, it was significantly more abundant in upland mixed-grass prairie than in lowland tallgrass prairie or tame hayfields. In Manitoba, it was negatively correlated with native vegetation and positively correlated with tame vegetation. In Wisconsin, its density was higher in barrens and dry prairies than in old fields, tame grasslands, small-grain fields, cornfields, mesic prairies, planted warm-season grasses, and hayfields. Density was positively correlated with percent coverage by woody vegetation, number of dead stems, low density of prostrate residual vegetation, amount of bare ground, and the proportion of plots that were burned. Density was negatively correlated with vegetation height and percent cover of standing residual vegetation. In Missouri, it used short cover (35% cover at a height of 1 cm and 10% cover at 25 cm) in a heavily grazed abandoned crop field. It was not observed in idle, grazed, hayed, or burned tallgrass habitat. In Iowa alfalfa fields, its abundance was directly related to vegetation density until alfalfa reached a height of 30 cm, when abundance became negatively related to vegetation height and density (Dechant et al. 2002a). On roadside surveys in Alberta, it occurred most often at stops characterized by cultivated lands mixed with native grasslands. Its occurrence was significantly higher at cultivated stops than at grazed or uncultivated stops. Its occurrence at grazed stops was significantly higher than at undisturbed areas. It occurred under both heavy and light grazing regimes, usually in association with shrubs. Uncultivated edges along agricultural lands, fencerows, and roadside ditches provided important habitat that is often lacking in native grasslands (Owens and Myres 1973). In Saskatchewan, the number of Vesper Sparrows observed per stop was 6 times higher in introduced vegetation than in native vegetation (Sutter and Brigham 1998). It was most abundant in planted pastures followed by hayfields and native pastures, and was significantly more abundant in planted than native pastures. Its abundance was correlated with planted grassland with increased cover by bare soil. There were no significant differences in nest survival rates among habitats (Davis et al. 2016).

In Michigan, the Vesper Sparrow avoided permanent pastures and pastures in hayfields. In Wisconsin, it was more abundant in continuously grazed pastures than in rotationally grazed or ungrazed pastures. In Alberta, it occurred in low numbers in early season tame and native pastures and deferred-grazed (after 15 July) native pastures and was absent in continuously grazed native pasture. In native pasture, it occurred in areas with moderate cover diversity and uniformly short grass. In tame pastures, it used areas with moderate amounts of herbaceous biomass, low to moderate variation in herbaceous height, and a moderate to high proportion of forbs relative to grasses. In Saskatchewan, it was equally abundant in lightly grazed mixed-grass prairie and lightly grazed crested wheat grass. Its occurrence was negatively correlated with vegetation height and clubmosses. In mixed-grass prairie, its abundance was positively correlated with forbs and broad-leaved grasses 10 cm or less tall and shrubs 20-100 cm tall. It was negatively correlated with broad-leaved grasses 20-100 cm tall. Its frequency of occurrence in native pasture was unaffected by grazing intensity. Heavy grazing removed virtually all plant and litter material resulting in more than 20% bare soil and more than 40% clubmosses, and presence of short plants with low vigour. Light grazing was associated with less than 10% bare soil and clubmosses, presence of robust and vigorous plants, and abundant litter and plant material. In Alberta, it was most abundant in deferred-grazed grasslands, followed by idle grasslands, continuously grazed grasslands, tame Dense Nesting Cover (DNC) for waterfowl, and idle native parkland. It was absent in idle deciduous upland, conventional hayfields, cropland, native DNC, shelterbelts, and wetlands. In Colorado, Montana, Nebraska, North and South Dakota, and Wyoming, densities were highest in moderately and lightly grazed shrubsteppe-grassland habitat characterized by vegetation averaging 20 cm tall with 9% bare soil (Davis et al. 2016; Dechant et al. 2002a).

In Iowa, the Vesper Sparrow was more common in cropland than CRP lands, which are typically characterized by dense grass cover, but it nested in both habitats. The same preference occurred in Minnesota, Montana, North and South Dakota, Indiana, and Michigan. It did not use CRP lands in Kansas, Missouri, or Nebraska but frequently nested in cropland. In Saskatchewan, it occurred in DNC and in idle grasslands and wheat fields. It was common in low nesting cover of red fescue and Kentucky bluegrass but absent from fallow cropland. In Alberta, it occurred in wetlands and wetland margins within all farmland types, and within DNC. It was present on 1-4-year-old tame DNC but absent in native DNC. In Manitoba, it was present in idle mixed-grass prairie but absent in DNC planted to either native or tame grasses (Davis et al. 2016; Dechant et al. 2002a). In Alberta, it used fields that were 70% cultivated pasture and 30% fescue more than delayed-mowed hayfields. It was absent in conventional hayfields (Jones and Cornely 2020). In Saskatchewan grasslands managed for waterfowl, numbers seen per plot were 0.02 in DNC (12.5% occurrence), 0.03 in native grassland (16.7% occurrence), and 0.02 in wheat (5.3% occurrence; Hartley 1994). In Iowa, CRP lands exhibited average characteristics that included 35 cm vertical cover (range 24-44 cm), 80% grass cover (range 47-98%), 22% forb cover (range 3-53%), 97% litter cover (range 93-100%), 36% vertical patchiness (range 18-56%), and 35% horizontal patchiness (range 6-65%). Density of the Vesper Sparrow was 20 times greater in cropland than CRP land. Nest densities in row crops increased with increasing crop residue from the previous year (Patterson and Best 1996). In Illinois, it occurred at a fairly high frequency in bare-field habitats such as row crops and plowed fields (Graber and Graber 1963). Camp and Best (1994) examined its usage of roadsides adjacent to cropland in Iowa. Strips along

roads were 6 m wide and consisted of a foreslope near the road, dropping to the bottom of a ditch, followed by a backslope up to a fence. All nests were in the foreslope area. Nest densities were positively correlated with the amount of bare ground and negatively correlated with vegetation height and density. Nests were in areas with shorter, sparser vegetation than generally occurred in roadsides, although the immediate nest site contained less bare ground than the area within 1 m of the nest. Vegetation characteristics at nests compared with the area within 1 m, respectively, included: vertical density, 4.1 and 5.1; vegetation height, 32.5 cm and 20.5 cm; grass cover, 52.1% and 40.0%; forb cover, 13.3% and 3.2%; and bare ground, 31.2% and 55.0%. Vegetation was most sparse in the foreslope where all nests were located due to mowing and presence of gravel from the road. Although density in roadsides was higher than in row crops, nesting success was low due to predation.

Other microhabitat preferences have been identified for the Vesper Sparrow. It occurred in green ash woodlands in South Dakota where it was present in early seral stages and absent in late seral stages. Early stage woodlands had less foliage density 1-2 m from the ground, were patchier, and had lower canopy cover (Rumble and Gobeille 1999). In Illinois, it particularly favoured edge shrub habitats, red clover fields, and shrub-grown areas (Graber and Graber 1963). In Wisconsin grasslands, populations were low and dispersed along field edges and fencerows. All territories contained posts and a fence line but none contained wire bales or tangles or trees (Wiens 1969). In the Prairie Provinces, it was in a guild associated mostly with coniferous forests; this study examined forested habitats only. It was associated with dry, nutrient-poor sites that were probably open jack pine stands (Kirk et al. 1996).

Considerable research was conducted on Vesper Sparrow usage of row-crop fields in Iowa. The cropping system there consists of planting corn and soybeans in alternate years. After planting, the area between the rows of crops was periodically cultivated to remove weeds. In Iowa, 58% of the land is in corn-soybean agroecosystems and this rate is 56% in Indiana. These areas provide considerable nesting habitat for the Vesper Sparrow, although nesting success tends to be very low. Within this ecosystem, there are patches that differ in vegetation structure and soil surface litter such as fencerows and weedy areas within cropped land. These provide essential habitat features. With the alternating crop system, soybeans are planted in fields that have corn crop residue from the previous year, and vice versa. Vesper Sparrow activities and early nests were initially in fields with corn residue. Once spring tillage began, most activity and nest placement shifted from 1 side of the fencerow in the territory to the other side that was most recently tilled. It may benefit from having different crops on either side of the fencerow. Agricultural operations on either side of the fencerow are asynchronous in these cases. Nesting sparrows were disturbed regularly and nests were often destroyed by agricultural activities, but only part of the territory was tilled at once, leaving a refuge. On plowed fields with little residual crop coverage, nests were scarce until crop plants began to develop. Later, as the crop canopy closed in mid- to late July, croplands became unsuitable for nesting. Early in the season, nests in crop fields were always in a clump of crop residue. Once the crop was about 10 cm tall, nests were placed at the base of growing plants in the crop row. Early nests were often near non-productive areas such as fencerows, washes, and weed patches, probably because they were the primary source of insect food at that time. Early nests were also in fields with the greatest amount of residual cover from the previous year's crop. Midseason nests were further

from non-productive areas because insect availability in crops greatly increased at that time. After 19 June, nests were closer to non-productive areas than in midseason. These nests were mostly in soybean fields because corn was too tall with a closed canopy by then and was no longer suitable nesting habitat. By mid-June, there was probably greater homogeneity in the distribution of food so birds did not have to nest close to non-productive areas. Although corn fields were unsuitable for nesting at this time, weedy areas under the corn canopy were heavily used for foraging. Having both soybean and corn fields within the territory provided suitable nesting habitat and preferred foraging areas in close proximity during the period when the probability of successful nesting was highest. In the last month of the breeding season, a high proportion of nests were in washes in soybean fields. These areas were open in an otherwise densely vegetated area. In spring, territories where fencerows had a greater number of shrub groups were occupied first. Early occupied territories tended to have greater crop residues in fields and less aerial extent of fencerow coverage. There was little correspondence between habitat characteristics associated with habitat preferences and those related to breeding productivity. This was due to the disruptive nature of agriculture. Radical instantaneous habitat changes may occur such as 100% of the crop residue being buried within a day. Consequently, the Vesper Sparrow may not be able to adjust its breeding behaviour to compensate for habitat changes made by agricultural practices (Best and Rodenhouse 1984; Rodenhouse and Best 1981, 1983, 1994). In contrast to agricultural fields, there is typically no difference in the vegetation at first and second nests in grassland habitat (Wray et al. 1982).

The Vesper Sparrow responds quickly to habitat changes. It colonizes new areas swiftly when habitat becomes suitable but disappears as old fields change into forest cover (Jones and Cornely 2020).

Some studies compared the habitat requirements of the Vesper Sparrow with those of other species. Wiens (1969) conducted a study on the ecology of grassland birds in Wisconsin. In addition to the Vesper Sparrow, the study area supported the Upland Sandpiper, Savannah Sparrow, Grasshopper Sparrow, Henslow's Sparrow, Bobolink, Eastern Meadowlark, and Western Meadowlark. The mean distance of Vesper Sparrow territories was 0 m from fencerows and 69.0 m from cultivated fields (range 5-180 m). Its mean effective vegetation height was low and differed significantly from all species except the Western Meadowlark. Compared with the Vesper Sparrow, vegetation density was greater in areas occupied by other species except in the single Western Meadowlark territory, where it was less. The total vertical vegetation density was significantly less for the Vesper Sparrow than for the Bobolink and Henslow's Sparrow. Light penetration to the ground was high, but not as high as for the Western Meadowlark. Coverage of low lawn-like vegetation was greater for the Vesper Sparrow than for all species except the Western Meadowlark. Forb density was higher and forb height was lower in Vesper Sparrow territories for all species except the Western Meadowlark. Litter depth was similar to that of the Western Meadowlark, Savannah Sparrow, and Grasshopper Sparrow but significantly less than in territories of the Bobolink, Eastern Meadowlark, and Henslow's Sparrow. Vesper Sparrow perches were 14.6% in grasses, 10.8% in heavy-stemmed forbs, 51.7% on wires, and 22.8% on posts. It used wires and posts much more and grass less than other species, and used forbs less than the other sparrows. Habitat was characterized as sparse low vegetation compared with dense low vegetation for the Western Meadowlark and tall dense vegetation for the Bobolink and Henslow's Sparrow. The Vesper Sparrow and Western Meadowlark were associated

with shallow loose litter. Territories often included trees or fence lines for the Vesper Sparrow, Eastern Meadowlark, and Bobolink, but not, or only occasionally, for the Henslow's Sparrow and Western Meadowlark. Species arranged in order of increasing vegetation richness (vegetation density and height and litter coverage and depth) were Western Meadowlark, Vesper Sparrow, Savannah Sparrow, Grasshopper Sparrow, Eastern Meadowlark, Bobolink, and Henslow's Sparrow. The range of difference in this ranking was small. Ecologically similar species performed their basic activities (nesting, foraging, singing, perching) in slightly different manners by differentially using the various substrates or using different vertical layers in the same substrate. In shrubsteppe vegetation, the Vesper Sparrow occupied a habitat niche in montane meadows that was most similar to that of the Savannah Sparrow. Its niche was somewhat similar to those of the Upland Sandpiper, Grasshopper Sparrow, Eastern Meadowlark, and Dickcissel (Rotenberry and Wiens 1980). In Michigan, the Vesper Sparrow was exclusively a ground nester, the Field Sparrow nested on the ground and in low shrubs, and the Chipping Sparrow nested exclusively in trees and shrubs (Evans 1964). In coniferous plantations in Wisconsin, the most common species were the Chipping Sparrow, Clay-colored Sparrow, and Field Sparrow and, to a lesser extent, the Vesper Sparrow. For plantations to be suitable for the Vesper Sparrow, they have to be young with an open canopy (Mossman et al. 1991).

The Vesper Sparrow demonstrates no clear preference for the edge or interior of habitat patches. It is likely that territories are selected based on the suitability of the vegetation structure and density of singing perches. In Colorado, it was significantly more abundant 200 m from edge than closer to edges between suburban development and upland or lowland habitats (Dechant et al. 2002a). In Wisconsin, the mean distance of territories from a wooded area was 246.0 m (range 10-370 m; Wiens 1969). In Alberta mixed-grass prairie, it increased with proximity to roads and exhibited no response to cropland edges. It was neither attracted to nor avoided wetland edges. It may have been attracted to roadsides because of the presence of fence posts for singing perches (Sliwinski and Koper 2012). In row crops in Iowa, it was an obligate edge species. Territories were centred along fencerows and did not extend into fields further than 80 m in 1 study and 110 m in another study. Interior portions of fields were avoided, probably because of the lack of suitable perches (Perritt and Best 1989; Rodenhouse and Best 1983).

The Vesper Sparrow does not appear to be area sensitive, but results are somewhat conflicting. In grassland habitat, it has nested in patches smaller than 4 ha (Beauchesne et al. 2004; Jones and Cornely 2020; Swanson 1996). In Illinois and Missouri, it was found in all sizes of habitat patches and considered highly tolerant of habitat fragmentation. Nonetheless, 10-100 ha was considered the minimum patch size to support a viable population (Herkert 1994a; Swanson 1996). In Maine, its abundance was significantly correlated with patch size. The approximate percentages of incidence were 1-2% in grasslands 1-2 ha in area, 38% at 10 ha, 62% at 100 ha, and 88% at 1,000 ha. Incidence reached 50% at approximately 20 ha. Although incidence increased with patch size, the smallest patches were not completely avoided (Vickery et al. 1994). In Iowa, it nested in 6-m-wide strips in roadsides (Camp and Best 1994), suggesting that it was not area sensitive. In agricultural row crops in Iowa, it was restricted to areas within 80 m or 110 m of edge (Perritt and Best 1989; Rodenhouse and Best 1983), suggesting that large fields would support lower densities than smaller fields. In North Dakota, its probability of detection was significantly negatively correlated with forest patch

size. Its rate of incidence was 80% in 1-ha forests, 55% in 10-ha woodlots, 20% in 100-ha woodlands, and 10% in 1,000-ha woodlands (Grant and Berkey 1999). Johns (1993) reported it being more abundant in large than small woodlots and considered it area sensitive. It occurred in the full range of sizes of woodlots that were examined, from 0.04-30 ha.

Almost all Ontario Vesper Sparrow nests were on the ground, although one was elevated in a grass clump. Many ground nests were in slight depressions or hollows and one was excavated by the bird. Of 129 nests, 68.2% were hidden in or under grass or forb clumps, 20.9% were under or at the base of small trees and shrubs, 6.2% were exposed, 3.1% were beside logs or dead branches, and 1.6% were under dead branches (Peck and James 1987, 1998b).

Almost all nests are on the ground in a small depression, with the exceptions being 1 nest in Ontario and 2 of 176 nests (1.1%) in British Columbia. The 2 British Columbia nests were in shrubs. Nests are frequently near small patches of bare ground or where the vegetation is sparse and low. First nests may be well concealed in an excavation in the ground under cover of prostrate dead herbaceous stems. Nests along gravel roads or in previous year's alfalfa or corn fields are often at the base of a grass tussock, thistle, dandelion, some other plant, or a clod of dirt. Some nests are almost completely exposed from above during egg laying but may be hidden by new growth by the time eggs hatch. Two nests on Vancouver Island were in a mixed forb-grass area concealed in a clump of English plantain and a third nest was in a rocky area against the side of some mowed Scotch broom. In Michigan, nests were oriented toward the north, possibly for protection from the afternoon sun. In British Columbia, there was vegetation on the southwest side of 87% of nests, significantly different from random, and they had a lower ambient temperature. Nests with a southwest orientation are potentially subjected to temperatures that are lethal to embryos for a short time. Nests sometimes have a ramp at the front and nests in sedges have a characteristic awning formed by bent sedge blades (Beauchesne et al. 2007; Berger in Austin 1968; Campbell et al. 2001; Jones and Cornely 2020; Wiens 1969).

The Vesper Sparrow is territorial and most activity is conducted within the territory. Adults frequently forage in nearby shrubs and woodland edges outside the territory. Territories are established shortly after arrival in April but boundaries are rather indistinct initially. The number of birds stabilizes in May. Territory configuration becomes established then and remains fairly constant for the remainder of the breeding season. In row-crop fields where food resources are patchily distributed, territory selection in fields may be related to the abundance and availability of food for nestlings. In Iowa croplands, preferred territories contained more shrubs and crop residue. In agricultural fields, territories typically straddle a fencerow. In grassland, territorial boundaries often follow fencerows or trails for a distance, often resulting in irregular boundaries. In Montana, 1 territory was L-shaped because of a sudden change in vegetation from mixed grasses to broad-leaved forbs. The area of forbs was avoided, possibly because the Vesper Sparrow had difficulty perching on the plants. Territory size is variable and dictated largely by food availability. Territory sizes of 0.29-8.19 ha have been reported; larger territories are often associated with cropland. In Wisconsin grassland, territories averaged 0.89 ha (range 0.61-1.09 ha). Territory size varied over the season and was significantly larger 28 May to 10 June. Average territory sizes in different periods were: 20-26 April, 1.09 ha; 15-25 May, 1.29 ha; 28 May to 10 June, 1.46 ha; and 14-25 June, 0.89 ha. In

Montana grasslands, territories averaged 1.02 ha (range 0.61-1.60 ha). In Michigan, territories averaged 2.59 ha, with averages of 1.53 ha in open fields and 1.03 ha in fields with standing dead trees; territories were 0.48-0.72 ha in cultivated fields. In Oregon grasslands, territories averaged 1.3 ha (range 0.4-5.2 ha). In Montana, 60 territories averaged 1.65 ha (range 0.29-3.04 ha); 3 territories in Montana montane meadows averaged 1.96 ha. In Iowa croplands, territories averaged 3.05 ha in 1 year and 3.57 ha the next year. Another Iowa study in cropland determined that the average territory size was 2.3 ha with a range of 1.8-3.2 ha (Best and Rodenhouse 1984; Dechant et al. 2002a; Jones and Cornely 2020; Perritt and Best 1989; Reed 1985; Rodenhouse and Best 1983, 1994; Wiens 1969).

Based on limited data, natal philopatry rates appear to be very low. Zero of 45 banded nestlings returned in Michigan (Dechant et al. 2002b).

Adult site fidelity rates are variable, based upon limited data. In Michigan, 6 of 8 banded adults (75.0%) returned the following year, and 5 of 16 (31.3%) returned the year after that. One male returned to the same territory in 4 years and 1 adult was recaptured at the same site 6 years later. Combining the returns for the 2 years, 11 of 24 adults (45.8%) returned. In Iowa cropland, 4 of 26 males (15.4%) and 2 of 11 females (18.2%) returned; the total return rate of adults was 6 of 37 (16.2%). All returned to the same fencerow they used the previous year and 2 males occupied the same territory. All returning birds nested successfully the previous year. There appeared to be no apparent advantage to returning to the same area because breeding habitat was abundant. Site fidelity to row-crop fields may be disadvantageous because some birds may return to suboptimal habitat. The amount of crop residue may vary considerably and fencerows may be altered or removed (Berger in Austin 1968; Best and Rodenhouse 1984; Dechant et al. 2002a).

Limiting Factors

Eggs have been reported in Ontario from the last week of April until the first week of August with most present in the last week of May and throughout June (Peck and James 1987). In Algonquin Park, eggs are present from late May to early July, nestlings are present from late June to late July, and recently fledged young have been observed in early August (Tozer 2012).

There is no information on how long nest building takes or if there is a time interval between nest completion and initiation of egg laying. Eggs are probably laid at the rate of 1 per day. It is unknown when incubation is initiated in relation to clutch completion. The incubation period is 11-14 days, but mostly 12-13 days. The incubation period at 4 Ontario nests was 11 to less than 13 days. The normal nestling period is 9-14 days (average 9.6 days in Michigan). If nestlings are disturbed, they may leave the nest when they are as young as 7 or 8 days (Berger in Austin 1968; Evans 1964; Jones and Cornely 2020; Peck and James 1987).

Ontario egg dates suggest that 2 broods may be raised in a year, but this has not been confirmed; the same is true in British Columbia and Quebec. In Ontario, a second clutch was reported in a nest that had contained young a week previously. In Wisconsin, only a single brood was raised. Double-brooding has been confirmed in Michigan, West Virginia, and New York. Michigan birds regularly raised 2 broods and 1 female successfully raised 3 broods. Renesting is common if a nest is lost. In West Virginia, an average of 3.6 nesting attempts were made per year, with averages ranging from 3.4 to 4.1 in individual years. Clutches of 2-6 eggs have been reported in Ontario (average 3.65 eggs). Fifty-nine percent of clutches contained 4 eggs and only 2 clutches

of 6 eggs were reported. Elsewhere, clutches of 3-6 eggs have been reported, with a normal range of 3-5 eggs and a mode of 4 eggs. Mean clutch sizes elsewhere include 3.8 eggs in Alberta; 4.0 in Saskatchewan; 3.8, 3.9, and 3.5 in 3 years in West Virginia; 3.6 in Michigan; 3.75 in Illinois before 15 July and 3.37 later; and 3.7 in Ohio, with mostly 4-egg clutches in May and 3-egg clutches in June and July. The slight but nonsignificant decline in clutch size with the advancing season may be due to shorter day length, diminishing food resources, and tapering off of the endocrine reproductive system (Berger in Austin 1968; Campbell et al. 2001; Dechant et al. 2002a; Gaudet et al. 2020; Graham and Cotter in Gauthier and Aubry 1996; Jones and Cornely 2020; Ludlow et al. 2014; Peck and James 1987; Wiens 1969; Wray et al. 1982).

The age at first breeding is 1 year. No information is available on the proportion of yearlings that nests and if there is a floating, nonbreeding population. The mating system is monogamous. It is probable that the pair bond persists throughout the breeding season, but this has not been verified. Most returning adults do not remate but 1 pair reunited in a subsequent year in Michigan (Dechant et al. 2002a; Jones and Cornely 2020).

In agricultural land in Iowa, food items were obtained mostly from the ground, but the Vesper Sparrow also gleaned the foliage of short plants and hovered to capture insects from vegetation as tall as 25 cm. It occasionally scratched vigorously with both feet at a potential food source, such as crop residue. It often pecked rapidly, suggesting that numerous small items were captured and ingested. It occasionally foraged at a single site for several minutes and walked as far as 50 m between foraging bouts. In Wisconsin grasslands, all foraging was in grasses 5 cm or shorter. Its behaviour of foraging in very short grass differed from that of all other grassland species. The Vesper Sparrow was not observed foraging in medium-stemmed forbs. It forages wherever food is most abundant. In Michigan grasslands, a considerable proportion of food captured for nestlings was obtained from a nearby woodlot rather than being caught within the breeding portion of the territory. Edges and interspersion of habitat types may be important in supporting high sparrow densities. In Iowa croplands, both sexes foraged almost exclusively in their territories. Only late in the season and after an adjacent territory had been abandoned did adults forage off their territories. At this time, flights longer than 300 m were occasionally made. In agricultural cropland, it alters its foraging locations throughout the breeding season in response to the distribution of food. It forages mostly in or near uncropped or weedy areas throughout the season, but proportionately more foraging occurs away from these areas later in the season. In April and May, 68% of foraging observations occurred within 1 m or in an uncropped or weedy area. In June, when insects were colonizing young crops, it walked along rows of corn gleaning insects. In July and early August when insects and foraging activity was more evenly distributed, 50% of foraging still occurred within 6 m of a non-productive area. Foraging was concentrated in a small proportion of each territory. Large areas of cropland, especially more than 50 m from a non-productive area, were rarely used for foraging. Of 21 birds that had the option of foraging in soybean or corn fields, 13 preferred to forage in soybean fields, 7 preferred to forage in corn fields, and 1 had no preference. Soybean fields had greater crop residue from the previous year's corn crop, and the Vesper Sparrow significantly preferred to nest in fields with greater crop residues. Fields with more crop residue had more elevated song perches, more concealing cover, and greater abundance of arthropods. Foraging occurred mostly in open or sparsely vegetated areas in cropland in April and May. In June,

uncropped areas with perennial vegetation, such as fencerows and grassed waterways, became unsuitable for foraging because of dense plant growth, and the proportion of time spent in these areas declined dramatically. During June, crop fields remained sparsely vegetated but provided a source of insect prey. In July and August, annual weeds in washed-out areas and cropland provided both insects and seeds for food. Overall, it tended to forage in field margins during the breeding season. The scarcity of insects in crop fields may contribute to the larger territories that it usually has in croplands (Best and Rodenhouse 1984; Evans 1964; Judd 1901; Rodenhouse and Best 1983, 1994; Wiens 1969).

In Michigan, the frequency of occurrence of food items in nestlings' feces included 30% odonates, 90% orthopterans, 50% true bugs, 60% soft-winged bugs, 100% beetles, 100% lepidopterans, 60% flies, 20% hymenopterans, 90% spiders, and 80% plant material. The frequency of occurrence of items in gizzards of nestlings was 100% orthopterans, 64.3% true bugs, 92.9% soft-winged bugs, 78.6% beetles, 71.4% lepidopterans, 35.7% flies, 42.9% hymenopterans, and 21.4% plant material. Larvae or nymphs of lepidopterans, orthopterans, beetles, and soft-winged bugs were preferred to adults. Nestlings ate significantly higher frequencies of soft-winged bugs, lepidopterans, flies, and spiders and lower frequencies of plants than adults. Nestlings were fed by frequency 58.3% rapidly flying insects, 66.7% sluggish larvae, and 100% insects that are active on the ground compared with 12.5%, 15.6%, and 93.8% for adults, respectively. While searching for food for nestlings, adults spent less time on open ground and more in active flight or in higher vegetation strata than while foraging for themselves (Evans 1964; Jones and Cornely 2020).

Judd (1901) examined the contents of 130 adult stomachs. The diet over the entire year consisted of 69% vegetable matter and 31% animal matter. In winter, the Vesper Sparrow eats vegetation almost exclusively; the summer diet consists of 90% invertebrates. The use of animal foods declines in late summer and early autumn. Vegetation comprises only 10% of the July diet and begins to increase steadily by early August until it comprises the entire winter diet. In addition to seeds, which are the staple of the vegetation part of the diet, it eats fruits of mulberries, blackberries, and strawberries, and buds of beech, maple, and apple. Seeds consisted of 11% grain, 16% grasses, and 42% weeds. The grain included oats and wheat gleaned from stubble fields, horse droppings, or roadsides. It is less partial to grass seeds than other sparrows, but selects much the same species: foxtails and crabgrasses and, to a lesser extent, timothy and paspalum. Weed seeds are more prevalent in the diet, including ragweeds, amaranths, lamb's-quarters, sunflowers, smartweeds, and purslane. Ragweed and amaranth seeds comprised 16% of the entire diet; purslane and sunflowers were preferred over amaranths and lamb's-quarters. The animal food consists almost entirely of insects. The diet included of 12% beetles, 11% grasshoppers and other orthopterans, 5% hairless caterpillars, and 2% bugs, ants, and other hymenopterans. Beetles and grasshoppers formed the bulk of the insect food and constituted a third of the May diet. As grasshoppers become more common as the season progresses, they become dominant in the diet. It is very partial to beetles and still eats them when grasshoppers are abundant and when they are available in winter. Scarab, click, and ground beetles and weevils are preferred to other beetle families. Scarab beetles are very abundant in pastures where it nests and these form 4% of its annual diet. Weevils constitute 4% of the annual diet and 20% of the June diet. Grasshoppers and other orthopterans predominate over all other insect prey from June to September. The Vesper Sparrow eats mostly short-horned

grasshoppers and these constituted 41% of the July diet. In May, 21% of the diet consisted of cutworms, armyworms, and other smooth caterpillars. It also eats leafhoppers, flies, spiders, snails, and earthworms; these collectively represent about 3% of the entire diet. Evans (1964) examined the Vesper Sparrow's diet in Michigan. In spring, the frequency of occurrence in 12 adult gizzards was 41.7% orthopterans, 8.3% true bugs, 25% soft-winged bugs, 66.7% beetles, 25.0% lepidopterans, 16.7% hymenopterans, 16.7% spiders, and 100% plant material (16.7% wiregrass, 58.3% panic grass, 16.7% foxtails, and 50.0% Indian grass). Beetles were represented mostly by ground beetles and weevils. The frequency of occurrence of food items in summer of adults and fledglings was 5% odonates, 80% orthopterans, 65% true bugs, 55% soft-winged bugs, 85% beetles, 5% lepidopterans, 5% flies, 40% hymenopterans, 35% spiders, and 95% plant material (5% flatsedges, 10% wiregrass, 95% panic grasses, and 5% wood-sorrel). Plant material represented 59% of the spring diet and 44% of the summer diet. Among beetles, leaf and click beetles became common in the diet along with ground beetles and weevils. The primary bugs in the diet were leafhoppers, plant bugs, assassin bugs, and meadow spittlebugs. Adult grasshoppers were more abundant in the summer diet. Ants were the main hymenopteran food but it also ate ichneumonid wasps and other parasitic wasps. Plant material remained common in the summer diet, particularly panic grass seeds. Jones and Cornely (2020) reported the results of additional diet studies, and noted that adults frequently ate ants that entered the nest. In Utah, 116 stomachs contained 1,300 insects from 10 orders, 3,158 seeds, and 1 pseudoscorpion. Adult insects predominated in the diet, but larvae, nymphs, pupae, and eggs were also eaten. Dominant animal prey items were soft-winged bugs (about 28.7% of the diet, mostly spittlebugs and aphids), beetles (26.9%, mostly weevils and leaf beetles), hymenopterans (17.0%, mostly ants), true bugs (14.2%, mostly seed bugs), orthopterans (8.5%, mostly locusts), lepidopterans (6.5%, almost entirely caterpillars), and flies (3.1%). Miscellaneous invertebrates in the diet included green lacewings, odonates, caddisflies, and spiders (Knowlton and Nye 1948). In Washington, the diet was predominantly seeds early in the season, but grasshoppers became much more abundant in the diet from June to August. Grasshoppers constituted over half the biomass of food items, but seeds represented 88% of items consumed (Rotenberry 1980). In southeastern Washington State, it was highly insectivorous throughout the breeding season. From June through August, grasshoppers were most important in the diet, often comprising more than 50% of the biomass consumed. Nonetheless, grass seeds dominated the diet numerically and represented 88% of food items. In Minnesota, a third of the diet consisted of seeds, mostly those of ragweeds, purslane, sunflowers, lamb's-quarters, foxtails, crabgrasses, knotweeds, and grain. In Montana, the summer diet consisted of 50.5% insects (grasshoppers, leaf beetles, and weevils) and 20% needle grass. Grasshoppers and beetles formed the bulk of the diet in early summer and seeds were important later in the year. Animal foods included beetles, orthopterans, hymenopterans, true bugs, spiders, caterpillars, flies, soft-winged bugs, thrips, and odonates. Plant seed species in order of abundance were bluegrass, needle grass, lamb's-quarters, satin grass, bush-clover, and Indian grass. Grass seeds predominated in the spring diet with panic and Indian grasses most frequently consumed. It commonly ate seeds throughout the summer, especially those of panic grasses. In western North Dakota, 67% of the spring diet was comprised of grasshoppers. In Montana, the early season diet was comprised of 7% grass seeds, 26% spiders, 11% beetles, 18% ants, 20% caterpillars, and 17% grasshoppers and leafhoppers. After invertebrates became abundant, the diet consisted of 5% grass seeds, 20% spiders, 11% beetles, 22% ants, 26% caterpillars, and 15% grasshoppers and

leafhoppers. The dietary breadth of the Vesper Sparrow declined by 48% after prey became more abundant (Cutting et al. 2016).

Evans (1964) compared the diets of the Vesper, Chipping, and Field sparrows in Michigan. There were very few differences in the diet of the 3 sparrows but he concluded that there was no competition for food because of its abundance. The Vesper Sparrow ate orthopterans more frequently than the other 2 species, but the difference was significant only from the Field Sparrow. The Vesper Sparrow ate true and soft-winged bugs less frequently than the other 2 species, but the difference was significant only for soft-winged bugs. The Chipping Sparrow ate significantly more lepidopterans than the other 2 species. The Vesper Sparrow continued to eat seeds in summer, particularly those of panic grasses. The other 2 sparrows ate seeds less frequently in summer but ate both grass and weed seeds. The only difference in the nestling diet was that Vesper Sparrow nestlings ate significantly fewer true bugs than Chipping Sparrow nestlings.

The Vesper Sparrow is commonly parasitized by the Brown-headed Cowbird. Rothstein (1975) considered it an acceptor of cowbird eggs. Peer et al. (2000) and Klippenstine and Sealy (2008) artificially parasitized Vesper Sparrow nests with real and artificial cowbird eggs painted similarly to real cowbird eggs, and with blue eggs. They also parasitized some nests with undersized eggs that resembled Vesper Sparrow eggs. Real and artificial cowbird eggs were accepted in all nests but 20.75% of blue eggs were rejected by grasp ejection or puncture ejection. Eighty percent of undersized eggs were rejected. Natural and artificial cowbird eggs may not have been ejected due to their close resemblance to Vesper Sparrow eggs and the risk of ejecting one of their own eggs. The Vesper Sparrow does not appear to be significantly harmed by parasitism and both species may fledge from a nest. In Illinois, the mean clutch size was 1.3 eggs in parasitized nests and 3.6 eggs in unparasitized nests. Saskatchewan parasitized nests had smaller clutches and hatched and fledged fewer young. Parasitized nests were significantly closer to field edges than unparasitized nests. Woodlands and thickets may provide perches for female cowbirds watching for activity that will reveal a nest location. One study found that parasitized nests were not significantly closer to edge or significantly less concealed than unparasitized nests. Nests are more apt to be parasitized in April and May when few other species have initiated nesting (Berger in Austin 1968; Dechant et al. 2002a; Jones and Cornely 2020). In Ontario, 52 of 494 nests (10.5%) were parasitized (Peck and James 1998b). From 1966 to 1984, 15 of 44 nests (34.1%) in Grey County were parasitized compared with 3 of 46 nests (6.5%) in Middlesex County from 1877 to 1966 (Peck and James 1987). Throughout the Vesper Sparrow's range, parasitism rates vary considerably from 0 to 61%, but tend to be low. Parasitism rates include 6 of 246 nests (2.4%) and 0 of 53 in North Dakota; 0 of 10, 25 of 41 (61.0%), 1 of 27 (3.7%), and 1 of 6 (16.7%) in Iowa; 13 of 44 (29.5%) in Iowa croplands; 2 of 53 (3.8%) in Alberta; 1 of 181 (0.6%) in Washington; 23 of 195 (11.8%) in Alberta, Saskatchewan, and Manitoba; 0 of 70 in West Virginia; 3 of 74 (4.1%) in southern Quebec; 9 of 112 (8.0%) and 3 of 14 (21.4%) in Ohio; 9 of 89 (10.1%) and 4 of 25 (16.0%) in Michigan; 4 of 52 (7.7%) in Illinois; and 3 of 215 (1.4%) in British Columbia (Berger in Austin 1968; Camp and Best 1994; Campbell et al. 2001; Dechant et al. 2002a; Gaudet et al. 2020; Granfors et al. 2001; Grant et al. 2006; Jones and Cornely 2020; Ludlow et al. 2014; Patterson and Best 1996; Rodenhouse and Best 1981; Vander Haegen et al. 2015; Wray et al. 1982).

Habitat loss and agricultural practices are the greatest limiting factors to the Vesper Sparrow. Conversion of suitable habitat to urban development is linked to its decline between atlases in Hamilton and Niagara Region, and in many areas throughout its range. Abandonment of marginal agricultural land and subsequent natural succession results in loss of suitable habitat. Declines in Algonquin Park and the Kingston area were attributed to natural succession, and much of the farmland in the southern Canadian Shield has reverted to forest (Black and Roy 2010; Curry 2006; Swanson 1996; Tozer 2012; Weir 2008).

Farming practices have changed significantly since the 1950s, and most changes have been detrimental to the Vesper Sparrow. At that time, farms were small with a few head of livestock and some pasture and hayfields. As small farms became less economically viable, harvesting machinery became more efficient, and numerous fencerows were eliminated to create larger fields. This was detrimental to the Vesper Sparrow because its territory is often centred on fence lines and it avoids the interior of row-crop fields. The practice of removing fencerows is still continuing. Fewer farmers continued to raise livestock, so the need for pastures and hayfields declined. Many fields were converted to row crops, habitat that is inferior to pasture and hayfields. Early hay crops were dominated by red clover and other clovers in the same genus. Clover fields were preferred habitat because the vegetation was short and supported abundant invertebrates. These clovers were largely replaced by alfalfa for hay. Alfalfa grows tall and dense and is marginal to unsuitable nesting habitat. The chronology and frequency of hay mowing also changed. Red clover crops were cut only once a year in mid-July. This allowed enough time to raise a first brood. Alfalfa is cut 2 or 3 times a year with the first cut in mid-June or earlier. In Iowa, the Vesper Sparrow was present in both the first and second alfalfa cuts. Its density did not differ significantly before and after mowing, although its overall density was low. Density tended to be higher 2 and 4 weeks after mowing than prior to mowing. Mowed alfalfa fields may be slightly better habitat than unmowed fields. Nests that are initiated in alfalfa fields are typically destroyed by mowing. Approximately 250,000 eggs and young are lost annually in Canada due to mowing, cultivation, and other agricultural practices. The estimated annual mortality rate in the Canadian Carolinian and Great Lakes–St. Lawrence forest regions is approximately 34,000 (Frawley and Best 1991; Graber and Graber 1963; Graham and Cotter in Gauthier and Aubry 1996; Jones and Cornely 2020; Tews et al. 2013). Wolcott et al. (2023) recommended that grassland management be deferred until August to protect both nests and fledglings.

In Iowa, corn and soybean crops are cultivated regularly after they are planted until the crop canopy closes in. Cultivation disturbs the soil between the crop rows and destroys any nests that are not in rows. In Ontario, no cultivation occurs after the crop is planted, and a single herbicide application is applied shortly after crop plants emerge. In both Iowa and Ontario, the first tillage and planting occur after the first nests are initiated. Consequently, almost 100% of first nests in corn and soybean fields fail. In Iowa, nest success rate was 9% prior to 15 June and 28% thereafter. Once the crops were about 10 cm tall, nests were placed in the crop rows and about 50% survived tillage. Since no tillage occurs in Ontario fields at this time, success rates should be higher than reported for Iowa. In Iowa, birds nesting in row crops appeared to represent sink populations, failing to produce enough young to replace themselves (Best and Rodenhouse 1984; Rodenhouse and Best 1983, 1994).

In Wyoming, mowing occurred in sagebrush habitat and was designed to reduce shrub growth and promote herbaceous plant growth. Abundance of the Vesper Sparrow increased by 5.38% for every incremental 10% increase in the amount of the point-count circle that was mowed (Carlisle et al. 2018).

Grazing alters vegetation structure and composition and has the potential to affect habitat suitability. In British Columbia, grazing resulted in significant changes in plant community structure and species composition, but had no effect on Vesper Sparrow abundance. In a second study, grazing converted habitats of robust grasses and shrubs to less robust, mat-forming grasses and forbs, and vegetation height was reduced. Nest sites had greater cover of late-seral bunched and tufted grass species, typical of ungrazed areas, than random sites. Nest survival rates were greater when the nest site had taller vegetation. Nests in shorter grasses had a higher risk of predation. Grazing reduced both the availability of suitable nesting habitat and nesting success (Harrison et al. 2010, 2011). In western native pastures, the frequency of occurrence of the Vesper Sparrow is unaffected by grazing intensity (Dechant et al. 2002a). In Illinois, moderate grazing that left 20-40% of vegetation cover taller than 25 cm was beneficial (Swanson 1996).

Responses to fire by the Vesper Sparrow depend upon the habitat and intensity of the fire. Forest fires are usually beneficial because they may create temporary habitat where none previously existed. Fire suppression may have had limited effects on it in Ontario because the bulk of its population occurs south of the areas that are most vulnerable to forest fires. Fires in shrubby areas may decrease habitat suitability, particularly if the fire is intense and kills shrubs. In shrubsteppe vegetation in Washington, fire converts sagebrush habitat to annual grasslands dominated by the nonnative downy brome. Historically, fires there were probably infrequent, occurring every 50-100 years, patchy, and uneven, resulting in a mosaic of sagebrush and native grasses in different stages of succession. Now fires are frequent, severe, and large, eliminating shrubsteppe vegetation. A fire in 2000 caused more than 90% mortality of shrubs, grasses, and forbs over 85% of the area and only 15% of the area burned in a mosaic pattern. Abundance of the Vesper Sparrow declined in the 2 years following fire, increased in the following 3 years until it approximately reached prefire levels, then declined in the final 2 years of the study (Earnst et al. 2009). Fires in grasslands tend to be beneficial because they reduce the litter depth and eliminate thatch from previous years' growths, making the habitat more suitable. After a fire in native fescue grassland in Saskatchewan, the Vesper Sparrow was the only species that exhibited a preference for burned over unburned prairie in the first year. In Idaho, it was absent from control areas, prior to the burn on the treatment plot and 1-2 years postburn, but appeared 3-7 years postburn. Colonization of grassland areas shortly after a burn or increases in abundance have been observed in other areas (Dechant et al. 2002a; Jones and Cornely 2020; Pylypec 1991; Swanson 1996). In Saskatchewan, its density in mixed-grass prairie was higher 1 year postburn and lower 2-3 years postburn than in an unburned mixed-grass site. In Wisconsin, it appeared on a restored prairie 3 years after it was burned. In another area, it was most abundant 2 years postburn and declined 3-5 years postburn. In Iowa, it was more abundant in burned than unburned roadsides. In Illinois, it was most abundant the first growing season after a burn, absent the second year, and uncommon the third year (Dechant et al. 2002a). In South Dakota, it occurred only on unburned grasslands and avoided burned areas (Swanson 1996). The effects of fire appear to be short lived and are probably initially beneficial by reducing litter depth, dead

vegetation from previous years, and possibly vegetation height and density. Intense fires could potentially kill shrubs and make habitat less suitable.

Some studies examined the effects of edges, vegetation structure, and other factors on nest success. In North Dakota, distance from edge was the most important factor determining nest survival. Percent coverage by tall shrubs was the second-most important factor; percent coverage by Kentucky bluegrass was also important. Nest survival was highest near aspen woodland edges and declined as the distance from woodland increased. Survival increased with increasing coverage by Kentucky bluegrass and tall shrubs. Nest survival was greatest for the best concealed nests. The thirteen-lined ground squirrel was the dominant predator and was most abundant in prairie interior (Grant et al. 2006). Nests near edge in Iowa croplands were significantly less likely to be successful than those distant from edge. Nests destroyed by predators averaged 13.5 m from unproductive areas for crops compared with 25.5 m for successful nests. Few predators search croplands for prey so nests near unproductive areas were more vulnerable to predation. No relationship was found between nest concealment and nest success. No territory characteristics were significantly related to nesting success but the number of washes and amount of crop residue were almost significant. Seventy-five percent of territories without a successful nest did not contain a wash and territories with 2 successful nests had a mean of 1.1 washes (Best and Rodenhouse 1984; Rodenhouse and Best 1983). In Alberta, nest survival was unaffected by temperature or precipitation, and the relationship between nest visibility and survival was highly variable (Ludlow et al. 2014). At West Virginia reclaimed mine sites, percent litter cover was 63.2% at successful nests and 53.7% at unsuccessful nests, percent bare ground was 32.9% at successful nests and 44.8% at unsuccessful nests, and vertical density was 15.3% at successful nests and 11.6% at unsuccessful nests. These characteristics indicate better concealment for successful nests that should be more resistant to avian predation. The main predators were snakes and birds, and snake predation rates appear to be constant in differing vegetation communities. Creating temporary grasslands surrounded by woodlands and pastures tends to concentrate predators and result in sink populations (Wray and Whitmore 1979; Wray et al. 1982). Nest success in relation to edge and vegetative characteristics is variable depending upon the types of predators that are present and where they are most abundant or most likely to search for prey.

Studies have been conducted on the effects of gas and oil development facilities and trails on abundance of the Vesper Sparrow. In Saskatchewan, old oil and gas wells are point sources for nonnative plant species such as crested wheat grass and yellow sweet clover. Nest locations relative to wells did not differ from random but the proportion of nests within 100 m of trails was higher than expected by random. The number of young fledged per nest was higher close to trails but did not vary with distance to wells or gravel roads. It appeared to select nest sites near trails and fledged more young from these nests (Ludlow et al. 2015). In Alberta and Saskatchewan, Sutter et al. (2016) studied the effects of active pipeline construction on the Vesper Sparrow. They compared plots close to the pipeline with those 600 m from it. Nests were evenly distributed in distant plots. In close plots, the number of nests within 50 m of the pipeline was higher than expected. Differences in vegetation near the pipeline may have been an important factor in nest-site selection. Daily nest survival declined slightly with increased exposure to pipeline activity; birds nesting near the pipeline tended to fledge fewer young. In Alberta, its abundance declined with increasing proximity to roads

and as far as 236 m from gas wells. Clutch size decreased with increasing road proximity and nesting success declined as the density of gas wells increased. Noise did not appear to be a factor because results were similar at quiet gas wells and noisy oil wells (Daniel and Koper 2019). In Saskatchewan, Sutter et al. (2000) compared abundance of the Vesper Sparrow along roads and trails. Roads had ditches and often fences. Trails consisted of a single pair of tire ruts through homogeneous habitat. It was significantly more abundant along roads, probably due to the dense grassy vegetation in roadsides and presence of fences that provided elevated song perches. In Colorado, it was significantly more abundant in mixed-grass prairies without trails than along recreational trails (Dechant et al. 2002a).

In North Dakota, the Vesper Sparrow appeared to be unaffected by wind facilities. It demonstrated no avoidance of wind turbines (Shaffer and Buhl 2015).

Declines in eastern populations have been attributed to pesticides. It appears to be unaffected by chemicals used to control grasshoppers (Jones and Cornely 2020). In Ontario cornfields, there was no difference in its abundance before and after treatment of corn rootworm with fonofos and terbufos, or between treated and control fields (Dechant et al. 2002a)

Weather is usually not a major limiting factor except in years of prolonged periods of rain or thunderstorms. This may result in nestlings dying of exposure. It can also affect the timing of agricultural activities which in turn can affect nesting success (Jones and Cornely 2020; Perritt and Best 1989). In Wyoming, all nests were abandoned when a rain storm in the second week of June was followed by 10-15 cm of snow (Schroeder 1972). During extremely hot weather and drought in North Dakota, females abandoned their nests during the incubation period. Populations declined in drought years and increased slightly at the end of the drought but remained 52% lower than prior to the drought (Jones and Cornely 2020). One study correlated the abundance of the Vesper Sparrow for 1980-2005 with the number of ponds present in May and a monthly index of soil moisture. There were no significant relationships between these parameters and its abundance (Niemuth et al. 2008). In South and North Dakota, Montana, and Wyoming, the Vesper Sparrow was significantly affected by weather. It responded negatively to the amount of precipitation received in both the current and previous years (Gorzo et al. 2016).

Dechant et al. (2002a) considered the keys to management of the Vesper Sparrow to be providing areas of dry sparse vegetation or edge habitat between forests and fields and providing elevated song perches. Specific recommendations included burning or mowing roadsides every 3-5 years to maintain vegetation quality, mowing only in early spring or late summer, delaying spraying and mowing in CRP lands to avoid the peak nesting period, leaving more corn residue in fields, and reducing the number of mechanical field operations in crop fields.

Cumming et al. (2014) examined the relationships between climate and Vesper Sparrow distribution and abundance in Canada. The main split between good and poor habitat was vegetation class, with higher abundance in mixed forest and cropland ecosystems. Within good habitat, predicted abundance was higher where the standard deviation around the August maximum temperature was less than 2.4°C. Within poorer habitat, highest abundance was found in areas with a May leaf-area index of less than 13.5 and mean net annual primary productivity less than 0.33. They interpreted this as a description of the open vegetated areas that it prefers. Price

(2004) concluded that the breeding range of the Vesper Sparrow might contract in southern Ontario if the average summer temperature increased by 2°C. In Alberta, Nixon et al. (2016) predicted the response of the Vesper Sparrow to climate change. The area of suitable climate within the province was projected to increase by less than 10% by the 2050s and by about 20% by the 2080s. The projected change in the amount of suitable habitat was 0% in the 2050s but by the 2080s it was projected to decrease by almost 30%.

Status

Prior to European settlement and the subsequent deforestation, the Vesper Sparrow was probably present but rare in the east. The open xeric sites it inhabited were probably maintained by fires, First Nations, erosion of loose sands by wind on sand dunes, diseases, insect damage, flooding, and beaver activity. Native prairies and savannahs probably supported some populations in Ontario. It responded very favourably to forest clearing and the establishment of farmland. By 1900, it was common throughout the eastern portion of its range and was one of the characteristic species where forests had been cleared. Declines as a result of agricultural intensification were apparent as early as the 1930s. Populations continue to decrease due to continued intensification of agricultural lands, natural succession, and conversion of farm land to urban areas. Agriculture is the main reason why the Vesper Sparrow is a common breeding bird in the province, but is also the main reason why populations are declining (Askins et al. 2007; Best and Rodenhouse 1984; Jones and Cornely 2020; Swanson 1986).

McIlwraith (1894) considered the Vesper Sparrow a common summer resident in southern Ontario, and it was found in essentially every grass field in the Hamilton area in 1866. It was still abundant in the Hamilton area in the 1930s and 1940s, but has since declined (Curry 2006). In Elgin County, it was a common summer resident in 1891 and 1954, but an increasingly uncommon breeder in 2000 (Lancaster et al. 2004). In the Kingston area, it was very common in 1909, fairly common in 1973, common in 1989, and common but declining in 2008 (Weir 2008). In Muskoka and Parry Sound districts, it was one of the most common summer residents in 1901 and was still abundant in southwestern Parry Sound District and northeastern Muskoka District in 1928. As late as 1948, it outnumbered the Savannah Sparrow as a breeding species. By 1980, it was only fairly common (Mills 1981). Sheppard et al. (1936) considered it abundant in Niagara Region. Black and Roy (2010) considered it a rare breeder in Niagara Region. Baillie and Harrington (1937) considered it a common breeding species from the southern boundary of the province north to southern Kenora District and Moose Factory. It was uncommon in most of northern Ontario, possibly due to the scarcity of suitable habitat, but its range appeared to extend westward to Lake of the Woods. Smith (1957) considered it uncommon in the Clay Belt portion of the Boreal Forest Region, but common around Timmins. In the Shield portion of the Great Lakes–St. Lawrence Forest Region, it was uncommon in jack pine stands near Gogama (James and Peck 1995a). In Algonquin Park, it is a rare breeder where it has been declining since about 1990, probably due to natural succession (Tozer 2012). The first atlas showed that the range of the Vesper Sparrow included all of southern Ontario north to the Kenora area in the west and Lake Abitibi in the east. No breeding records were obtained from the Moosonee area. It was absent in the urban area of Toronto, the heavily forested landscapes of Algonquin Park, southwest of Lake Nipissing, and in the boreal forest. It was uncommon in the province (Rising in Cadman et al. 1987). James (1991) considered the Vesper

Sparrow a common summer resident north to southern Georgian Bay and Ottawa, rare north to Sioux Lookout and Timmins, and formerly occasional to Moosonee.

The second atlas revealed no change in the overall distribution of the Vesper Sparrow. A breeding observation was obtained in northern Ontario in the Boreal Forest Region near North Caribou Lake. No sightings occurred in the Moosonee area. Its probability of observation declined province-wide and in every region where it occurred, except for the Boreal Forest Region where it is rare. Declines were greatest south of the Shield and in the southern portion of the Shield. Off-Shield losses were probably due to agricultural intensification and urbanization; on-Shield declines were probably related to natural succession. It was most abundant south of the Shield. Highest abundance occurred in the agricultural areas of southwestern Ontario and between the north shore of Lake Ontario and the southern edge of the Shield from Port Hope to Napanee (Rising in Cadman et al. 2007).

Breeding Bird Survey results indicate that the Vesper Sparrow decreased at annual rates of 2.37% in Canada and 3.71% in Ontario 1970-2021. It decreased annually at rates of 2.65% in Canada and 3.48% in Ontario 2011-21. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young are incapable of flight when they leave the nest but are quick and agile at moving through the vegetation. After leaving the nest, fledglings remain quiet and hidden in the vegetation. They remain semidependent upon the adults until they are 30-35 days old, usually remaining in the vicinity of the territory during this period. If the female initiates a second brood, the male cares for the fledglings from the first brood (Berger in Austin 1968; Jones and Cornely 2020).

In Oregon at 2 sites, the fledgling survival rates were 47.1-75.0% and 52.0-78.3%, the highest known rates for a grassland species. Fledglings remained in the natal areas an average of 70.4 days and 82.4 days, with an overall average of 78.1 days; 83.8% of 105 fledglings remained on site more than 50 days. Six juveniles (3.1%) dispersed either short distances of 3 km or longer distances of 14 km. The high persistence may be because juveniles undergo a preformative moult that usually occurs on the natal site. Nearly all juveniles that survived the first 2 weeks spent 2-4 months at the natal site (Altman et al. 2024).

Once they are independent, juveniles and adults congregate together, often in the company of other grassland sparrows. In Algonquin Park, approximately 15 were seen on 11 July and 50 on 3 August on an abandoned airfield. In other areas, flocks have been observed congregating along roadsides and fencerows and in weedy and shrubby fields. Birds remain in flocks until autumn migration. Not all families join these flocks. Some late-nesting birds and their families continue to frequent pastures and fields in the vicinity of the breeding area until autumn migration (Judd 1901; Leighton et al. 2002; Tozer 2012).

MIGRATION

The Vesper Sparrow migrates opportunistically, especially in autumn, in response to food availability. In the east, the normal northern extent of the wintering area is South Carolina, Georgia, Alabama, Mississippi, and Oklahoma. It is a nocturnal migrant that moves in small groups, although flocks of

25-300 have been recorded in spring and 50-100 in autumn. Flocks arrive in waves, sometimes in the company of Savannah Sparrows (Jones and Cornely 2020).

In Iowa, females arrived within a week of the first male (Rodenhouse and Best 1983). In southern Ontario, migrants arrive in early April or very late March, with the peak of migration in mid-April and some birds still migrating until the end of April. Migrants arrive in the southern Shield in mid- or late April. Autumn migration occurs throughout September and early October, with peak movements in early October. Some persist in the province into November and rarely into early December (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

During migration, the Vesper Sparrow inhabits fields and habitats similar those used during the breeding season. In Algonquin Park, most spring migrants are observed at an old airfield, but it also occasionally occurs on road margins, hydro cuts, at old sawmill sites, and in other clearings (Tozer 2012). During spring migration in Ohio, it inhabited better-drained upland fields and pastures. It was most abundant in sparsely vegetated fields and in close-cropped pastures and meadows. It never occurred in large flocks in spring, with a maximum of 15 in well-organized flocks, and these occurred only early in the season. During the last half of migration, individuals became scattered over fields and pastures (Berger in Austin 1968). In British Columbia, it occurs in open grassy or weedy areas of many types during migration. These include overgrazed pastures and ranges, stubble fields, pastures, prairies, airports, openings in aspen parkland, south- and west-facing unforested or sparsely forested hillsides, road margins, clear-cuts, regenerating burns, dry agricultural fields, playgrounds, sand spits, and dunes (Campbell et al. 2001). Jones and Cornely (2020) described the migration habitat of the Vesper Sparrow as pastures, barren to overgrown fields, grassy or weedy ditches and fencerows, and weedy areas bordering cultivated fields, roadsides, and hedgerows.

The Vesper Sparrow is occasionally killed at communication towers during migration (Jones and Cornely 2020).

In Arizona, both native and nonnative grasslands were burned, reducing the amount of shrubs, eliminating litter, and increasing herbaceous cover. Grass cover was not changed significantly, especially in nonnative grasslands where an exotic love grass still averaged about 90% coverage. The Vesper Sparrow was significantly more abundant during autumn migration in burned portions of both types of grasslands for 2 years postfire, but numbers reverted to prefire levels 3 and 4 years postfire (Bock and Bock 1992).

James (1991) considered the Vesper Sparrow a common migrant in the province. Daily counts seldom exceed 100 birds (Curry 2006; Lancaster et al. 2004; Tozer 2012; Weir 2008).

Captures of migrant Vesper Sparrows at Long Point Bird Observatory declined at a nonsignificant rate of 1.9% per year 1961-88. Trends by period were: 1961-70, –8.2%; no data for 1970-79; and +21.9% 1979-88 (Hussell et al. 1992).

WINTER

During winter, the Vesper Sparrow frequents areas in the east that have an average minimum January temperature of at least –1°C. Within this area, it inhabits patches of cleared land and openings within forests. Abundant populations are restricted primarily to areas with stunted and sparse vegetation (Root 1988).

James (1991) considered the Vesper Sparrow rare and occasional in winter north to London and Kingston. Birds wintering in Ontario are well outside their normal winter range and should be considered extralimital. It is also uncertain if wintering birds successfully overwinter, if they succumb to severe weather, or move further south if weather conditions deteriorate. Limited data suggest that wintering birds are much less frequent than they were formerly. It is probable that the Vesper Sparrow is absent in Ontario in some winters.

LeConte's Sparrow

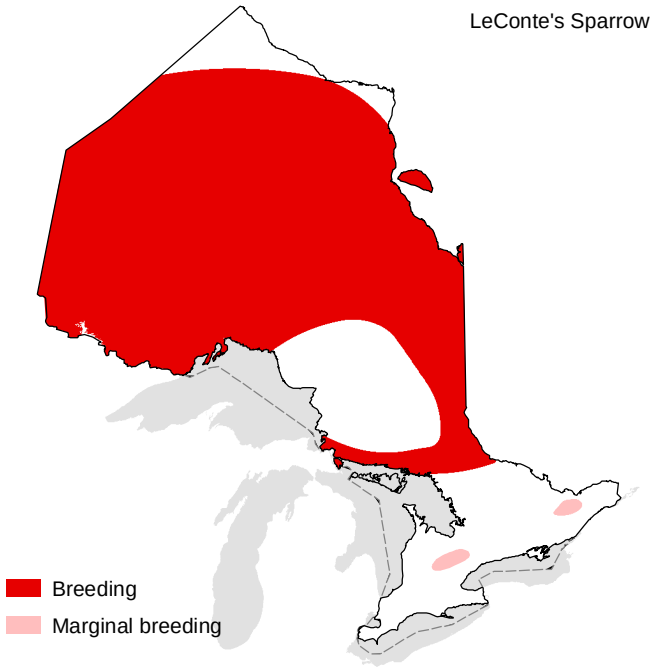
Ammospiza leconteii

BREEDING SEASON

Habitat Requirements

One Ontario LeConte's Sparrow nest was on damp ground at the edge of a swamp and another was on a grassy dyke between stands of wild rice. Near Moosonee, it nested in a graminoid-dominated tidal marsh. In Rainy River District, it nested in a wet meadow bordering a lake. Characteristic nesting habitat appears to be wet areas or their edges (Peck and James 1987, 1998b).

In the Hudson Bay Lowland, 2 nests along the James Bay coast north of the Swan River were in extensive sedge fens (Coady in Cadman et al. 2007). Near Hearst, the LeConte's Sparrow nested in a 5-year-old clear-cut in lowland coniferous forest. There was extensive growth by grey alder in low-lying areas and trembling aspen and beaked hazel on better-drained ridges. The total vegetative cover was 76%: 36% ground cover, 19% low shrub cover, 5% tall shrub cover, and 16% tree cover by balsam fir, trembling aspen, white birch, and white spruce (Welsh and Fillman 1980). Near Wawa, it nested in a sphagnum bog with a few stunted black spruces with areas of nutrient-poor open fen and meadow marsh. It inhabited about 2 ha of the fen, which was bordered by alder thickets with a



few dead balsam poplars and a mixed forest dominated by trembling aspen and white birch. The occupied area had a ground cover of sphagnum moss and was dominated by few-seeded sedge and awl-fruited sedge; Canada bluejoint was also present. The meadow marsh portion of the wetland was flooded to a depth of 0.5 m in late May but the water gradually receded by late June. This area remained damp but without standing water (Patrikeev 2006). One was seen in June in Algonquin Park at the edge of a beaver meadow bordered by alders. This may have been a breeding bird (Tozer 2012). Beaver meadows have the potential to provide suitable habitat throughout the heavily forested Shield.

South of the Shield, Villard and Bracken (1989) reported breeding by the LeConte's Sparrow south of Ottawa. The landscape was agricultural with scattered woodlots. The nest was in a vernally inundated ditch separating 2 cultivated fields. The ditch was 135 m long, 2.5 m wide, and 1 m deep. The adults were seen most frequently around a clump of reed canary grass. The ditch was densely vegetated with tufted vetch, Canada bluegrass, smooth brome, pussy willow, meadow willow, and dark green bulrush. Prior to taking up residence in the ditch, the pair was regularly observed in an alfalfa field, but moved to the ditch after the field was mowed. For at least a decade, LeConte's Sparrows nested in the grassy flats of Holland Marsh, but abandoned this area in the 1940s when it was converted to market gardening. After this, it persisted for a few years in a marsh north of Bradford until it was cultivated (Devitt 1967). In 1985, breeding was confirmed south of Luther Marsh (Sandilands and Campbell in Cadman et al. 1987). The site was an idle agricultural field dominated by rank growth of reed canary grass and smooth brome (personal observation).

Throughout Canada, the LeConte's Sparrow nests in freshwater and salt-water marshes, moist meadows and meadow marshes that are often adjacent to moister wetlands, open fens, prairies and other natural grasslands, idle agricultural lands, and old fields dominated by grasslands. Key habitat components include tall dense grasses and sedges with a deep litter layer. It is not a true grassland species because it also nests regularly in graminoid marshes and fens. In Quebec, it occurs in rather wet habitats such as large marshes of sedges and grasses, including salt-water marshes dominated by cordgrass. It frequents broad open areas thickly carpeted with dead grass and rank herbaceous growth. There is usually a scattering of low shrubs or tall herbaceous plants or grasses such as reed canary grass present. These meadows may be nearly pure sedge communities or mixed communities of grasses and sedges. It also nests in pastures, dense wet meadows, peatlands with abundant grasses and sedges, and fallow or recently abandoned agricultural land where shrub growth is not overly advanced. Although it often occurs in wet habitats, it also inhabits dry areas

(Boulva and Browne 1965; Létourneau and Aubry in Gauthier and Aubry 1996). Erskine (1977) reported that it was associated with fens in the Boreal Forest Region. In the Prairie Provinces, it was in a guild of birds that nested in wet marshy fens or young aspen stands less than 9 years old. It was associated with wetter habitats (Kirk et al. 1996). In Saskatchewan, Hartley (1994) reported 1.34 birds per plot with 100% occurrence in Dense Nesting Cover (DNC), 0.46 birds per plot with 94.4% occurrence in planted native grasses, and 0 in wheat. Near Saskatoon, it was associated with damp areas adjacent to lakes and sloughs where the vegetation was lush. More rarely, it bred in alfalfa fields (Leighton et al. 2002). It bred in native and tame DNC 3-5 years old, including fields planted to intermediate and tall wheat grass, alfalfa, and sweet clover. It occurred in low nesting cover of Kentucky bluegrass and red fescue. In 1 area of Saskatchewan, it was present only in organic farmland and upland DNC and was more abundant in the latter habitat. It was more abundant in wetlands in organic farmlands than wetlands in conventional farmland or DNC. Its density was unaffected by the amount of cropland or wetland within 1.6 km (Dechant et al. 2002i). In Alberta, Tittler et al. (2001) considered it a species of clear-cuts rather than one of unharvested forests. It colonized clear-cuts by the third year after harvest and decreased with increasing basal area of trees. It occurred more frequently in tame than native pastures. In tame pastures, it preferred high grass biomass. In native pastures, it preferred low to moderate cover diversity and moderate to tall grass of uniform height. It was rare or absent in DNC less than 2 years old, increased in abundance through the fifth year, and decreased thereafter (Dechant et al. 2002i). In British Columbia, it nests in patches of sedges emerging from flooded lands. These habitats often contain scattered clumps of low-growing willows. It also inhabits drier sites with grasses, sedges, and willows. One study found that it occupied damp sites ranging from shrub carrs to fields where patches of tall black spruce were prevalent. Sedge meadow–shrub carr edges were the most commonly used habitat. One occupied location was dominated by creeping bentgrass close to a shrub carr complex. Preferred habitat had a plant association that included beaked sedge, horsetails, scrub birch, Labrador tea, sphagnum moss, and willows. It has nested in damp short-grass margins of grain fields, wet sedge verges of black spruce–tamarack muskeg, tall grasses at sewage lagoons, and patches of Labrador tea along shores of muskeg ponds (Campbell et al. 2001). In the Yukon, it nested in open wet meadows with dense and tall (0.5 m) grasses and sedges with scattered shrubs 0.5-1 m tall; the shrubs were used as singing perches. Moisture conditions at nesting sites ranged from wet to standing water (Sinclair et al. 2003).

In the United States, the LeConte's Sparrow nests predominantly in meadows adjacent to marshes, wet or flooded grass and sedge meadows, fallow fields, hayfields, undisturbed pastures, tallgrass prairies, planted cover including Conservation Reserve Program (CRP) lands, and hummocky alkaline fens. Many territories contain scattered low shrubs but others are devoid of shrubs. In territories within or near marshes, common plant species may include soft-stemmed bulrush, willow, prairie sedge, spikerushes, water parsnip, wild mint, and bugleweed. In grassland habitats, it may be associated with cordgrass, river grass, common reed, squirrel-tail grass, smooth brome, Kentucky bluegrass, quack grass, creeping bentgrass, barnyard grass, timothy, reed canary grass, and wheat grass. It occasionally nests in hayfields dominated by timothy and alfalfa and rarely nests in small-grain fields. It occurs most often in moist or wet habitat but also nests in drier areas

(Dechant et al. 2002i; Igl and Johnson 1995, 1999; Lowther 2020b; Murray 1969; Peabody 1901; Walkinshaw 1937; Walkinshaw in Austin 1968; Winter et al. 2005).

Once shrub coverage becomes too dense or taller than about 1 m, habitat becomes unsuitable for the LeConte's Sparrow. In North Dakota, its abundance decreased with increasing tree cover. Its probability of occurrence was 50% when there was 0% woodland cover within a 500-m radius. Its probability of occurrence decreased to 30% at 20% tree cover and to 0% at 60% tree cover (Grant et al. 2004). It tended to avoid areas with extensive woody vegetation (Johnson and Igl 2001). In Minnesota, Winter et al. (2005) found no evidence that it avoided trees when situating its nest. Nesting success increased slightly with increasing distance to trees but percent coverage by trees and shrubs did not affect nest success.

Some studies compared habitat where the LeConte's Sparrow is present to unoccupied sites, or nest sites to the remainder of the territory. In North Dakota where it was present, there was significantly deeper litter (4.3 cm compared with 2.8 cm), taller vegetation (55 cm compared with 51 cm), more smooth brome coverage (22.1% compared with 14.1%), more legume coverage (4.9% compared with 0.2%), less aspen coverage within 100 m (2.1% compared with 6.3%), less native herbaceous vegetation coverage (34.2% compared with 43.9%), and less aspen within 500 m than where it was absent. Its occurrence was greater in areas with taller, lusher vegetation dominated by cool-season nonnative plants such as smooth brome, quack grass, and sweet clover. There were 4 vegetation parameters that did not differ between occupied and unoccupied areas. Mean values for these parameters in occupied areas included 33.7% live vegetation, 14.9% shrubs shorter than 1 m, 2.4% taller shrubs, and 18.9% bluegrass coverage (Grant et al. 2004). In North Dakota in a wet year, it occurred throughout grassy floodplain habitat except in the wetland areas. Its population was densest in cordgrass, less dense in the sparser cover afforded by squirrel-tail grass, and rare in smooth brome in the dry upland habitat. In a dry year, it was confined to the cordgrass habitat. Both cordgrass and river grass provided thicker cover for nest sites. Both grasses are tall and grow in dense stands and most dead stems fall and form a thick mat of litter. Squirrel-tail grass is sparser and shorter and remains upright after drying. The largest patch of squirrel-tail grass was the driest area and was avoided. It typically sang from the concealment of clumps of cordgrass but occasionally from the top of a dock plant. Only 3 used 1-m tall stakes placed throughout the study area, and not until mid-July. Both the LeConte's and Nelson's sparrows nested at this site and both were most numerous in cordgrass, with the LeConte's Sparrow occupying some drier habitats and the Nelson's Sparrow occupying some wetter habitats. The LeConte's Sparrow preferred drier areas than the Nelson's Sparrow. Most areas occupied by the LeConte's Sparrow are flat and may be subject to flooding (Murray 1969). In fields where there is a slight slope, it tends to prefer higher areas (Lowther 2020b; Winter et al. 2005). In Minnesota, it spent most of its time in dense dead grass except in the morning and at sunset when it fed where living grass was sparse. It nested where dead grass was thickest, in lowland sections of prairie with luxuriant growths of denser grasses and vetch (Peabody 1901). In Minnesota, nest sites had significantly less bare ground (0.5% compared with 3.3%), more litter coverage (45.3% compared with 38.7%), less woody cover (0.2% compared with 1.4%), shorter vegetation (37.3 cm compared with 46.8 cm), and lower visual obstruction (19 cm compared with 26 cm) than random areas within the territory. There were 3 parameters that were not significantly different for nests and the remainder of the territory. Mean values for these characteristics at nests

included 37.6% grass cover, 15.6% forb cover, and 6.1 cm litter depth. Compared with random sites, nests were in areas of less bare ground and woody vegetation with higher litter cover. It chose nest sites surrounded by shorter and less dense vegetation. Its density decreased with either high or low amounts of bare ground, increased with taller vegetation at 1 site, and varied among years. Moderate ground cover was probably beneficial because it provided a balance between foraging efficiency and cover from predators. Site-specific vegetation parameters were more important in predicting its density than factors such as patch size and proportion of tree cover in the landscape (Winter et al. 2005). In North Dakota, it was associated with a high amount of grass cover, especially broad-leaved introduced species (Dechant et al. 2002i).

There is some uncertainty as to whether the LeConte's Sparrow exhibits area sensitivity. In Montana, North and South Dakota, and Minnesota, results were inconclusive because it occurred in only 4 of the studied regions and was common enough to analyze results at only 1 site. It showed no evidence of area dependency overall with 2 positive and 4 negative coefficients. Patch size was a positive influence on frequency of occurrence at 1 site, but results were not significant. Johnson and Igl (2001) did not identify any minimum patch-size requirements. Winter et al. (2005) found no evidence of area sensitivity in Minnesota. The mean patch size in their study area may have been too large to detect area sensitivity. Patch size had no influence on nesting success. South of Ottawa, Villard and Bracken (1989) confirmed nesting in a ditch that was only 0.03 ha in area. This strongly suggests that it is not area sensitive, but may just be an example of site tenacity. The pair was originally associated with an alfalfa field of unspecified size. Once the field was mowed the sparrows moved to the ditch. Near Wawa, 2-3 pairs nested in a 5.8-ha wetland and the fen portion of it that they inhabited was only 2 ha (Patrikeev 2006). The existing evidence suggests that the LeConte's Sparrow can adapt and nest in very small patches but more research on its area sensitivity is required.

Ontario nests were either on the ground or 5-17 cm above it, mostly in tall grasses or sedges. One nest was underneath a flattened clump of rushes, one was supported by Canada bluegrass stems, one was well hidden under and inside a clump of dried graminoids and could not be seen from above, one was under an old mouse nest, and one was attached to dried and living sedge stems and a small leatherleaf under loose cover of sedges and grasses (Patrikeev 2006; Peck and James 1987, 1998b).

In dry habitats, the nest is usually on the ground and may be sunk into it. In damp areas, nests are as high as 20 cm above the substrate. In North Dakota, the maximum height of nests was 5 cm. In Minnesota, mean nest height was 2.6 cm; 1 nest was 20 cm from the ground in another Minnesota study. Although 1 nest was scantily concealed, most are well hidden within and under dead plant material. In Minnesota, 96% of 44 nests were within dead plant material; average coverage by surrounding vegetation was 86.9%. The surrounding vegetation is typically grasses or sedges and less frequently rushes or spikerushes (Campbell et al. 2001; Lowther 2020b; Murray 1969; Peabody 1901; Walkinshaw 1937; Walkinshaw in Austin 1968; Winter et al. 2005).

Breeding territories may be clumped leading some authors to conclude that the LeConte's Sparrow is loosely colonial. Apparent clumping of territories in some areas is probably a result of habitat distribution. Males defend territories and all activities by both sexes occur within the territory.

Territories rarely overlap and, when they do, this occurs at different times. Once territorial boundaries are established, they remain fairly stable throughout the season. Any boundary changes are small and typically occur when a neighbouring male disappears. If he is not replaced, some of his territory may be absorbed by the neighbour. If the disappearing male is replaced, there may be slight modifications to the boundary as a result of interactions with the newcomer. In North Dakota, territories were 0.1-0.5 ha (average 0.2 ha). In 1 Minnesota study, 4 birds had territories of approximately 0.2 ha and, in another Minnesota study, mean minimum territory size was 0.47 ha (Lowther 2020b; Murray 1969).

No information is available on natal philopatry. Very few nestlings or fledglings have been banded and no recoveries have been made. It is probable that natal philopatry rates are very low because adults exhibit low site fidelity.

Although adult site fidelity rates are low, few studies banded many birds. In North Dakota, 1 of 7 males (14.3%) returned in the following year and 0 of 6 females returned. In Minnesota, 1 of 93 adults (1.1%) returned, a female (Murray 1969; Winter et al. 2005).

Limiting Factors

Eggs have been found in Ontario nests in the first 3 weeks of June (Peck and James 1987), and probably occur into the first week of July based upon the timing of young in a Wawa nest (Patrikeev 2006). No information is available on how long it takes to build the nest, the amount of time that elapses between nest completion and initiation of egg laying, the egg-laying interval, or when incubation begins relative to the completion of the clutch. The incubation period is probably 12-13 days, but this is uncertain and possibly based upon a single nest. No information is available on the nestling period. One Wawa nest with nestlings was checked on 2 dates and the nestlings were still in the nest when they were at least 7 days old (Patrikeev 2006; Walkinshaw 1937; Walkinshaw in Austin 1968).

Double brooding has not been confirmed and egg dates from most locations suggest that the LeConte's Sparrow raises only a single brood. Renesting has been confirmed after nest loss. All Ontario nests contained 4 or 5 eggs (mean 4.38 eggs). Clutches of 4-5 eggs have been reported throughout its range, with 4 eggs most frequent. In Minnesota, the mean clutch size was 4.51 eggs. Clutch size declined significantly with the season at a rate of 0.03 egg per day (Lowther 2020b; Patrikeev 2006; Peck and James 1987; Walkinshaw in Austin 1968; Winter et al. 2005).

The LeConte's Sparrow is probably capable of breeding when it is 1 year old and breeds annually thereafter. No information is available on the mating system but it is probably predominantly monogamous (Lowther 2020b). Near Wawa, Patrikeev (2006) found 2 nests 150 m apart and thought that they might belong to the same male which would be indicative of polygynous nesting.

Near Wawa, young were fed small green caterpillars, moths, spiders, a sphinx moth caterpillar, and 2 grasshopper abdomens (Patrikeev 2006). The only diet information for adults is based upon the contents of 15 stomachs collected in Missouri in spring and autumn. The diet consisted of 82.9% plant material and 16.9% animal matter by volume. The vegetable matter consisted of seeds including a trace of three-seeded mercury, a trace of redtop, 0.7% bentgrass, 30.2% big and little bluestem and unidentified bluestem, a trace of sedges, 0.7% yellow stargrass, 13.2% early forget-

me-not, a trace of wood-sorrel, 2.9% panic grass, a trace of field milkwort, 16.9% yellow foxtail, 14.7% Indian grass, 2.2% prairie dropseed, a trace of low hop clover, and 0.7% unidentified material. The animal matter consisted of 3.7% spiders, a trace of insect fragments, a trace of beetle fragments, 0.7% leaf beetles, 3.7% weevils, 0.7% stink bugs, 0.7% caterpillars and moths, a trace of ants, and 7.4% leafhoppers (Easterlea 1962). Foraging typically occurs on the ground under cover of vegetation (Lowther 2020b).

The LeConte's Sparrow is an infrequent host of the Brown-headed Cowbird. The effects of parasitism on it have not been determined and it is uncertain if it is able to fledge its own young from parasitized nests. It is probable that clutch size and nest success are diminished in parasitized nests. In Ontario, 0 of 10 nests were parasitized, 0 of 36 nests in Wisconsin were parasitized, 4 of 14 nests (28.6%) were parasitized in Minnesota, 1 of 50 nests (2.0%) in Minnesota were parasitized, and 5 of 5 nests were parasitized in North Dakota (Patrikeev 2006; Peck and James 1987, 1998b; Lowther 2020b; Murray 1969; Peabody 1901; Winter et al. 2005).

It is uncertain if habitat loss is a significant limiting factor for the LeConte's Sparrow in Ontario. The threat of habitat loss in the Canadian Shield northward is low and forest management that involves clear-cutting may provide temporary habitat (Welsh and Fillman 1980). South of the Shield, the amount of suitable habitat has declined significantly since the mid-20th century, but the distribution and abundance of this sparrow within this region is not well known. The field that supported it near Luther Marsh was plowed the year after it nested (personal observation).

In some areas, it is necessary to disturb grasslands periodically to halt invasion by woody growth. Hayfields that are mowed annually are unsuitable habitat. In North Dakota, the LeConte's Sparrow was never observed in fields of squirrel-tail grass that had been mowed the previous year even after the stubble was replaced by luxuriant growth. In addition to removing the litter area, mowing can result in direct mortality of eggs or nestlings. In Saskatchewan, it preferred tame hayfields that were mowed every 3-8 years, management that produced stands of introduced broad-leaved grasses that were attractive to it. At another North Dakota site, highest densities occurred in hayfields that had been mowed 1 year previously, provided that tall grass growth was available for nesting. In a Minnesota tallgrass prairie, idling habitat for more than 1 year allowed too much litter accumulation for the habitat to be suitable. The optimum frequency of mowing is highly variable and site-specific and depends on how fast shrubs invade the habitat and how long the field takes to grow sufficiently tall grasses and accumulate enough litter to be suitable for the LeConte's Sparrow (Dechant et al. 2002i; Lowther 2020b; Murray 1969).

Grazing is another method of retarding natural succession, but it appears to be less effective. In Alberta, Manitoba, and Saskatchewan, the frequency of occurrence of the LeConte's Sparrow was higher in hayed than grazed fields. In North Dakota, it was absent both in grazed prairie and prairie that had been left idle for 5-19 years and had grown up with significant shrub coverage. In Minnesota and Wisconsin, it used both grazed and ungrazed pastures provided that adequate litter was maintained. With grazing, there is also the risk that cattle will trample or lie on nests (Dechant et al. 2002i; Renken and Dinsmore 1987). In most of southern Ontario, grazing intensity is too high to be compatible with the LeConte's Sparrow.

Prescribed burns are often used to kill woody vegetation. In western grassland habitats, the LeConte's Sparrow was absent in areas that were never burned or that were burned in the same year. In North Dakota, it was absent in areas that had not been burned for 7 to more than 80 years, and also in areas that had been burned less than a year previously. Highest density occurred 2 years after fire, declining to half that density 6 years after fire, and disappearing thereafter. In that area, it would probably benefit from a short burn cycle of 2-4 years. In Minnesota, it was absent the year of burning but present the following year after litter and vegetation growth increased (Dechant et al. 2002i; Lowther 2020b; Madden et al. 1999).

The LeConte's Sparrow is adversely affected by drought and is much more abundant in wet than dry years. In Rainy River District, counts were much higher than usual after a prolonged wet period. In Saskatchewan, it was more common in 2 wet years than during a dry year. In North Dakota CRP lands, density per km^2 in 4 drought years was 0.03 compared with 5.4, 21.2, and 21.8 in the following 3 years with above-average rainfall. It was absent in a dry year where the highest counts in the Yukon were made in the previous year. In Texas, it was most abundant during the wettest year of a 3-year study. In Minnesota, it was scarce during a dry year. In North Dakota, it responded positively to moisture and the number of ponds present in May, an indicator of moisture. It is capable of responding quickly to changing habitat quality and this adaptability results in low site-fidelity rates. Other factors that result in the drying of soils and subsequent changes in vegetation have the potential to create local conditions similar to drought. Agricultural drainage may reduce soil moisture and decrease habitat suitability, and these drier areas are more likely to be converted into active agricultural land (Coady in Cadman et al. 2007; Igl and Johnson 1995, 1999; Lowther 2020b; Niemuth et al. 2008; Peabody 1901; Sinclair et al. 2003; Villard and Bracken 1989; Winter et al. 2005).

Nixon et al. (2016) analyzed the projected response of the LeConte's Sparrow to climate change in Alberta. They predicted that its area of suitable climate would shift northward out of the province and that the area of suitable climate would decrease by 12% in the 2050s and 50% by the 2080s. They predicted that there would be a decline of suitable land cover within its area of suitable climate. The decline of suitable cover was projected to be 40% in the 2050s and 80% in the 2080s.

Status

The LeConte's Sparrow is a very unobtrusive species that is easily overlooked. Its song is similar to that of an insect and singing is often done below the vegetation so that it is seldom seen. The weak song is frequently drowned out by other birds' songs but it sings after sunset when it is more easily detected. Its call note resembles that of a small mammal and when disturbed, it tends to run on the ground under the vegetation instead of flying. When it is flushed, it flies only a short distance before diving back into the vegetation. The abundance and distribution of the LeConte's Sparrow is rather poorly known throughout its range because of these behaviours.

McIlwraith (1894) had no records of the LeConte's Sparrow for Ontario although it is probable that it was a breeding species at that time. Baillie and Harrington (1937) stated that, prior to then it was known to occur only north of latitude 48°N in Thunder Bay and Algoma districts. The population along the James and Hudson bay coasts was unknown at that time. In 1937, small colonies were discovered in Waterloo Region, near Toronto, and at Holland Marsh. The latter population persisted for over a decade until its habitat was destroyed (Devitt 1967). Murray (1969) considered the

population along the shores of James Bay and Hudson Bay to be almost disjunct, but acknowledged that it was rare in the Canadian Shield in Ontario east to eastern Quebec. The first atlas revealed that greatest concentrations occurred in the central areas of the James Bay coast and in the northwest in the Boreal Forest Region and Hudson Bay Lowland. It also occurred in Rainy River District and near Thunder Bay with very scattered records in the Shield portion of the Great Lakes–St. Lawrence Forest Region and the Boreal Forest Region. A single record of fledged young near Luther Marsh was the only breeding evidence obtained south of the Shield. The atlas represented the best available information on the LeConte's Sparrow's breeding distribution, but its range and abundance was probably underestimated. Sandilands and Campbell (in Cadman et al. 1987) concluded that it should occur in some inland blocks of the Hudson Bay Lowland and that it should be looked for in marginal farmland in the south and near the southern edge of the Canadian Shield. Villard and Bracken (1989) reported fledged young south of Ottawa. They were uncertain whether its sparse occurrence in the east was actual or an artifact of its discrete mouse-like behaviour. James (1991) considered the LeConte's Sparrow rare to locally uncommon at widely scattered locations in the north from Thunder Bay and Timmins to the north coast. He concluded that it was virtually absent in the south, but with recent records from Dundas and Wellington counties and near Sudbury. In the Hudson Bay Lowland, Wilson and McRae (1993) concluded that breeding undoubtedly occurred from Ekwan south to Moosonee.

The second atlas demonstrated that the LeConte's Sparrow was more widespread and common than was determined during the first atlas. It was observed in many more blocks in the Hudson Bay Lowland and particularly in the Boreal Forest Region and the Shield portion of the Great Lakes–St. Lawrence Forest Region. Despite this, it remained scattered in distribution, with the highest probabilities of observation occurring in the Boreal Forest Region and western portion of the Great Lakes–St. Lawrence Forest Region and the Hudson Bay Lowland. There were only 2 records south of the Shield: 1 east of Orangeville and 1 south of Ottawa. Its probability of observation increased significantly since the first atlas and more than doubled for the entire province, with significant increases in the Great Lakes–St. Lawrence Forest Region, Boreal Forest Region, and Hudson Bay Lowland. Most of the increase was attributed to an improvement in atlasser familiarity with the species. The areas of highest concentrations were in the south-central James Bay coast, western Rainy River District, and in the Dryden area. Despite the significant increase in observations between atlases, Coady (in Cadman et al. 2007) concluded that its range and abundance were still probably underestimated. Patrikeev (2006) confirmed the LeConte's Sparrow breeding near Wawa and concluded that it likely occurred in low densities throughout Algoma District wherever suitable habitat is present.

Breeding Bird Survey (BBS) results suggest that the North American population is declining. During 1966-2015, it decreased at a rate of 2.5% per year rangewide (Lowther 2020b). During 1970-2021, BBS results determined that the LeConte's Sparrow decreased in Canada at an annual rate of 2.17% and increased in Ontario 0.102% annually. During 2011-21, it decreased at annual rates of 5.65% in Canada and 8.53% in Ontario. The short-term trends were of low reliability; the long-term Canadian trend was highly reliable and the long-term Ontario trend was of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Almost nothing is known of the LeConte's Sparrow during the postfledging period. South of Ottawa, 3 fledged young were observed in a drainage ditch where nesting had occurred. They behaved in the same manner as the female, remaining in dense vegetation until they were flushed and then going back to safety a short distance away (Villard and Bracken 1989). Near Luther Marsh, young were observed in the field where the male's territory was located (Craig Campbell, personal communication). In South Dakota, Skadsen (1987) observed an adult with 2 young in dense white clover. The habitat consisted of tallgrass prairie dominated by bluestem, blazing-star, goldenrod, and sweet clover. The young ran through thick vegetation and flew 4.6-6 m when flushed before dropping back into the vegetation.

There appear to be no observations of independent juveniles. It is unknown whether they congregate into flocks and if they remain within the natal area until autumn migration is initiated.

MIGRATION

The LeConte's Sparrow is occasionally killed at towers indicating that it is a nocturnal migrant. Low counts of less than 1 bird per year per site suggest that birds migrate singly or are widely spaced. It is unknown if daytime migration occurs. In South Carolina, 82.8% of specimens collected were female. This may indicate that females winter further south than males (Lowther 2020b; Murray 1969; Walkinshaw in Austin 1968).

The LeConte's Sparrow arrives on the breeding grounds in late April or early to mid-May after a prolonged migration. Near the northern extent of its range, spring migration may be rapid with birds travelling directly to the breeding areas and seldom seen at stopover areas (Campbell et al. 2001; Murray 1969). In Elgin County, there is only a single spring record on 14 May (Lancaster et al. 2004). The 2 Hamilton spring records were on 4 and 14 May (Curry 2006). The earliest record for Simcoe County is 24 May (Devitt 1967). In the Kingston area, there are 4 spring records from 9 to 22 May (Weir 2008). In Algonquin Park, there are sightings from mid-April to late May (Tozer 2012). Near Wawa, singing males were present on 21 May and display flights were observed on 27 May (Patrikeev 2006).

The LeConte's Sparrow leaves the breeding range in September but does not reach the wintering area before early November (Murray 1969). Wilson and McRae (1993) observed one at Moosonee on 1 September. It is observed regularly in Algonquin Park in autumn, mostly from late September to mid-October (Tozer 2012). The 2 autumn records from Muskoka and Parry Sound Districts were on 29 September and 9 October (Mills 1981). One was seen at Luther Marsh on 11 September (personal observation). There are 6 autumn records for the Kingston area: 23 July, 20 August, 1 September, 3 September, 27 September, and 18 December (Weir 2008). The July and August records may be of postfledging birds rather than migrants. The latest autumn record in Simcoe County is 11 September (Devitt 1967). In the Hamilton area, there are 2 autumn records on 6 and 17 September and a winter record on 12 January (Curry 2006).

Habitat selected during migration is similar to breeding habitat. Prime migration habitat in Algonquin Park consists of fields with tall grasses, sedge meadows, drained beaver ponds, marshes, and vegetation at margins of lakes (Tozer 2012). In the Hamilton area, migrants have been observed on the shore of Dundas Marsh, in tall grasses along a creek in Oakville, and in Bronte Woods (Curry

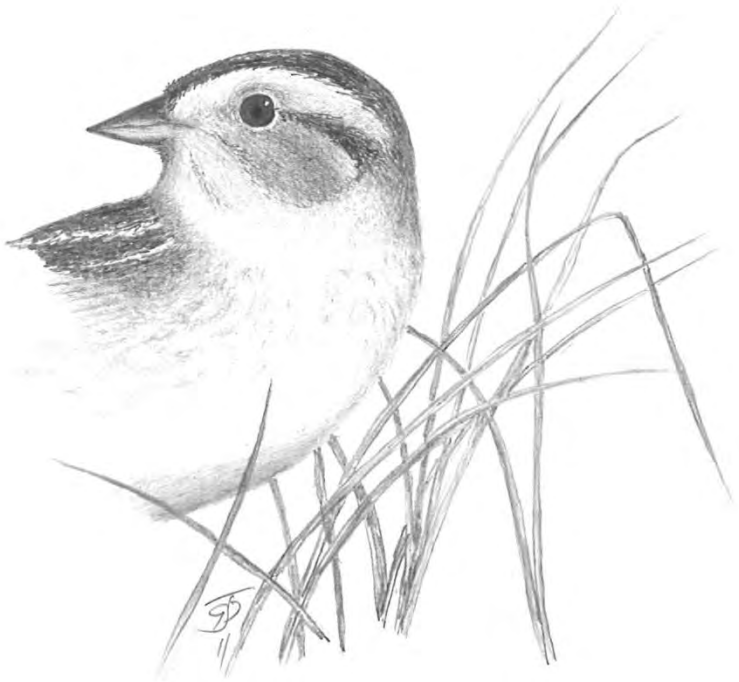
2006). An autumn migrant at Luther Marsh was in an abandoned pasture adjacent to the marsh. It was dominated by goldenrods with an understorey of dead grasses (personal observation). In British Columbia, migrants frequent wet or moist habitats adjacent to marshy lakeshores, wet meadows, patches of sedges, overgrown meadows, tall grasses adjacent to wetlands, and roadside ditches vegetated with dead grasses and willows (Campbell et al. 2001). In the United States, migrants have been observed in tall grasses of dry fields near marshes, open prairies overgrown with ironweed, occasionally on dry bluffs, fields of switchgrass, old fields and weedy areas in Kansas, large open grassy fields and low-lying wet flat areas with rank vegetation in Arkansas, grasslands and marsh edges in Iowa, and stands of cordgrass in a matrix of shorter annual forbs and spikerushes in Kansas (Lowther 2020b; Powell and Nyari 2007; Robertson et al. 2012; Walkinshaw in Austin 1968).

Although the LeConte's Sparrow is occasionally killed during migration by striking television and communication towers and other tall structures, the incidence of this is rare (Lowther 2020b).

James (1991) considered the LeConte's Sparrow a rare migrant. All regional books concur and some regions have no records of migrants. Undoubtedly many migrants pass through undetected because of its reclusive behaviour and the fact that relatively little effort is spent birding in its preferred habitat.

Nelson's Sparrow

Ammospiza nelsoni

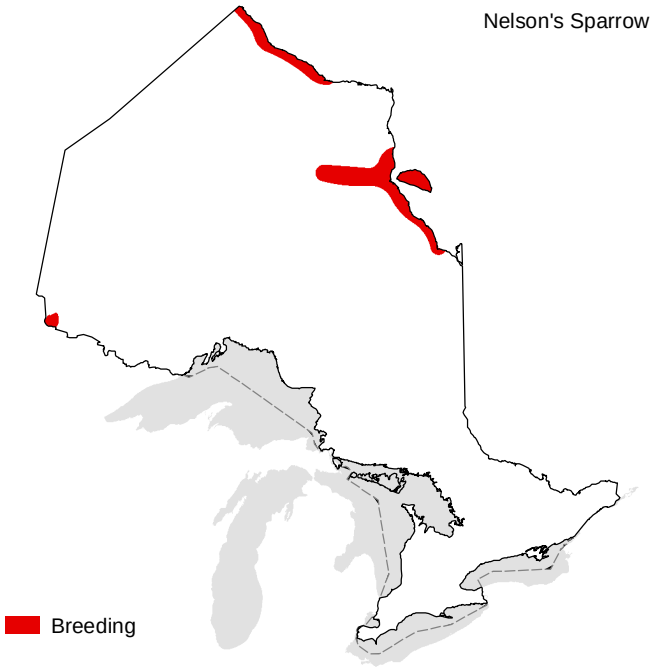


BREEDING SEASON

Habitat Requirements

The Nelson's Sparrow is a highly localized species that occurs as 3 geographically separated subspecies. The prairie subspecies breeds from extreme northeastern British Columbia, northern Alberta, central Saskatchewan, southern Manitoba, and extreme northwestern Ontario (in the Rainy River area) to northeastern South Dakota. The James Bay subspecies breeds on the southern coasts of Hudson Bay and James Bay. The Acadian subspecies breeds along the St. Lawrence River and the Atlantic Coast south to Massachusetts. Its range along the St. Lawrence River extends to almost the extreme western portion of Quebec, but does not include Ontario (Campbell et al. 2001; Murray 1969; Ouellet in Gauthier and Aubry 1996; Shriver et al. 2020). The James Bay subspecies has the best representation in Ontario, but breeding birds in Rainy River District appear to be of the prairie subspecies (James 1991). The northern extent of the James Bay race is uncertain because birds at

Churchill are apparently of the prairie subspecies (Jehl 2004). It is likely that birds along the Ontario coasts of Hudson Bay and certainly James Bay belong to the James Bay subspecies.



All Ontario nests were on the southwest coast of James Bay close to the bay. One was in a grassy area in a clearing along a moist ditch, one was at the edge of a brackish pool on the coast at the mouth of the Nettichi River, and another was in an area of dry grasses, sedges, and forbs 30-40 cm tall (Peck and James 1987, 1998b).

Todd (1963) stated that the James Bay subspecies nested solely in saltwater marsh habitats but it nested in brackish marshes in the Moose Factory area (Murray 1969). During both atlases, it was observed in some inland locations in the Hudson Bay Lowland, indicating that it also breeds in freshwater habitats (Coady in Cadman et al. 2007; Rising in Cadman et al. 1987). This race breeds most frequently in coastal graminoid marshes dominated by saltmeadow rush, meager sedge, chaffy sedge, red bulrush, and common arrowgrass. This habitat is a band approximately 1.6 km wide above the high-water tide. Occupied habitat in Rupert Bay on the southeastern shore of James Bay in Quebec was dominated by Canada bluejoint, northern reedgrass, chaffy sedge, red fescue, sweet grass, bogbean, field horsetail, and Baltic rush. It often breeds where willow and dwarf birch is present (Hill in Austin 1968; Shriver et al. 2020).

The prairie subspecies has the largest range and occupies a greater variety of habitats than the other 2 subspecies. It has been stated that it differs from the other subspecies by nesting in only freshwater habitats (Hill in Austin 1968) but this may not be the case if this is the subspecies that occurs at Churchill. It also nests on margins of salt lakes in North Dakota (Rolfe 1899). It is most frequent in wetlands, particularly marshes, but also occurs in native and planted grasslands and rarely in agricultural lands. In British Columbia, the Nelson's Sparrow nests only in wetlands, including marshes and wet meadows with stands of emergents and willows. It occurs in damp sedge meadows and marshes bordering woodland lakes, among dead and living willows between creeks and grassy meadows, and on willow-covered islets in lakes. In occupied marshes and sedge meadows, clumps of dead and living willows were invariably present interspersed between large areas of grasses or sedges (Campbell et al. 2001). In Alberta, it inhabits marshes in woodland areas and prefers those with scattered willows, and nests in cattails and wet grassy meadows around woodland lakes. In aspen parkland, it was absent in mixed-grass native pastures and uncommon in planted pastures. Planted pastures had lower percentages of grass and shrub cover, higher cover by forbs and bare ground, fewer shrub clumps, and taller grasses and forbs than mixed-grass pastures.

In Alberta pastures subjected to late-season grazing, it was recorded only on a site subjected to the highest intensity of grazing. The biomass lost to grazing was 71% but vegetation height was not reduced significantly. It was more abundant in seeded native Dense Nesting Cover (DNC) than in tame DNC. It was rare or absent in tame DNC less than 2 years old. Its abundance increased with age of DNC until the fifth year, after which abundance decreased. In Manitoba, it nested in unmowed or hayed habitats on hydro transmission line corridors and road rights-of-way that were at least 30 m wide (Leston and Koper 2017). In the Boreal Forest Region, the Nelson's Sparrow also nests in fens. Species that provide nesting cover in marshes include cattails, hard-stemmed bulrush, river bulrush, saltmarsh bulrush, river grass, slough grass, wheat sedge, water smartweed, mints, manna grass, common reed, bluejoint, cordgrass, and water sedge (Campbell et al. 2001; Dechant et al. 2002h; Erskine 1977). In Saskatchewan, Minnesota, and many other areas, the Nelson's Sparrow occupies wetter portions of marshes among cattails, bulrushes, and slough grass. It is uncommon in Saskatchewan grasslands managed for waterfowl, with 12.5% occurrence in DNC, 5.6% occurrence in native grasslands, and 0% in wheat (Hartley 1994; Shriver et al. 2020). Typical habitat in Manitoba consists of a dense mix of cattails, grasses, and tall herbaceous plants with scattered willows. One study found it only in native grasslands and not in tame or seeded native DNC. Another Manitoba study had a single detection in hayfields planted to tame grasses and legumes. It was not observed in native DNC, DNC planted to tame grasses and legumes, or idle native grassland (Dechant et al. 2002h; Shriver et al. 2020). In Minnesota, it nests in prairie marshes and open peatlands that have a permanent water level of a few cm. It is not found in deeper cattail marshes or in marginally wet meadows. Breeding territories contain a low density of shrubs, grasses, and forbs more than 30 cm tall; shorter forbs are more abundant. Some wetlands used were surrounded by bands of tamarack, aspen thickets, and patches of tall grass. At another Minnesota site, it nested in vegetation in damp soil at the edge of a wetland dominated by sphagnum moss and sedges. Another Minnesota study found that graminoid density in territories was high and exceeded 180 stems per m^2. It also occurs in low density Conservation Reserve Program grasslands (Coffin and Pfannmuller 1988; Dechant et al. 2002h; Igl 1996). At 1 North Dakota site, the Nelson's Sparrow nested in a river floodplain. It occurred in wetter areas dominated by cordgrass and was less frequent in stands of river grass and at edges of common reed stands. It never occurred in upland areas dominated by squirrel-tail grass (Murray 1969). In North Dakota, it occurred in low density in fields planted to a mixture of alfalfa and wheatgrass, but was absent in grazed grasslands and idle prairie (Renken and Dinsmore 1987). The Nelson's Sparrow perches on the tallest available sites including fences, shrubs, and trees (Shriver et al. 2020).

The Acadian subspecies nests on islands in the St. Lawrence River not far from the Ontario border. This subspecies is most common in saltwater marshes, but also occurs in brackish and freshwater marshes, fallow fields, drainage ditches, peatlands, hayfields, and grasslands (Hill in Austin 1968; Nocera et al. 2007a; Shriver et al. 2020). In Quebec, the Nelson's Sparrow breeds predominantly in saltwater and brackish marshes, but also in freshwater marshes. It is sometimes found in idle fields and fields of forage crops adjacent to saltwater marshes. In the St. Lawrence River estuary, it occupies the upper level of saltwater marshes dominated by saltmarsh cordgrass interspersed with numerous tidal pools in lower elevations. The upper edges of saltwater marshes are dominated by prairie cordgrass, which is used for cover and perching. In some areas, it occurs in the shrub layer of

saltwater marshes. In a brackish marsh in the Gaspé Peninsula, it nested in a dense stand of hard-stemmed bulrush. At freshwater islands, it occurs in tall grasses of wet meadows. Grasses may include reed grass and rye grass and it may also nest in higher but moist meadows of northern blue flag and marsh cinquefoil (Hill in Austin 1968; Ouellet in Gauthier and Aubry 1996; Seutin and Simon 1988). In New Brunswick and Nova Scotia, it breeds in meadows dyked for the production of hay, especially along ditches where brackish water occasionally backs up. It occurs in the St. John valley in a freshwater environment dominated by arrowheads and white waterlilies. Nova Scotia hayfields that were occupied were dominated by timothy, meadow foxtail, bluegrasses, and reed canary grass. Ditches and wetter sections of hayfields were dominated by prairie cordgrass. The presence of ditches in fields was strongly correlated with its occupancy and reproductive activity, with uncut ditches providing a damp environment with tall coarse grass. It was positively correlated with the height of May vegetation and the abundance of orthopterans, caterpillars, and spiders. It was negatively correlated with the presence of alfalfa. In Prince Edward Island and the St. Lawrence River area, it breeds in short grasses, bogs, and a few ditches. It also nested in a dry marsh grown up to shrubs with scattered dead pine stubs that were remnants of a former forest (Hill in Austin 1968; Nocera et al. 2007a, 2007b; Owen et al. 2025). In Nova Scotia and Maine, the Nelson's Sparrow is associated with coastal saltwater marshes and brackish and saltwater marshes in lower reaches of rivers. These marshes are typically dominated by saltmarsh cordgrass at the lowest elevation, and marsh hay cordgrass and chaffy sedge at middle and higher elevations. Other plants such as saltmeadow rush were patchily distributed at lower elevations. These marshes may contain salt ponds, salt pans (depressions with little or no vegetation and high salinity levels), saltmeadow rush, and saltgrass. In both male and female home ranges, marsh hay cordgrass and vegetated pan habitat was more frequent than at random sites. Saltmarsh cordgrass was less frequent in home ranges than at random sites. There were no differences in the amount of saltmeadow rush, saltgrass, and unvegetated pan habitat in home ranges and random sites, and there were no differences in the vegetation characteristics of male and female home ranges. Mean habitat characteristics in male and female home ranges, respectively, were 28.8% and 18.8% marsh hay cordgrass, 17.8% and 27.6% saltmarsh cordgrass, 21.4% and 14.6% saltmeadow rush, 0.6% and 1.2% saltgrass, 1.3% and 0.5% unvegetated pan, and 20.3% and 18.8% vegetated pan. Many saltwater marshes that support the Nelson's Sparrow contain common arrowgrass. Nests are frequently within patches of saltmarsh cordgrass, with marsh hay cordgrass occurring in drier areas and more important for perching. In other areas, it may nest in marsh hay cordgrass to avoid having the nest flooded by daily tides. Females remain close to the nesting area but males may also use higher elevations of grass, cordgrass, old fence posts, shrubs, stumps, stakes, and spruce trees as perches. Nests tend to be at the upper area that is affected by tides, with full tide flooding only to the roots of the grasses (Hanson and Shriver 2006; Hill in Austin 1968; Norton 1927; Shriver et al. 2010).

Hanson and Shriver (2006) concluded that the Acadian subspecies was not affected by marsh isolation. Proximity of other marshes was not an important variable explaining its density.

Although 1 study determined that marsh size was important in determining density, the Nelson's Sparrow does not appear to be area sensitive. Hanson and Shriver (2006) concluded that marsh area was important in determining density of the Acadian Nelson's Sparrow in marshes as large as 10 ha. Densities in marshes smaller than 5.0 ha and 10.0 ha were lower than in larger

marshes. There was no significant difference in densities in marshes 10-435 ha. Densities increased with the presence of adjacent dykes. Although densities increased with increasing marsh size up to 10 ha, it did not avoid small wetlands. It nested in marshes as small as 1-2.3 ha. In Maine and British Columbia, it nested in very small marshes (Campbell et al. 2001; Hill in Austin 1968). In northern Minnesota, the average size of occupied wetlands was 130 ha (range 15-250 ha). In North Dakota, it occurred in wetlands 5.0-6.4 ha (Dechant et al. 2002h). The prairie subspecies may require larger habitat patches than the other subspecies. Marshes used in Minnesota were quite small and isolated (Coffin and Pfannmuller 1988).

Murray (1968) compared habitat usage of the Nelson's and LeConte's sparrows in a riverine marsh in Minnesota. Both were most numerous in cordgrass but some Nelson's Sparrows were in wetter habitats and some LeConte's Sparrows were in drier habitats. Nelson's Sparrow was never observed in upland stands of squirrel-tail grass but LeConte's Sparrow occasionally nested in this habitat.

Ontario nests were on or close to the ground. Elevated nests were supported by dead coarse grasses (Peck and James 1987, 1998b).

All subspecies place their nests either on the ground or as high as 25 cm above it. Mean nest height is approximately 5 cm. Ground nests may be sunk into the ground or placed on a clump of grasses. Elevated nests are attached to standing grasses or occasionally to a small shrub. Mean vegetation height at nests is 68.1 cm (range 30-90 cm). Nests may be partially or fully domed with dead vegetation from the previous year. A Maine nest was completely covered by a reclining mat of cordgrass and the female entered and left the nest through a narrow passage that was parallel to the culms of the cordgrass. The female may build more than 1 nest but eggs are laid in only a single nest. Nests do not appear to be reused (Campbell et al. 2001; Hill in Austin 1968; Murray 1969; Nordhagen et al. 2005; Norton 1927; Rolfe 1899; Shriver et al. 2020).

Both sexes of the Nelson's Sparrow are nonterritorial. Males may guard receptive females and fight with other males that approach, but no territory is defended. Two to 3 females may nest at the same time within 2-3 m of each other with little or no aggression. Home ranges of all males and females within a population completely overlap with both sexes wandering within the occupied habitat. Males fly from song perch to song perch, crisscross each other's paths, and use common song perches. In North Dakota, males often flew more than 150 m in a single flight but distances travelled in New Brunswick were as far as 800 m. In Maine, the mean size of core home ranges was 18.42 ha for males and 6.15 ha for females. The total home range was 119.68 ha for males and 43.58 ha for females. Twenty-seven percent of females and 45% of males had 2 core areas. The mean distance between core areas was 161.40 m for females and 204.28 m for males. When birds had 2 core areas, they were not used simultaneously and usage of core areas was timed to coincide with separate lunar cycles. At this study area, most nests were flooded during the spring tide and females moved within the study area to construct a second nest during the subsequent lunar cycle. Home ranges of males and the distance between core areas were significantly larger than for females because males attempt to maintain close proximity to females during renesting attempts. In New Brunswick, core areas consisted of patches of isolated wet meadows as far apart as 800 m. At another New Brunswick site, the 95% home ranges averaged 22.17 ha (range 0.30-215.11 ha) and the mean

50% core area was 3.01 ha (range 0.07-29.04 ha). Male home ranges (mean 25.45 ha compared with 9.03 ha) and core areas (mean 29.04 ha compared with 2.95 ha) were significantly larger than those of females (Owen et al. 2025). Birds at a Quebec site had much smaller home ranges, with males restricting their activities to about 1.5 ha and females remaining in an area of 0.4 ha. Male dispersion is related to female dispersion which is influenced by the patchiness of suitable nest-site microhabitat (Murray 1969; Ouellet in Gauthier and Aubry 1996; Shriver et al. 2010, 2020). It is likely that home range size is influenced by the size of habitat patch, homogeneousness of the habitat, and size of the local breeding population. Breeding birds tend to be clumped and adjacent suitable habitat may be unoccupied. This suggests that the Nelson's Sparrow may be colonial but it has been suggested that absence of birds from potentially suitable nesting habitat may reflect chance associated with limited local recruitment. The lack of territoriality and its promiscuous mating system are indicative of true coloniality. If birds were spread evenly throughout habitat, it would be more difficult for individual birds to mate with multiple birds (Murray 1969; Ouellet in Gauthier and Aubry 1996; Shriver et al. 2020).

No information is available on natal philopatry and there is limited information on adult site fidelity. In North Dakota, 1 of 3 males (33.3%) and 1 of 1 female banded the previous year returned (Murray 1969). Shriver et al. (2020) reported return rates of 39% for males and 32% for females based on a sample size of 101.

Limiting Factors

Eggs are likely to be present in Ontario nests from the third week of June until the third week of July (Peck and James 1987). The time it takes to build the nest is unknown. Eggs are laid at the rate of 1 a day and incubation begins with the laying of the penultimate or last egg. Hatching occurs over a 24-36 hour period, suggesting that incubation begins in earnest with the penultimate egg. No information is available on the incubation period. Disturbed nestlings may fledge when they are as young as 8 days, but normally fledge at age 10-11 days. Nest departure is synchronous with all young leaving within a few hours of each other (Shriver et al. 2020).

The number of broods that the James Bay subspecies raises is unknown. The other 2 subspecies are capable of raising 2 broods in a season. Because the female raises the fledglings without assistance from the male, second nests are not initiated until the first brood is independent. Renesting is common after nest loss by the Acadian subspecies. Renesting has not been documented for the prairie subspecies and no information on renesting is available for the James Bay subspecies. In Maine, replacement nests were not initiated until more than 10 days after the initial ones were flooded by spring tides. All Ontario nests contained 4 eggs, but the sample size is small. Clutches of 2-6 eggs have been reported but the normal range is 3-5 eggs; 4-egg clutches are most common (Dechant et al. 2002h; Hill in Austin 1968; Norton 1927; Ouellet in Gauthier and Aubry 1996; Peck and James 1987, 1998b; Rolfe 1899; Shriver et al. 2007, 2020).

Both sexes are capable of breeding when they are 1 year old. The Nelson's Sparrow is polygynandrous, which means that both sexes are promiscuous and may potentially mate with numerous individuals. The mating system is a form of male-dominance polygyny where a small proportion of males perform a disproportionate share of copulations. No pair bond is formed but males may guard specific females for periods ranging from 15 minutes to 43 hours. As a result of

this mating system, offspring in the same brood often have different fathers. The Nelson's Sparrow is the only North American marsh-dwelling polygynandrous species (Greenlaw 1989; Murray 1969; Seutin and Simon 1988; Shriver et al. 2007, 2010, 2020).

The Nelson's Sparrow forages on the ground in dense grasses within marshes or wet meadows, along ditch margins, at edges of shallow pools and mud pans, and around patches of beach wrack. The Acadian subspecies, and probably the James Bay subspecies, forages below the high-water level at low tide around tidal pools and channels. Birds did not move into the grass at higher levels to forage until the mud was submerged. Birds breeding in salt-marsh habitats may visit nearby hayfields to forage. Birds breeding in coastal areas probably feed mostly on marine invertebrates during low tide and terrestrial invertebrates during high tide. Prey items that have been found in the diet are consistent with those found in vegetation and from mud and water obtained by gleaning, pecking, and probing (Hill in Austin 1968; Shriver et al. 2020).

Young are fed invertebrate prey almost exclusively. Eleven Acadian subspecies nestlings had consumed 44.4% insects and 33.3% spiders. The insects in order of decreasing importance consisted of orthopterans, soft-winged bugs, beetles, true bugs, flies, and odonates (Shriver et al. 2020).

Judd (1901) examined 51 adult stomachs collected during the breeding season. It is possible that some of them were Saltmarsh Sparrows; the sample did not include any James Bay subspecies specimens. The diet consisted of 81% animal material and 19% vegetable matter, mostly grass seeds. The animal food consisted of 26% amphipods, spiders, and snails; 14% lepidopterans (a third were owlet moths); 12% bugs (half were leafhoppers); 7% orthopterans (mostly short-horned grasshoppers but some long-horned grasshoppers and crickets); 6% beetles (mostly weevils with some small ground beetles and occasional leaf, rove, tiger, and dung beetles); 5% flies (mainly midges and their larvae and smaller adult horse flies); 3% hymenopterans (ants and ichneumonid wasps); and 8% miscellaneous insects. The Nelson's Sparrow ate a larger proportion of flies than most birds except for flycatchers and shore-inhabiting species of the far north that feed almost exclusively on midges. Amphipods constituted 16% of the diet of saltwater birds but 0% of freshwater birds. Only saltwater birds ate snails and only freshwater birds fed on armyworms. Saltwater birds ate no vegetable matter other than grass seeds but 30.4% of freshwater birds had eaten other seeds, including those of smartweeds, lamb's-quarters, clovers, and dandelions. Saltwater birds fed on the seeds of grasses associated with saltwater marshes and occasionally wild rice. Freshwater birds ate seeds of other grasses, especially panic grasses. Other items it eats include wasps, earwigs, wolf spiders, fiddler crabs, and ribbon worms (Hill in Austin 1968; Shriver et al. 2020).

The Nelson's Sparrow is a rare host of the Brown-headed Cowbird. There are only 2 records of parasitism, both on the prairie subspecies. Based on the results of a single nest, it is possible that parasitism results in complete nest failure (Nordhagen et al. 2005; Shriver et al. 2020). The James Bay subspecies nests north of the range of the cowbird and is unlikely to be parasitized.

Habitat loss and degradation is currently not an issue in Ontario, but is an issue in other areas. It is sensitive to loss of saltwater marshes along the St. Lawrence River and Atlantic coast. In Quebec, 18% of saltwater marshes were destroyed 1945-76 due to agriculture, landfilling, and construction, but the Nelson's Sparrow still continues to inhabit most of its traditional sites. The Quebec James Bay hydro-development has the potential to alter habitat, the movement of ice, and salinity levels.

Along the Atlantic Coast, cutting marshes off from tidal influences by roads and ditching resulted in its decline. Prairie birds have been subjected to drainage of wetlands and fields. Those nesting in managed grasslands may be adversely affected by mowing, grazing, plowing, burning, channelization, recreation, and spraying for insects. In Nova Scotia, delaying hay harvest until 7 July enhanced reproductive success and still provided a good hay crop. Cutting again prior to late August allows a second crop to be harvested and gives time for grass to grow to suitable height for the next year (Campbell et al. 2001; Correll et al. 2016; Nocera et al. 2007a, 2007b; Ouellet in Gauthier and Aubry 1996; Shriver et al. 2020).

The prairie subspecies may be affected by the amount of rainfall received. Responses to wet seasons differed in British Columbia and North Dakota. In British Columbia, it was much more abundant during a very wet summer when water levels were much higher than usual. It was much more widely distributed, nesting in flooded areas such as ponds, densely vegetated ditches, and low fields (Campbell et al. 2001). In North Dakota, it was more abundant during dry years. In dry years, it nested in shallow-marsh and deep-marsh zones of wetlands. In wet years, it nested in cordgrass in wet-meadow zones (Dechant et al. 2002h).

The Nelson's Sparrow is one of few ground-nesting passerines that breed in flooded tidal marshes. These areas have predictable unusually high flood tides that occur every 26-28 days because of the lunar cycle. In Maine, the elevation of nests was a significant predictor of nest success, with successful nests significantly higher than unsuccessful nests. Vegetation parameters did not affect nest success. Second nests were initiated an average of 10.3 days after the flood tide. There was no significant difference in nest initiation dates for birds that had successful or unsuccessful first nests. There were 2 options to achieve successful nesting: constructing nests at high enough elevations to avoid flooding or initiating renesting immediately after nest loss to ensure that nesting was complete before the next flood (Shriver et al. 2007). Flooding of nests has not been documented for the James Bay subspecies, but it is possible that it occurs. The terrain in this area is extremely flat so even a minor increase in water levels could flood extensive areas.

Status

McIlwraith (1894) and Baillie and Harrington (1937) were unaware that the Nelson's Sparrow bred in Ontario. It was first confirmed as a breeder in 1939 when a juvenile was collected at Attawapiskat. Nests were found at Fort Albany and Nettichi Point in 1942; it was most abundant at Fort Albany where 50 were counted on 2 separate dates (Baillie 1960). Manning (1952) concluded that it probably bred in fair numbers in the long grass coastal barrens of the western James Bay coast north to the Albany River. The first atlas revealed that it nested along the southern portion of James Bay and at scattered locations along Hudson Bay. There were 3 records of birds in the north away from the coast. One may have represented a late migrant but the other records were in July, suggesting that these were birds breeding in freshwater habitat. A single bird heard in Rainy River District was likely of the prairie subspecies (Rising in Cadman et al. 1987) and at least 5 were reported there during the 1979 breeding season (Speirs 1985). James (1991) considered the Nelson's Sparrow an uncommon summer resident along the northern coasts where it was most abundant along the southern James Bay coast. He noted that there were summer records from western Rainy River

District. Wilson and McRae (1993) concluded that it was common along much of the James Bay coast but uncommon and local along the Hudson Bay coast.

The second atlas revealed that there had been no significant change in the probability of observation of the Nelson's Sparrow since the first atlas. There was also no significant change in its abundance. Breeding evidence was found again far inland along the Attawapiskat River confirming that it breeds away from the coast in freshwater habitat. A bird singing in early June at Cat Lake may have been a late migrant of the James Bay subspecies or a nesting bird of the prairie subspecies. It was once again documented in the Rainy River area, but breeding of this population has yet to be confirmed. Thirty-five singing males were heard in a small area near Shegogau Creek on the James Bay coast north of Moosonee (Coady in Cadman et al. 2007).

POSTFLEDGING PERIOD

Young can run on the ground and climb in vegetation upon leaving the nest, but are not capable of flying short distances until they have been out of the nest for 3-5 days. They initially disperse in grass a few metres from the nest. In the Bay of Fundy, fledglings remain in grass above the high-tide level while adults forage for food items for them at lower elevations. Small flocks of juveniles and adults form once the juveniles are independent, and juveniles predominate in these flocks. Along the Atlantic coast, these flocks typically contain 10-40 individuals, but flocks in excess of 100 commonly occur. There appears to be some wandering in autumn prior to migration (Hill in Austin 1968; Shriver et al. 2020).

MIGRATION

The Nelson's Sparrow is thought to migrate only at night. All races overwinter along the Atlantic coast from North Carolina to Florida and around the Gulf of Mexico to southern Texas. The James Bay subspecies winters in South Carolina, Georgia, northern Florida, and Alabama. The migration route from the breeding grounds tends to be north-south to the southern Great Lakes area, with numerous records of migrants in the Toronto area and central New York (Hill in Austin 1968; Shriver et al. 2020).

The Nelson's Sparrow is a late spring migrant and the last sparrow to arrive in the Churchill area (Jehl 2004). Because males are nonterritorial, they do not need to arrive early on the breeding grounds to vie for the best territories. There are few records of spring migrants in the province. The single spring record for Hamilton is 20 May (Curry 2006) and Fleming (1907) had a record for Toronto on 10 June. The 4 spring records for the Kingston area span the period 20 May to 5 June (Weir 2008). Wilson and McRae (1993) observed a singing male at Brant on 26 June. It leaves the breeding grounds in September and the peak of migration in southern Ontario is from late September to mid-October. Movement is often associated with strong cold fronts (Pittaway 1997). Wilson and McRae (1993) last saw it at Ekwan on 9 September and on 12 September at Longridge.

In Algonquin Park, autumn migrants occur in wet sedge and marshy areas where they favour extensive stands of sedges, grasses, bur-reeds, bulrushes, and beggarticks but not cattails. Habitats are typically large marshes and wetlands along rivers and lakeshores where the water is as deep as 30 cm (Tozer 2012). In the Kingston area, migrants are found predominantly in cattail marshes (Weir 2008). In Renfrew County, migrants were observed in grasses and sedges that were waist high. In Dundas, most birds occur in a narrow band of waist-high manna grass bordering cattails between a

small pond and the open water of the bay. Autumn migrants at Hillman Marsh were in a zone of grasses, sedges, and beggarticks between the shore and cattails. In southern Ontario, it usually inhabits marshes bordering large lakes and rivers, but not in deep-water marshes or dense stands of cattails. It tends to concentrate where grasses and sedges are knee to waist high and sometimes taller, and where the ground is moist to slightly wet. It is occasionally found in drier sites where lake levels have receded. It may occur in communities of bulrushes, sedges, cordgrass, reed canary grass, manna grass, and other similar grasses, and sometimes in a mix of cattails, beggarticks, or smartweeds (Pittaway 1997).

During autumn migration in Kansas, Nelson's and LeConte's sparrows often occupied stands of cordgrass in a matrix of shorter annual forbs and spikerushes. They often occurred in the same area at the same time, but rarely within 10 m of each other (Powell and Nyari 2007).

The Nelson's Sparrow is a rare migrant in Ontario, or at least rarely observed. It passes through southern Ontario regularly but is rarely seen because few people search the appropriate habitat at the right time. Eighteen were seen on 8 October at Hillman Marsh. Maxima seen in the Hamilton area were 10 on 28 September and 8 on 29 September. Maxima in the Kingston area were 6 on 1 October and 3 on 3 October, and the maximum count at Algonquin Park is 10 on 3 October (Curry 2006; James 1991; Pittaway 1997; Tozer 2012; Weir 2008).

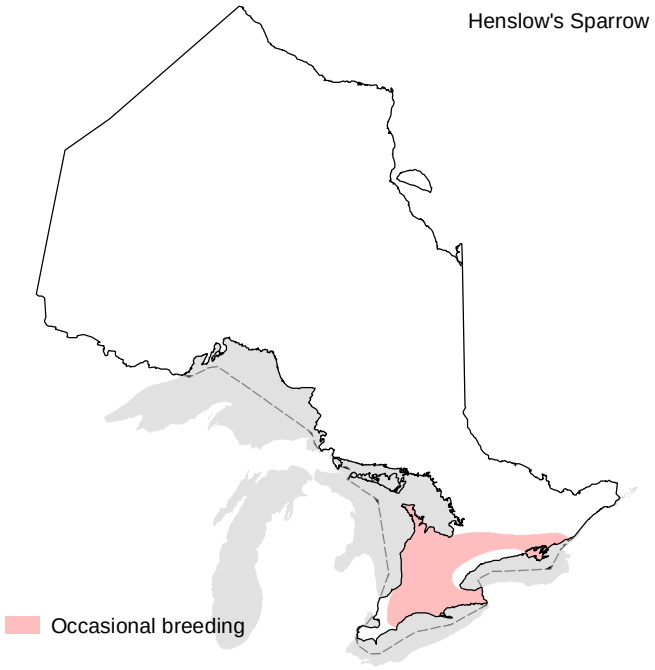
Henslow's Sparrow

Centronyx henslowii

BREEDING SEASON

Habitat Requirements

In Ontario, the Henslow's Sparrow has nested in hayfields, meadows, and pastures, all with characteristically tall growths of grasses, legumes, and forbs. Several nests were in wet or damp fields and 1 field contained scattered small shrubs (Peck and James 1987). It has nested in abandoned fields, ungrazed or lightly grazed pastures, fallow fields with a high clover and alfalfa content often mixed with timothy, grassy swales in open rolling farmland, wet meadows, infrequently mowed fields with a thick layer of thatch, and tallgrass prairie on Walpole Island (Austen et al. 1995; Pearce et al. 2010). In Haldimand County, it nested in a pasture containing many small tributaries lined with dogwoods. The site was dominated by tall grasses with even taller forbs (Speirs 1933). Many occupied sites contain tall common mullein stalks that are used as singing perches. Speirs and Orenstein (1967) reported it in Durham Region in an old field dominated by bluegrasses and other grasses, with asters and goldenrods and some encroachment by raspberries, dogwoods, and other shrubs; a hayfield on a hilly sandy moraine dominated by clover, timothy, and alfalfa with a good



deal of mullein and other forbs; a very hilly hayfield; and an area of mixed farmland consisting of hay, corn, and oats. It appeared to prefer old fields and hayfields with clover and alfalfa. In Simcoe County, it nested in moist weedy fields and sometimes in clover fields or wet meadows bordering marshes. It formerly nested in Holland Marsh before it was cleared and drained for market gardening (Devitt 1967). In Wellington County, it nested in a 160-ha abandoned pasture dominated by grasses 30 cm or taller, including timothy, quack grass, and orchard grass, with some areas of reed canary grass and scattered common mullein (personal observation). Near Brockville, it nested in an old hayfield that consisted of 90% orchard grass and 10% shrubs and forbs. The grasses were 0.5-1 m tall and the shrubs were less than 0.5 m tall, but the field was becoming invaded with shrubs. The thatch layer was 7-10 cm high and trees less than 10 m tall bordered the field on 3 sides. There was a marsh on the fourth side (Austen and Cadman 1993). The site that was occupied at Luther Marsh in Dufferin County (Brewer 1977) was dominated by smooth brome. Some historical Ontario locations contained or were adjacent to low-lying areas that were seasonally flooded during spring. Canada bluejoint and reed canary grass were common in these areas. Wet areas may contain the most stable vegetation communities and be less likely to be invaded by shrubs (Pearce et al. 2010). Reed canary grass forms dense monotypic stands that typically preclude establishment by other species. Although it is often stated that it occurs in wet low-lying areas, it also inhabits dry areas, including hilltops (Knapton 1984a).

Optimal Ontario habitat includes a high percentage of grasses, moderate to high density of grasses, a thick mat of ground cover from previous years' vegetation, dense vegetation at least 0.5 m tall, no current disturbance due to grazing, and low coverage by shrubs. Intermediate moisture regimes or low-lying areas are considered essential by some authors, but this is not the case. The Henslow's Sparrow avoids fields that are frequently mowed, cultivated or grazed, and recently burned grasslands. Sites that meet all or most of its habitat requirements are becoming increasingly scarce in Ontario (Austen et al. 1995; Heagy 2011; Knapton 1984a; Kraus 2015; Pearce et al. 2010).

Knapton (1984a) described the habitat at 5 occupied Ontario sites. The Aberfoyle site consisted of 70% grass cover with a high density of grass, 51 cm mean height of dense vegetation (range 48-54 cm), maximum height of grasses and forbs 88 cm and 116 cm, and high litter density. The Hockley Valley site consisted of 50% grass cover with a high density of grass cover, 82 cm mean height of dense vegetation (range 56-104 cm), maximum height of grasses and forbs 100 cm and 146 cm, and moderate litter density. The Rockton site consisted of 50% grass cover with a moderate density of grass cover, 30 cm mean height of dense vegetation (range 26-34 cm), maximum height of grasses

and forbs 80 cm and 100 cm, and moderate litter density. The Tiny Marsh west site consisted of 40% grass cover with a moderate density of grass cover, 29 cm mean height of dense vegetation (range 25-31 cm), maximum height of grasses and forbs 54 cm and 76 cm, and moderate litter density. The Tiny Marsh east site consisted of 60% grass cover with a high density of grass cover, 42 cm mean height of dense vegetation (range 25-48 cm), maximum height of grasses and forbs 76 cm and 102 cm, and high litter density. Both the Rockton and Hockley Valley sites lacked one or more of the optimum habitat requirements. Sites in Ontario and New York had 50-80% grass coverage, often with vetches, bird's-foot trefoil, and strawberries; dense vegetation 30-80 cm tall; grass and forb height 89-115 cm; and woody vegetation (willow, dogwood, or staghorn sumac) 76-183 cm tall.

Some studies examined landscape features that may affect occupancy of grasslands by the Henslow's Sparrow. Murray et al. (2008) used Breeding Bird Survey (BBS) data in the Midwest. Its abundance was most closely related to the amount of grassland within 800 ha. Thogmartin et al. (2006) also analyzed BBS data and found that higher abundance occurred in grasslands surrounded by forest; it was positively associated with precipitation during warm months. The positive association with forests could be a result of the types of grasslands that occur within these landscapes. These grasslands tended to have greater topographical relief, less agricultural land, and more idle and Conservation Reserve Program (CRP) lands. In New York, Peterson (1983) measured the distance to the horizon in the 4 cardinal directions. The mean distances to the horizon of 4 occupied sites were 7.3-15.6 km (average 10.25 km), significantly greater than the mean of 3.3 km for unoccupied sites. All occupied sites were on or near hilltops with sweeping panoramic views to distances greater than 35 km in some cases. Sites in valleys with hills or treelines rising above the grassland were not occupied, and even a single treeline or forest edge at a short distance precluded occupancy. At 2 occupied sites, adjacent areas that differed only in the presence of a treeline were unoccupied. The requirement for a lack of treelines and long panoramic views does not appear to be the case in Ontario. The only known occupied site in 1992 and 1993 was a small field with trees bordering it on 3 sides (Austen and Cadman 1993). In Pennsylvania, the distance to the nearest grassland and the surrounding land cover were unrelated to occupancy probability. Forested landscapes did not appear to be effective barriers to dispersal and colonization, even when more than 80% of the landscape was unsuitable habitat (Hill and Diefenbach 2014). Many colonies in New England, New York, and Pennsylvania were in river valleys (Hyde 1939), contrary to Peterson's (1983) findings.

The optimal habitat conditions identified for Ontario are the same for the Henslow's Sparrow throughout its range. Inhabited areas are typically dominated by grasses 0.5 m or more in height, the grass layer is very dense, and there is a deep thatch or litter layer from previous years' vegetation. In Pennsylvania, it was most likely to occupy fields with a larger grass component and low coverage by forbs (Hill and Diefenbach 2014). In North Carolina where pine trees had been planted, occupied areas had a dense ground cover of grasses, sedges, and ferns (Lynch and LeGrand 1985). In Iowa, occupied fields were dominated by smooth brome 45-85 cm tall, 5-20% of the area was covered with forbs, and there were dense standing dead grass stems from the previous year (Melde and Koford 1996). In Kentucky, it occurred in fields of orchard grass with some forbs such as wild carrot. In Missouri, numbers increased markedly as grass heights exceeded 15 cm in prairies (Knapton 1984a). In Pennsylvania, habitat at nests consisted of 2% bare ground, 22% forbs, 66% grasses, and

1% shrubs. The thatch layer was 4 cm deep, grasses were 57 cm tall, and forbs were 32 cm tall (Hill and Diefenbach 2013). In Michigan, habitat consisted of vegetation dominated by nonwoody vegetation, particularly grasses and sedges, that was dense or at least had dense patches, and presence of litter (Robins 1971a). In New York, all occupied sites were heavily dominated by grasses and most contained sedges. Subdominant herbaceous species composition had little importance in habitat selection and herbaceous species may not be required; 1 site was pure timothy (Peterson 1983). In Kansas, forb coverage was not important when selecting territories (Zimmerman 1988). In Illinois, important habitat characteristics included litter density and depth, standing dead residual vegetation, and vegetation height and density. Occupied areas were dominated by sedges, dropseeds, cordgrass, meadow fescue, and bluegrass. Occupied areas had a greater vegetation density between 0 and 25 cm and a higher percentage of standing dead residual vegetation than unoccupied areas (Herkert 1994a, 1994b). At a military base in Kansas, vegetative characteristics that were consistently associated with occupied sites included high litter coverage and dense homogenous vegetation. In spring, it used sites that had retained higher cover by standing dead vegetation and deeper litter; those differences disappeared by summer (Cully and Michaels 2000). At reclaimed mines in Indiana, its presence was positively associated with percent coverage by grasses, grass species diversity, percent coverage by smooth brome, and percent coverage by broomsedge. It was marginally associated with vegetation height and negatively associated with forb species diversity (Bajema et al. 2001). In Wisconsin, occupied areas had lower coverage and density of forbs, significantly taller forbs, higher vertical vegetation density and mean effective height with a lower proportion of vegetation occurring in the 0-10 cm layer, considerably less coverage by lawn-like vegetation, and deeper, more compact, and more extensively distributed litter than unoccupied areas (Wiens 1969). In Wisconsin, its abundance was positively correlated with maximum vegetation height and density and percent coverage by standing residual vegetation. It was negatively correlated with bare ground (Swanson 1996). In western shrubsteppe vegetation, it was positively correlated with litter depth (Rotenberry and Wiens 1980). In Quebec, it nested in a wet meadow of sedges and grasses. Another site was in the upper part of a gently sloping field with dense smooth brome and timothy 1.2-1.5 m tall (Bannon in Gauthier and Aubry 1996). The vegetation that the Henslow's Sparrow inhabits may be rather irregular in height and density or uniform, but the ground cover is usually quite dense and at least 30-60 cm tall (Graber in Austin 1968). There is no difference in its rates of occupancy or nest survival in native and planted grasslands, and the species of grass that are present do not appear to be important. It has been documented breeding in little bluestem, smooth brome, paspalum, Kentucky bluegrass, tall ryegrass, cordgrass, wiregrass, broomsedge, perennial rye grass, orchard grass, redtop, timothy, big bluestem, switch grass, reed canary grass, Canada bluejoint, Indian grass, sweet grass, beach grass, and muhly grass (Arnold and Garza 1998; Ells 1995a; Graves et al. 2010; Herkert 1994b; Hill and Diefenbach 2013; Hyde 1939; Jaster et al. 2013; Schulenberg et al. 1994; Skipper 1998; Winter 1999).

Some studies reported that the Henslow's Sparrow is intolerant of any woody vegetation within its territory; others concluded that short shrubs may be widely scattered throughout the territory. It is universally agreed that invasion of grasslands by tall shrubs and saplings render habitat unsuitable. In New York, it occurred in fields with no woody vegetation at 1 site. At another site, shrub coverage was less than 1% and the density of shrubs with an average height of 0.5 m was less than 10 per 250

m^2. In Kansas, densities of trees taller than 4 m were significantly lower in territories (0.54 per ha) than in random sites (6.67 per ha). In Ohio, grasslands used for nesting included scattered shrubs that provided singing perches. In Missouri, territories contained no shrubs with a diameter at breast height greater than 2.5 cm and few or no smaller woody stems (range 0-1.00 per ha). Males avoided areas with woody vegetation taller than 1 m. In Illinois, occupied areas had no or very sparse coverage by shrubs. In Kansas and Ohio, its abundance was negatively correlated with woody vegetation. Daily nest survival was negatively correlated with the amount of woody vegetation surrounding the nest. In Indiana, nest survival increased with increasingly open habitat. At a Pennsylvania reclaimed mine site, all standing woody vegetation was pulverized to a maximum height of 0.3 m and spring sprouts were sprayed with herbicide. There was no difference in nest survival between control and treatment areas, suggesting that woody vegetation did not affect survival. In Massachusetts, it nested in wet meadows grown up in steeplebush and in fields invaded by hazel and blackberries. It may nest in young plantations where the conifers have not yet overtopped the grasses. In New York, woody vegetation at occupied sites was either nonexistent or limited to a very few widely scattered low hawthorns, dogwoods, or raspberries that comprised less than 2% coverage. Almost any woody vegetation appeared to decrease suitability. In Texas, the amount of woody vegetation on 4 transects through territories was 3.4%, 12.1%, 14.3%, and 6.8%. At 1 Kansas site, it used open grassland with few trees. Presence of low woody vegetation did not reduce usage of areas, but shrubs were scattered in distribution. In Indiana, sites with more than 50% shrub coverage were avoided (Arnold and Garza 1998; Crimmins et al. 2016; Cully and Michaels 2000; Galligan et al. 2006; Graves et al. 2010; Herkert 1994b; Hill and Diefenbach 2013; Hyde 1939; Pearce et al. 2010; Peterson 1983; Pruitt 1996; Smith and Smith 1992).

Many studies concluded that the Henslow's Sparrow prefers moist low-lying areas, but it has nested in a wide range of moisture regimes. Vegetation characteristics are much more important in habitat selection and moisture regime may either be a secondary characteristic or not important at all. The apparent preponderance of wet habitats may be because these areas are less likely to be cut for hay, burned, or converted to other land uses than drier sites. In New York, it often nested on hilltops with a variety of moisture regimes. In Texas, it nested in a 105-ha field divided by a drainage canal. The western part of the field was higher and drier than the eastern part, and all Henslow's Sparrows nested in the western part. In Michigan, it appeared to prefer an intermediate moisture regime. In Kansas, it nested near the crest of a hill. In another New York study area, it occurred in a variety of moisture regimes from dry and well-drained to 30% seasonally or continually moist with numerous clumps of sedges and grasses. In prairies in Kansas, it was significantly more abundant in sites with deep silty clay loam than shallower soils. The clay soils supported a greater above-ground biomass of grasses. It tends to occupy flatter slopes of fields with a maximum slope of 7° (Arnold and Garza 1998; Herkert et al. 2020b; Hyde 1939; Peterson 1983; Pruitt 1996; Robins 1971a; Smith and Smith 1992; Zimmerman 1988).

Several studies compared habitat at the nest with the remainder of the territory or habitat within the territory to unoccupied areas. In Minnesota, both the depth of the litter layer and the distance from the ground to the bottom of the litter layer were greater in occupied than unoccupied sites (Pruitt 1996). In Ohio, Graves et al. (2010) found no significant differences in habitat variables between occupied and unoccupied sites on reclaimed surface mines. In Kansas, the amount of

standing dead vegetation was greater in territories than in unoccupied sites. Grass coverage within and outside territories, respectively, was 83.3% and 70.0% and 78.6% and 79.2% over 2 years. There was significantly less woody cover within (0.7% and 0.8% over 2 years) than outside (1.8% and 2.7%) territories. Grass height was significantly higher within (23.7-73.3 cm) than outside (31.2-50.7 cm) territories on all soil types. There was no significant difference in forb coverage within (12.0% and 14.4%) and outside (12.6% and 15.0%) territories. The Henslow's Sparrow's association with standing dead vegetation may be because it helps protect nests from predation, parasitism, and microclimate extremes. Dead vegetation and the litter associated with it may inhibit growth of new vegetation, providing a more open substrate (Zimmerman 1988). In Illinois, occupied areas had taller vegetation than unoccupied areas (27.5 cm compared with 19.8 cm for grasses and 47.2 cm compared with 30.1 cm for all vegetation). In occupied areas, vegetation was denser, particularly within 25 cm of the ground, and there was a higher proportion of dead plant material (45.0% compared with 13.6%) than in unoccupied areas (Herkert 1994b). At another Kansas site, mean vegetative cover and density, litter cover, and structural heterogeneity were higher at occupied sites in spring than at survey points. By summer, there were no significant differences between occupied and unoccupied sites (Cully and Michaels 2000). In Indiana, there were significant differences in habitat parameters for occupied and unoccupied sites, respectively: 5.4 cm and 3.8 cm litter depth; 79.1% and 70.9% litter coverage; 68.1% and 57.5% grass coverage; 15.8% and 7.5% coverage by smooth brome; 4.1% and 0.6% coverage by broomsedge, and 2.0 and 1.7 grass species diversity (Bajema et al. 2001). In Wisconsin, territories contained no fence posts, fence lines, wire bales or tangles, or trees. It is possible that suitable habitat simply did not contain these features rather than them being actively avoided. The percent coverage by vegetation in occupied and unoccupied areas, respectively, was 97% and 97% grass cover, 86% and 64% very narrow-leaved grass cover, 36% and 58% narrow-leaved grass cover, 20% and 31% forb cover, and 1% and 3% bare ground (Wiens 1969). In Missouri, coverage by grasses and standing dead vegetation was greater within than outside territories (Swanson 1996).

Other studies examined microhabitat characteristics within territories. In Kansas, vegetation at nest sites consisted of little bluestem, sedges, forbs, and a few shrubs. Cover within the 1 m^2 around nests consisted of 10% standing dead little bluestem, 10% alive little bluestem, 25% sedges, 20% forbs (blazing-star and hemp dogbane), and 5% bare ground; litter depth was less than 2 cm. Spaces around grass clumps may enable birds to disperse quickly through the grasses once the young fledge (Schulenberg et al. 1994). On Ohio surface mines, areas within 100 m of the nest averaged 2.3% woody vegetation coverage and there were 2.7 woody patches within a 100-m radius (Graves et al. 2010). In Missouri, 82% of nests were among layers of thick litter. There were no differences in any habitat variables between successful and unsuccessful nest sites. Habitats at successful and unsuccessful nests, respectively, were 3.3 cm and 3.7 cm litter depth, 43.0 cm and 40.7 cm vegetation height, 27.1% and 33.1% litter cover, 51.4% and 49.4% grass cover, 19.1% and 16.2% forb cover, 1.8% and 1.1% woody cover, 0.6% and 0.2% bare soil, 89.6% and 91.7% cover at the nest, and 7.0 cm and 7.9 cm nest height (Winter 1999). Wisconsin territories had less than 2% woody cover, 74% herbaceous cover (which probably included grasses), 24% litter cover, less than 2% bare ground, and 88 cm maximum vegetation height (Swanson 1996).

Although singing perches are a common component of Henslow's Sparrow territories, they may not be essential. It occasionally nests in uniform grass communities where there are no perches. In these cases, it sings from below the grass canopy (Peterson 1983). In Missouri, it was very selective and sang predominantly from woody vegetation less than 1 m tall. In Minnesota and Michigan, males returning in early spring sang while perched on last year's standing dead vegetation (Pruitt 1996; Robins 1971a). In North Carolina, it was never observed singing from a fence or exposed snag, but sang mostly from the tops of pine and deciduous saplings that had not yet overtopped the dense ground vegetation. One sang from a bare pine branch 4.6 m above ground, but such behaviour was rare. Most perched or sang in the middle of a sapling or by clinging to the stalk of a herbaceous plant (Lynch and LeGrand 1985). In Michigan, it sang from just below the top of the vegetative cover. Invading woody plants and grid stakes provided perches above this level, but were used infrequently (Robins 1971a). Another Michigan study determined that it used elderberries and other shrubs, but especially dead mullein stalks, as perches (Hyde 1939). In Wisconsin, perchs consisted of 3.3% grasses, 59.7% heavy-stemmed forbs, and 37.0% medium-stemmed forbs (Wiens 1969).

Several studies compared microhabitat features of Henslow's Sparrow's territories to those of other grassland species. In New York, the Savannah Sparrow had the closest habitat requirements, but it tolerated nearby treelines and forest edges whereas the Henslow's Sparrow did not (Peterson 1983). In Pennsylvania, the Henslow's Sparrow preferred taller vegetation and was less tolerant of woody vegetation than the Grasshopper Sparrow (Hill and Diefenbach 2013). In Missouri, Winter (1999) compared habitat at nests of the Henslow's Sparrow and Dickcissel. Henslow's Sparrow nests had deeper litter (3.5 cm compared with 1.9 cm), shorter vegetation (42.0 cm compared with 46.1 cm), greater cover by litter (29.6% compared with 11.6%), less cover by forbs (17.9% compared with 26.0%), less woody plant coverage (1.5% compared with 5.2%), and less bare soil (0.4% compared with 4.8%). Henslow's Sparrow nests had a higher percentage of cover (90.3% compared with 67.7%) and were located closer to the ground (7.2 cm compared with 18.4 cm). Henslow's Sparrows never placed their nests in or immediately adjacent to woody vegetation. Dickcissels preferred forbs and shrubs as a nesting substrate. In Wisconsin, Wiens (1969) compared the microhabitats of the Henslow's Sparrow with those of the Vesper Sparrow, Savannah Sparrow, Grasshopper Sparrow, Bobolink, and Eastern and Western meadowlarks. Habitat of the Henslow's Sparrow was the most distinctive of the 7 species. It exhibited preference for either the highest or lowest value for each parameter. It selected the highest levels for grass-leaf narrowness, forb-leaf smallness, forb-stem straightness, total vertical vegetation density, and litter depth. It selected the lowest values for forb coverage, forb stem thinness, forb density, coverage of effective height of less than 5 cm, vegetation density 0-10 cm from the ground, and light intensity at 0-10 cm. Forbs were significantly taller and coverage by dead forbs was greater in Henslow's Sparrow territories than in territories of other species. The most distinctive feature was the density of the vegetation selected. Vertical density was greater in Henslow's Sparrow territories than in those of any other species, with low vegetation contributing the least to this density. There was little bare ground or area covered by low vegetation in territories. The Henslow's Sparrow spent more time in forbs than Savannah and Grasshopper sparrows despite having fewer forbs in its territories. Species arranged in the order of increasing habitat richness (vegetation density and height and litter coverage and depth) were Western

Meadowlark, Vesper Sparrow, Savannah Sparrow, Grasshopper Sparrow, Eastern Meadowlark, Bobolink, and Henslow's Sparrow.

Some studies concluded that the Henslow's Sparrow is adversely affected by edge; others found no edge effects. In Pennsylvania, density was highest in grasslands with small perimeter-to-area ratios of less than 0.141 km per ha, but it was detected in areas with ratios as high as 0.16 km per ha. It was less likely to occupy small grasslands, especially if they had complex shapes. Hill and Diefenbach (2014) concluded that it may avoid edges because lower densities occurred in small grasslands with large perimeter-to-area ratios. In Illinois, it was more inclined to nest in the interior of fields than within 50 m of a wooded area. In Missouri, nest success was lower less than 50 m from a shrubby edge, presumably because of mammalian predation (Herkert 2002; Winter and Faaborg 1999). In North Carolina, it was dispersed randomly or evenly in fields (Lynch and LeGrand 1985). In Ohio, mean distance of nests from woodlands was 161.1 m, but this was not compared with random sites (Graves et al. 2010). In Kentucky and Tennessee, it was 59% more abundant at points distant from a road than at points on roadsides. This may have been a result of the distribution of habitat. The mean percent land cover by old field was greater 600 m from roads and the mean percent land cover of forest was greater at roadside points. Sample sizes were small and Lituma and Buehler (2016) cautioned against drawing any conclusions about its road avoidance. In Kansas, 13.9% of singing males were within 100 m of woodland edge and 19.0% were within 100 m of savannah habitat. Grassland areas were used significantly more than other habitats. In Wisconsin, the mean distance from territory boundaries was 175.0 m from woods (range 90-240 m), 22.5 m from a fence line (range 5-50 m), and 40.0 m from a cultivated field (range 10-100 m). Territories appeared to be situated randomly from these features (Wiens 1969). There appears to be no evidence that the Henslow's Sparrow consistently avoids edge.

Most studies concluded that the Henslow's Sparrow is area sensitive, but it has been documented nesting in some very small patches. In Ontario, it is generally agreed that it requires grasslands at least 30 ha but that grasslands larger than 50 or even 100 ha may be required to maintain a viable population. Nonetheless, it has nested in much smaller fields in the province. A 3-ha field was occupied in 2 consecutive years near Brockville. Extensive searches for the Henslow's Sparrow were made in Ontario in those 2 years, including much larger patches, and this was the only record for it (Austen and Cadman 1993; Kraus 2015; Pearce et al. 2010). In Missouri, it was 1.8 times more abundant on prairies larger than 110 ha than on smaller prairies (Pruitt 1996). Another Missouri study determined that it was significantly affected by fragment size, but the extent to which patch size affected its density varied greatly among years. Vegetation characteristics were more important in determining its density. Nest success was not affected by patch size (Winter and Faaborg 1999). In New York, it occupied fields 36-100 ha (mean 66 ha). Occupied fields were significantly larger than the mean of 19 ha for unoccupied fields (Peterson 1983). Smith and Smith (1992) concluded that it required 30 ha in New York. In Illinois, grassland size appeared to be the most important factor influencing occupancy. It occurred in only 1 grassland smaller than 100 ha, but occasionally occurred within small patches (1 ha) of unburned prairie within a larger (120 ha) matrix of burned forest (Herkert 1994b). In the same study area, the Henslow's Sparrow occurred on 73% of transects with suitable habitat in grasslands larger than 100 ha, but on 0% of transects with suitable habitat in smaller patches. It rarely occurred in grasslands as small as 10 ha. The area at

which the probability of occurrence was 50% of the maximum was 55 ha (Herkert 1994a). Also in Illinois, Walk and Warner (1999) studied 9 grasslands 7-120 ha in size. It was not documented on the 3 smallest grasslands that were 7, 17, and 32 ha. It occurred in 1 of 4 years on patches 40 ha and 44 ha and occurred more frequently on larger patches. The minimum area requirement for the Henslow's Sparrow was estimated at 75 ha, the area when the frequency of occurrence was 50% of its maximum. Based on data from Maryland, Skipper (1998) concluded that it required a minimum of 28 ha of grassland in the east, but Ells (1995a) reported it nesting in a 6.9-ha field in Massachusetts. In Pennsylvania, Hill and Diefenbach (2014) determined that grassland area itself was insufficient to explain occupancy patterns, but it was less likely to occupy small grasslands with complex shapes. They detected it in grasslands as small as 12.9 ha. Occupied fields in Kansas averaged 29.7 ha (range 9.8-39.1 ha; Schulenberg et al. 1994). In Minnesota, 2 fields with a combined area of 23.1 ha were used in 15 years (Pruitt 1996). In Iowa, fields that supported it were 16-65 ha (Melde and Koford 1996). In Kentucky and Tennessee, almost all nests were in the largest fields. A few nests were in fields as small as 4 ha; all were within 10 km of larger fields (Giocomo et al. 2008). In Michigan, it nested regularly in a 12.1-ha field (Robins 1971a). Studies in Missouri, Kansas, and Ohio demonstrated that it can occur in small fragments (Winter 1999). In Ohio, 6 occupied fields averaged 12 ha and the smallest was 8 ha. Three occupied CRP grasslands averaged 13 ha (range 1-26 ha; Swanson 1996). In Missouri, it was absent in a 28-ha isolated prairie but present in a 16-ha fragment that was 1.6 km from a larger prairie where it was present. Although it may be sensitive to habitat fragmentation in some areas, nesting success does not appear to be affected by patch size. Density increased with the total area of grassland in the landscape and with decreasing distance among grassland patches (Herkert 2002). In most areas, including Ontario, the Henslow's Sparrow appears to be area sensitive. The minimum size of grassland it requires varies geographically, largely depending upon the regional abundance of grasslands and its own abundance. Where it is rare, it is most likely to occupy the best habitats and these are most likely to consist of the largest patches of habitat. It may occasionally occur in smaller than normal patches within a region, but populations in smaller patches are less likely to be sustainable and birds may exhibit lower site fidelity to small sites (Pearce et al. 2010; Pruitt 1996).

Ontario nests were well hidden in and supported by clumps of tall vegetation that was often dead growth from previous years. Nest heights varied from being on the ground to 20 cm above ground (Peck and James 1987; Richardson 1933).

In Michigan, Hyde (1939) summarized 3 types of nest locations. Most nests were built at or near the bases of thick clumps of grass with the base of the nest 5-7.6 cm above ground. Dead grasses at the base of these clumps formed arched roofs over the nests. Some nests were 15-50 cm above ground and fastened to vertical stems of growing forbs and grasses. These nests were associated with advanced growth later in the season. They were usually deeply cupped and not arched over. Approximately 10% of nests were depressed into the ground and were either arched over by projecting earth or protected by dense vegetation. One nest was in a shallow, open saucer of grasses among young green vegetation that afforded no concealment. One nest was in a shrubby cinquefoil. A Kansas nest was 10.2 cm from the ground in a hollowed-out clump of little bluestem 37-39 cm tall. In many areas, nests are in clumps of little bluestem, but they have also been concealed in smooth brome, orchard grass, big bluestem, and Indian grass. Some nests are woven

into the supporting grasses; others are loosely attached. Nests are not reused and a new nest is built for each clutch (Guzy et al. 2002; Melde and Koford 1996; Reinking and Hendricks 1993; Robins 1971a; Schulenberg et al. 1994; Wiens 1969; Winter 1999).

The Henslow's Sparrow has often been described as being colonial or loosely colonial. Territories may be clumped together, but they may also be evenly or randomly distributed, and it may also nest solitarily. It is not a true colonial nester. There are 4 potential reasons why territories are sometimes clustered: the occupied area may have some microhabitat feature that makes the area more optimum than unoccupied areas; the presence of conspecifics may be a cue that it is a good breeding location; clumping of territories may provide enhanced protection from predators such as the Northern Harrier, with alarm notes being given when a sparrow detects a hawk; and having territories close to each other may facilitate extra-pair copulations. There is great variation in the stability of territories and their boundaries. In some areas, boundaries remain fairly constant throughout the season. In other areas, boundaries may be constantly shifting, even in response to human disturbance early in the season, and some males may occupy more than 1 territory in a season. In Michigan, 10 males had a single territory that remained stable over the season, 2 males had 2 successive territories, 2 males had 3 territories, and 4 males had 4 territories. Over the season, shifting of territories, disappearance of singing males, and colonization by new males were common. For males with 4 territories within a season, individual territories persisted for 28-30, 32-34, 22-23, and 34-35 days. In Maryland, some males remained on the same territory from early March until mid-August. Others began singing in early August in areas that were previously unoccupied. Usually singing in these areas lasted for only 3-4 days and then the territory was abandoned. During the nestling period, singing is greatly reduced but the territory is still defended. In Michigan, territories were not defended after mid-September although birds remained in the area for another month. These territories were distinct units separated by a buffer on all sides. The average distance between territories varied inversely with population. The distance between territories was 14 m in July when the population was at its peak and 131 m in September when the population was at its lowest. Thirteen of 22 territories (59.1%) in Pennsylvania overlapped. One territory in Oklahoma was about 1 ha. In Michigan, territories averaged 0.32 ha. Most territories were smallest there at the beginning of the season and increased the remainder of the year, but this was not true for all individuals. Mean territory size was 0.25 ha in the first half of May, 0.25-0.36 ha from May through July, and 0.65 ha in September. In Missouri CRP lands, there were no significant differences in territory sizes in warm-season native grasses and cool-season nonnative grasses. Mean territory sizes in native grasses over 2 years were 0.38 ha and 0.42 ha (range 0.03-1.11 ha) compared with 0.31 ha and 0.36 in nonnative grasses (range 0.01-1.25 ha). Territories averaged 0.18 ha on reclaimed surface mines in Pennsylvania. In Texas, 6 territories averaged 1.01 ha (range 0.15-1.91 ha). In Wisconsin, the average territory size was 0.61 ha (range 0.28-1.09 ha). Mean territory sizes changed with season there as well: 0.36 ha 5-9 May, 1.17 ha 15-25 May, 0.81 ha 28 May to 10 June, and 0.81 ha 14-25 June (Arnold and Garza 1998; Dornak 2010; Graber in Austin 1968; Herkert 1994b; Herkert et al. 2020b; Hyde 1939; Jaster et al. 2013; Lynch and LeGrand 1985; Pruitt 1996; Robins 1971a; Schulenberg et al. 1994; Skipper 1998; Wiens 1969).

Natal philopatry is low, although few nestlings and fledglings have been banded. In Michigan, 0 of 18 nestlings and 2 juveniles returned the following year. In Maryland, 0 of 36 fledglings returned;

0 of 9 juveniles returned in Missouri. In Ohio, 0 of 13 banded juveniles returned (Ingold et al. 2009; Jaster et al. 2013; Pruitt 1996; Skipper 1998).

Even in the core of its range where the Henslow's Sparrow is most abundant, adults exhibit low site fidelity. Throughout its range, birds may be present at a site for 1 to a few years and then disappear inexplicably. These same areas may be recolonized in subsequent years. In many areas, fields may be occupied for only 1 or 2 years. Based on BBS data, it returned to an entire route (30 km^2) in only 50% of years and was occasionally conspicuously absent from broader regions, with only 63% prevalence at a scale of 31,000 km^2. It was not consistently present (with prevalence greater than 75%) until the resolution was broadened to cover 126,000 km^2. It was concluded that the Henslow's Sparrow was nomadic in successive breeding seasons across multiple scales. It may not return to sites where it previously nested even if there have been no changes in habitat. Nomadism may be associated with the spatial and temporal patchiness of suitable breeding habitat and is a sound strategy given that habitat suitability is often ephemeral due to succession, mowing, and fire. Settling suitable habitat as it is encountered upon arrival in the breeding areas rather than homing is advantageous. It appears to track disturbance cycling across the landscape, moving among high-quality habitats characterized by patches that have been idle or only lightly disturbed for 2 or more years. At broader scales, it may respond to droughts, late springs, and regional variation in land use (Austen and Cadman 1993; Austen et al. 1995; Coffin and Pfannmuller 1988; Committee on the Status of Species at Risk in Ontario [COSSARO] 2011; Dornak 2010; Dornak et al. 2013; Hyde 1939; Pruitt 1996; Wiens 1969). In Maryland, 5 of 37 males (13.5%) and 0 of 14 females returned for an overall return rate of 5 of 51 adults (9.8%). Returning males settled an average of 93.4 m from the banding location (range 56-165 m; Skipper 1998). In Missouri, 5 of 32 males (15.6%) returned the following year and all occupied the same territory. One of 13 females (7.7%) returned to the same field (Jaster et al. 2013). In Ohio, 10 of 101 adults (9.9%) returned. All returns were by birds that had been banded in unmowed areas and all but 2 (80.0%) returned to unmowed areas. No birds banded on mowed areas returned to these areas when they were mowed again the following year. Two birds returned in 2 consecutive years and one returned in 4 consecutive years (Ingold et al. 2009). In Kansas, 0 of 13 adults returned even though the site still supported 37 pairs. Return rates of adults in other areas were: 1 of 5 (20.0%) in Minnesota, 0 of 24 in Michigan, 2 of 7 (28.6%) in Texas, and 0 of 17 in Missouri (Arnold and Garza 1988; Herkert et al. 2020b; Pruitt 1996).

Limiting Factors

Eggs have been reported in Ontario nests from the beginning of June until mid-August, with most present from the second week of June through the first week of July (Peck and James 1987). It takes 3-6 days to complete the nest. It is unknown whether egg laying starts as soon as the nest is complete. Eggs are laid at the rate of 1 a day and incubation begins with the laying of the last egg. The incubation period is 10-12 days. The nestling period is 9-10 days (Austen et al. 1995; Graber in Austin 1968; Herkert et al. 2020b; Hyde 1939; Robins 1971a; Winter 1999).

Egg dates suggest that the Henslow's Sparrow may raise 2 broods in Ontario, but this has not been confirmed. The extended egg-laying season with double peaks of activity suggest that 2 broods are raised in many, or most, other places. Two broods have been confirmed in Michigan and Kentucky. In Kentucky, 2 pairs successfully raised 3 broods. It is probable that 2 broods are raised in

most areas. Renesting is common if a clutch or brood is lost. In Michigan, a replacement nest was built 15 m from the first one 5-6 days after the original nest was destroyed. Clutches of 3-5 eggs have been reported in Ontario with most containing 4 eggs (mean 4.09 eggs). Clutches of 2-5 eggs have been reported elsewhere with 3-5 eggs the normal range and 4- and 5-egg clutches most common. In Kentucky and Tennessee, the mean clutch size was 3.8 eggs with a range in means in different years of 3.3-4.4 eggs. Other mean clutch sizes include 3.8 in Missouri, 4.06 in Indiana, 4.4 in Michigan, and 4.3 in Kentucky. In Kentucky and Tennessee, clutch size initially increased, peaked in mid-season, and then declined. In Missouri, clutch size tended to decrease with the season, but not significantly (Crimmins et al. 2016; Giocomo et al. 2008; Herkert et al. 2020b; Hyde 1939; Peck and James 1987; Reinking and Hendricks 1993; Robins 1971a; Skipper 1998; Winter 1999).

The age at first breeding is unknown, but it is likely that both sexes can breed in their first year. In Missouri CRP lands, only 19 of 54 males (35.2%) with territories were paired. There was no difference in pairing success in native and nonnative grasslands. No explanation was offered for the low pairing success. The sex ratio may have been male biased at this site, yearlings may have failed to attract a mate, possibly yearlings are not capable of reproducing, or habitat may have been suboptimal in areas where males remained unmated. The mating system is monogamous with no indication of polygyny. Extra-pair copulations were observed in Michigan and this may be a common mating strategy (Herkert et al. 2020b; Hyde 1939; Jaster et al. 2013; Wiens 1969).

In Wisconsin, the Henslow's Sparrow spent 93.6% of its foraging time in grass 11-15 cm tall and 6.4% of the time in grass 16-20 cm tall. It was not observed foraging in grass 0-10 cm tall or in the air, and it foraged in much deeper cover than other grassland species (Wiens 1969). In Michigan, about half the foraging trips by both sexes were outside the territorial boundaries. Males and females tended to forage in separate areas either within or outside the territory. Mean distances flown from the nest to forage were 30.8 m for males and 24.9 m for females. Each bird of a pair exhibited a strong directional bias in the area in which they foraged (Robins 1971b).

In Michigan, the primary food brought to day-old nestlings was smooth caterpillars, mostly owlet moths. These and soft abdomens of katydids, tree crickets, and grasshoppers were the chief items fed to young as old as 3 days. A greater variety of food items was fed to older nestlings, although orthopterans and caterpillars continued to dominate their diet. Young were also fed willow sawflies, spiders (including garden orbweavers), fireflies, and crickets. The food provided to young consisted of 80% orthopterans and caterpillars (Hyde 1939). In Michigan, the prey most commonly fed to nestlings consisted of caterpillars, primarily of snout moths, and scarab beetle larvae. These were provided to young on 44% of feeding trips. Other important prey included orthopterans (17%), leafhoppers (5%), and assassin bugs (5%). The latter 2 food items were small and probably formed an important part of the unidentified small insects that comprised 21% of the sample. Other invertebrate prey of lesser importance in nestlings' diet included cutworms, crickets, preying mantises, click beetles, fireflies, wasps, lacewings, dragonflies, spiders, and harvestmen. Smooth brome florets were fed on 2 days at 1 nest to nestlings 1 and 2 days old. Small insects and larvae were often brought several at a time and were the major food items fed to 1- and 2-day-old nestlings at all nests. Orthopterans were important foods over the entire nestling period, but most were fed to young in the 3 days prior to fledging. The wings of moths, hind legs of crickets and

grasshoppers, and forelegs of mantids were usually removed before they were fed to young. There were large differences in prey taken at various nests suggesting that adults were selecting prey based upon their availability, but there was no difference in the prey selected by the sexes at individual nests (Robins 1971b). In Illinois, food brought to nestlings consisted of 38.5% caterpillars, 30.7% orthopterans, 15.4% beetles, 7.7% hymenopterans, and 7.7% spiders (Herkert et al. 2020b).

In Michigan, 1 adult was observed eating a large katydid. Seventeen stomachs contained 82% animal food and 18% vegetable matter by volume. From April to September, animal food comprised 85-100% of the diet, except for 1 juvenile that had eaten only 10% animal food. Two stomachs collected in October contained only 9% and 15% animal matter. Orthopterans comprised 36.5% of the entire diet and more than 50% of the August and September diet; 17% of these were crickets and 8.2% were short-horned grasshoppers. Beetles comprised 19.3% of the diet and were found in all but 1 stomach. These included 6.5% weevils. Leaf beetles constituted 5.4% of the diet from April to September, mostly taken from leaves of goldenrods and evening-primrose. The Henslow's Sparrow also ate click beetles and ground beetles. From May to October, bugs comprised 12.2% of the diet, including milkweed bugs, stink bugs, and bug eggs. Lepidopterans comprised only 3.3% of the adult diet, fly remains or eggs were found in only 4 stomachs, and small amounts of hymenopterans, insect eggs, spiders, neuropterans, myriapods, and snails were found in stomachs. Grass seeds constituted 6.2% of the diet, about a third of the vegetation consumed. Grass seeds it ate included those of paspalum, foxtails, crabgrass, corn, and cutgrasses. Other seeds it ate were those of ragweed, smartweeds, sedges, beaked-rush, fox sedge, sheep sorrel, and violets (Hyde 1939). Judd (1901) analyzed 4 stomachs collected in summer and they contained beetles, owlet moth caterpillars, grasshoppers, bugs, and blackberries. The beetles consisted of ground, leaf, and click beetles, and weevils. Bugs were represented by soldier bugs and assassin bugs. Three collected in January in Texas had eaten a spider, grass fragments, and seeds of plants in the aster family.

The Henslow's Sparrow is an infrequent host of the Brown-headed Cowbird. This is because the nests are so well concealed and the cowbird appears to prefer to target woodland and shrubland species. In Missouri, no nests were lost due to parasitism, and both species fledged from parasitized nests. Sparrow clutch size was reduced by 0.9 egg as a result of parasitism. The number of young fledged per successful nests was 3.6 for unparasitized nests and 2.0 for parasitized nests. In Ontario, 1 of 12 nests (8.3%) was parasitized. Parasitism rates from other areas include 1 of 113 nests (0.9%) in Kentucky and Tennessee, 0 of 21 nests in Indiana, 1 of 1 nest in Kansas, 0 of 11 nests in Pennsylvania, 3 of 56 nests (5.3%) in Missouri, 1 of 135 nests (0.7%) in Indiana, 2 of 24 nests (8.3%) in Oklahoma, and 2 of 3 nests (66.7%) in Kansas (Crimmins et al. 2016; Galligan et al. 2006; Giocomo et al. 2008; Herkert et al. 2020b; Hill and Diefenbach 2013; Peck and James 1987; Rivers et al. 2010; Winter 1999; Zimmerman 1989).

Habitat loss and degradation are the greatest limiting factor for the Henslow's Sparrow. It is an early successional species with exacting microhabitat requirements. It is adversely affected if habitat is directly lost, if too much woody growth invades its habitat, or if disturbance results in loss of litter and dense standing dead vegetation. Historically, its habitat was maintained by wildfires, light grazing by bison, and periodic outbreaks by the Rocky Mountain grasshopper. Most native prairies have since been plowed under, there are essentially no wild herds of bison left, the Rocky Mountain

grasshopper is extinct, and fire is typically suppressed (Wells 2007). The Henslow's Sparrow now relies mostly on nonnative habitats for nesting, particularly in Ontario. It is dependent on human management such as prescribed burns, mowing, and grazing by livestock. This management is typically directed toward optimizing profit for humans and any benefits that may accrue to the Henslow's Sparrow are incidental. Where grasslands are managed for wildlife, waterfowl or upland game birds are typically the target species so any benefits to the Henslow's Sparrow are incidental (Pruitt 1996).

Forest clearing to create agricultural land enabled the Henslow's Sparrow to colonize Ontario, but agricultural practices are now the main cause of habitat loss. The losses are due mostly to conversion of pastures and unimproved hayfields to row crops and hayfields dominated by alfalfa. Many poorly drained fields were drained and converted to cropland. In Ontario, there has been a gradual loss of both summer fallow and pasture, with the area available in 1976 only half that of 1951. In 2006, there were 315,000 ha of summer fallow, natural pasture, and improved pasture in Ontario, a decline of 14% since 1996 and 61% since 1976. In Elgin County, low wet meadow habitat is almost gone; there are fewer marshes in Middlesex; there has been a decline in old fields in Oxford, Haldimand, and Norfolk; in Niagara, there are fewer uncultivated fields; there has been a loss of grassy fields and fallow land in Wellington; and successional changes have occurred in former fields in Northumberland. In 1937, there was a colony in Holland Marsh that persisted for about a decade until it was converted to market gardening. Early hay crops consisted of a mixture of grasses, clovers, and a small proportion of alfalfa. These were cut later in the season and often yielded only a single cut or a maximum of 2. Most hayfields are now planted to alfalfa which grows faster. It is cut much earlier in the season than traditional hayfields and 2 or 3 cuts are routinely made each year. In Ontario, habitat loss may also occur due to urbanization, but the effects of this are small compared with agricultural losses. Throughout its range, loss of habitat due to agricultural practices is the most significant limiting factor (Austen 1994; Austen and Cadman 1993; Austen et al. 1994, 1995; COSSARO 2011; Devitt 1967; Heagy 2011; Herkert et al. 2020b; Knapton 1984a; Lancaster et al. 2004; Pearce et al. 2010; Pruitt 1996; Swanson 1996).

Habitat may be lost due to natural succession or tree planting. In 1998, mowing and brush clearing was undertaken at Ostrander Point in Prince Edward County and this area attracted Henslow's Sparrows the next 2 years (Pearce et al. 2010). The site that was formerly occupied at Luther Marsh was planted to conifers and became unsuitable habitat by the early 1970s (personal observation). Many Ontario fields that it formerly bred in have succeeded to shrubland and forest and are no longer occupied (Austen et al. 1999). In Pennsylvania, Hill and Diefenbach (2014) conducted vegetation and breeding bird surveys on reclaimed mine sites 9 years apart. During this time, the amount of woody vegetation increased by 2.5 times and grass height and cover decreased. The Henslow's Sparrow decreased 49% between sampling periods. Surface mine habitats are ephemeral habitat for the Henslow's Sparrow unless regular maintenance occurs to arrest succession. In North Carolina pocosins that had been clear-cut and replanted to pines, habitat became unsuitable once the pines attained a height of 2.4-3.0 m (Lynch and LeGrand 1985).

Loss of grassland habitat has resulted in habitat fragmentation. There are fewer grasslands large enough to support Henslow's Sparrows. Smaller grassland patches have the potential to increase

predation and parasitism rates, but there are no real data to support or refute this. Because of its very specific habitat requirements and its requirement for large patches, only a very small proportion of Ontario agricultural grassland habitat is suitable. Remaining prairies are too small and fragmented to support populations. Assessments of former breeding sites since 1980 in 2002 and 2007-08 found that much of the former habitat now appears unsuitable due to changes in agriculture, conversion to shrublands, and development. Nonetheless, large areas of apparently suitable habitat remain in Grey, Prince Edward, Lennox-Addington, and Frontenac counties. The fact that these are unoccupied suggests that other factors may be affecting the Henslow's Sparrow, such as loss of wintering habitat, mortality between breeding seasons, local population losses due to small numbers of individuals, natural population fluctuations, or low site fidelity. The loss of wintering habitat is a real limiting factor to the Henslow's Sparrow. Perhaps the main reason for apparently suitable habitat remaining unoccupied in Ontario is the fact that this province is at the extreme northern extent of its range. When species decline as a whole, they may contract from the periphery of their range and breed only in their core range. It is also declining in states adjacent to Ontario so there is less likely to be recruitment from other areas (Austen 1994; Austen and Cadman 1993; Austen et al. 1995; Heagy 2011; Pearce et al. 2010; Pruitt 1996).

Prescribed burns are a common management technique used to arrest natural succession. If the fire is intense enough, it will kill shrubs and saplings that have become established. It also removes the litter layer and dead standing vegetation which usually makes the habitat unsuitable for the Henslow's Sparrow immediately after burning. At 1 Kansas site, it was absent at 4 sites where it had nested the previous year. This was because April burning removed the standing dead grass and litter. Rotational burning occurred every 3-4 years at this site and this activity appeared to be favourable for the Henslow's Sparrow (Schulenberg et al. 1994). On another Kansas prairie, it did not occur in areas that were burned in the spring. Over 2 years, 89 and 105 territories were mutually exclusive of burned areas. The most obvious difference between burned and unburned areas was the complete lack of litter and standing dead vegetation in burned areas. Areas that are never burned quickly become invaded with shrubs, so a 3-4-year rotational cycle of burning was recommended, with each tract being at least 30 ha in area. In Missouri, it occurred only on idle or lightly grazed, unburned prairie (Zimmerman 1988, 1989). In tallgrass prairies in Kansas, burns occurred in spring at frequencies of 1, 2, or 4 years. It was nearly absent in the year of the burn. More frequent burning was preferred there. In areas that had not been burned in 1-3 years, it was less abundant in areas burned every 4 years than those burned annually. Areas burned at shorter intervals had higher grass densities (Powell 2008). Also in Kansas, 96% of occupied areas had been burned 2 or 3 years previously. One occupied site was burned 4 years previously and no areas that had been burned in the same year were occupied. Burned sites reached the highest total vegetation cover and density in late spring rather than in summer, and this may have been important in establishing territories (Cully and Michaels 2000). At an Indiana site, burning every 3-5 years was necessary to manage succession. Densities usually peaked 1 year postburn. Some nested successfully during the same year following a spring burn, but density was lower in these areas (Crimmins et al. 2016). At another Indiana site, densities were highest 2 and 3 years after burning and declined in the fourth year. It preferred smaller fields in years 2 and 3, but larger fields in the first and fourth years postburn. Large grasslands may contain patches that did not burn and the effects

of shrub regrowth may be greater in smaller grasslands. A fire frequency of every 3 years would be beneficial for this population (Keating et al. 2023). In Illinois, burning had a significant effect and the Henslow's Sparrow was never encountered in a recently burned area. Densities in areas 2 years postburn were less than half of those 3 or more years postburn (Herkert 1994b). In Oklahoma, all nests were in areas that had not experienced spring burning (Reinking and Hendricks 1993). Periodic rotational burning is beneficial. This arrests succession and results in denser, more vigorous grass growth. In most cases, the habitat is unsuitable the year of the burn except for wet areas where not all litter and standing dead vegetation is burned. Many areas in the Midwest where prescribed burning occurs are devoid of Henslow's Sparrow because the frequency of burning is too high, preventing development of litter and dead vegetation layers. The optimum frequency of burning varies geographically and depends upon the soils, moisture regime, characteristics of the grassland, and how soon litter accumulates. In the case of small grasslands, the entire area is likely to be unsuitable habitat in the year of the burn (Herkert 2002; Pruitt 1996).

The Henslow's Sparrow avoids recently mowed areas. The frequency of mowing that occurs in privately managed hayfields severely limits or eliminates nesting. In Illinois, mowed areas were not completely avoided but densities in mowed areas were 90% less than those in unmowed areas. At a Kansas site, only areas that were not hayed the previous year were occupied. On reclaimed mines in Indiana, 252 Henslow's Sparrows were detected at point counts and many more were observed away from count areas; 0 occurred in hayed grasslands. It may use fields planted to switchgrass used in the production of biofuels. Due to the typical harvest regimes, these fields are likely to act as ecological traps, with a very small probability of any young being produced. CRP lands in Illinois and other states have been beneficial because these are typically planted to grasses and left idle for a 10-year period. Population gains as a result of CRP lands have not been sufficient to overcome losses. The CRP is a 10-year contract so much of this land may revert to agriculture. For lands remaining in the program, there may be a need to control succession for them to continue to provide habitat. Mowing is the preferred method of eliminating woody vegetation because the litter layer and standing dead vegetation typically recover faster. In Missouri, grasslands managed by mowing had almost 2 times as many Henslow's Sparrows as those managed by fire. In New York, maintenance mowing in mid-August allowed it to raise 2 broods while still leaving enough time for regrowth to provide dead vegetation for the next year. Even delaying mowing until mid-July may enable it to raise a single brood and at some sites this is done every other year. In Minnesota, it was recommended that a few small (0.4 ha or smaller) portions of a site be mowed, with 10% or less of the entire site being mowed. This slowed woody encroachment while maintaining enough area with standing dead vegetation, litter, and singing perches (Bajema et al. 2001; Cully and Michaels 2000; Hands et al. 1989b; Heagy 2011; Herkert 1994b, 1997, 2002; Knapton 1984a; Pruitt 1996; Robertson et al. 2012; Swanson 1996). Wolcott et al. (2023) recommended that grassland management be deferred until August to protect both nests and fledglings.

The Henslow's Sparrow avoids grazed areas unless the intensity of grazing is very low. It is absent in areas subjected to moderate or heavy grazing. The level of grazing pressure required for a reasonable economic return is not compatible with this sparrow. In 1 year of a 4-year study in Michigan, it was much more abundant in fields that were lightly grazed than in ungrazed meadows. Of more than 500 sightings of the Henslow's Sparrow in Indiana reclaimed mines, none occurred in

grazed areas. In addition to modifying the habitat so that vegetation is too short or sparse, cattle may trample or lay on nests. In Kansas, it was absent at a site until grazing had been halted for 2 years. It nested successfully in Missouri and New York in pastures grazed by cattle from mid-May to mid-October. Grass height averaged 30.4 cm or more in Missouri and 61 cm in New York. Light grazing after the nesting season may successfully inhibit succession while maintaining habitat and avoiding nest destruction by cattle (Bajema et al. 2001; Hands et al. 1989b; Herkert 2002; Hyde 1939; Ingold et al. 2009; Peterson 1983; Pruitt 1996; Swanson 1996).

Local populations may fluctuate with spring precipitation rates. In Illinois, population fluctuations were associated with the total amount of precipitation received January through April. Abundance tended to increase in years when the spring precipitation was greater than in the previous year and decline when spring precipitation declined (Herkert et al. 2020b). Zuckerberg et al. (2018) determined that its abundance was positively correlated with the amount of precipitation received in the previous summer and the amount of rain from June to August in the current breeding season. These studies suggest that the Henslow's Sparrow may be vulnerable to climate change.

Human disturbance is potentially a limiting factor. Vehicle traffic during a single night in a field caused boundaries of 2 of 6 territories to shift. Disturbance by birders and photographers has been considered a risk in Massachusetts and Ontario (Pruitt 1996). Hands et al. (1989b) recommended that human access to nesting fields should be prohibited to prevent disturbance.

Herkert (2002) offered management recommendations for the Henslow's Sparrow: provide 30 ha or more of contiguous grassland or a complex of smaller areas close together; create large grassy areas near small prairie fragments; remove woody vegetation within and along edges of grasslands to discourage predators; implement a rotational disturbance regime and never burn, mow, or otherwise disturb an entire site within a single year; conduct management treatments before birds arrive or after the young fledge; provide dense and moderately tall (higher than 30 cm) grassy vegetation; remove woody vegetation when it becomes taller than grass or herbaceous vegetation; use prescribed burns on a rotational basis to remove woody cover, and do this in early spring or late autumn; and create restoration areas that are larger than 50 ha and preferably larger than 100 ha.

Status

The Henslow's Sparrow was first reported in Ontario in 1898 at 3 locations: near Sarnia, at Lake St. Clair, and in Leeds County near Lansdowne where a nest was found. It was not seen in the latter region for another 52 years. It was later found breeding in the tallgrass prairies of Walpole Island. Some authors speculated that it always nested in the province; others assumed that the 1890s records represented the initial colonization. It seems most likely that the Henslow's Sparrow was not historically part of Ontario's avifauna and that it colonized the province as it shifted its range eastward and northward in response to forest clearing. It did not become established until 1881 in Michigan, 1894 in Ohio, 1880 in Minnesota, 1870 in Wisconsin, and 1887 in inland New York. It seems unlikely that it would have been present in Ontario much before its presence was confirmed. By the early 1900s, it was breeding regularly in Essex and Lambton counties and nested at Lake Joseph in Muskoka District in 1902. A large colony occurred at Long Point in 1927, it was fairly common in the London area by 1931 and one of the more common birds in the Rondeau area at this time. The late

1920s and the 1930s appear to have been the peak years for it (Austen and Cadman 1993; Austen et al. 1994, 1995; Heagy 2011; Hyde 1939; Knapton 1984a, 1984b; Weir 2008). Baillie and Harrington (1937) considered the Henslow's Sparrow a local summer resident in extreme southern Ontario, where it bred only south and west of York Region. Sarnia and Bradford appeared to mark its northern limit but it was fairly common in certain locations. The population and its range continued to increase through until the 1960s after which it began to decline. By 1966, its range had expanded northeastward to Ottawa and Morrisburg. It peaked in abundance in Niagara Region 1947-52 but remained uncommon until 1965. It may have nested on Manitoulin Island in 1952 and probably bred in the Vermilion Bay area in Kenora District in 1975 and 1976. The first breeding season record in the Hamilton area was in 1929 and it was encountered in 12 of 20 years 1931-50. During the 1930s and early 1940s, there was a colony in a large abandoned field that was subsequently developed. From the 1930s to 1970s, various small colonies were discovered. These only lasted for a few years before disappearing, only to have another small colony appear elsewhere. The last breeding record there was in 1981. In the mid-1960s, it was common in old fields and hayfields in Durham Region, but these sites are no longer extant. Results at Hamilton are typical of the entire province. Numbers probably peaked in the 1950s and 1960s and were followed by a precipitous decline in the 1970s and 1980s. The range contracted from the southwestern agricultural landscape, more northern areas, and the eastern part of the former breeding range. Large colonies were presented at Tiny Marsh with as many as 43 seen in 1978; this colony was last occupied in 1980. Colonies at Barrie, Holland Marsh, Luther Marsh, and in Chatham-Kent, Lambton, Middlesex, Haldimand, and Norfolk counties were abandoned. In Elgin County, isolated colonies numbering as high as 12 birds were reported annually in the 1930s and 1950s but there have been no breeding records there for over 3 decades (Austen and Cadman 1993; Austen et al. 1994; Brewer 1977; Curry 2006; Devitt 1967; Heagy 2011; Knapton 1984a, 1984b; Lancaster et al. 2004; Speirs and Orenstein 1967). During the first atlas, the Henslow's Sparrow was documented in only 38 squares, not all of which were occupied in each year of the atlas. Only 1 colony larger than 10 pairs was found. It was considered unlikely that the provincial population exceeded 50 pairs. Most records were concentrated in the Kingston area and, to a lesser extent, in Wellington and Dufferin counties in the general vicinity of Luther Marsh (Knapton in Cadman et al. 1987). In 1983, the known population was 25-29 individuals at 13 sites; in 1982, only 6 individuals were detected and 17 were found at 7 sites in 1981 (Austen 1994; Austen and Cadman 1993; Austen et al. 1994, 1995; Knapton 1984a). James (1991) considered the Henslow's Sparrow a rare to locally uncommon summer resident in the south north to Bruce County and Kingston.

Numbers continued to decline after the first atlas. A concerted effort to find the Henslow's Sparrow in 1992 and 1993 found only a single singing male each year, both at the same location. In 1988-90, searches for it were made in Grey, Wellington, and Dufferin counties and totals of 2, 1, and 0 were detected in those 3 years. In 1989, a site with 10 territories was located in Haldimand-Norfolk, but it was abandoned during the breeding season. By the early 1990s, it was concluded that the province supported fewer than 10 pairs. Nonetheless, several singing males were found in 1999 and 2000 at a site in Prince Edward County that was managed for Henslow's Sparrows in 1998. At least 7 singing males were found in Halton Region in 2000 (Austen 1994; Austen et al. 1994, 1995; Knapton 1993; Pearce et al. 2010). The second atlas demonstrated an 86% decline in its probability of

observation since the first atlas. It was documented in only 9 squares in the province and probable breeding evidence was attained in only 3 squares. These included 2 birds in Chatham-Kent, a singing male that remained at least a week in Grey County, and as many as 4 birds in Halton Region in 2001. It was absent in the Kingston and Luther Marsh areas. Three of the 4 records from the Carolinian Forest Region were in native tallgrass prairie remnants or restorations. It was concluded that breeding pairs, if present at all, are likely to be very few in any given year. The species is difficult to detect and its habitat is often not checked by birders, so it is easily overlooked (Tuininga in Cadman et al. 2007). From 2000-09, the Henslow's Sparrow was reported from only 16 sites, including those documented in the atlas. Most records were of single males singing on a single day with no subsequent occurrence in either the same or following years. The most recent record of a pair is the 2005 Chatham-Kent observation reported in the atlas. The population in recent years has barely been above 0 and there is no evidence that any young have been produced in several decades. The Natural Heritage Information Centre in Ontario has 73 element occurrences. Sixteen are considered extirpated and 51 are historical. Only 6 were documented in the past 20 years and none are ranked as high-quality occurrences (COSSARO 2011).

Prior to European settlement, the Henslow's Sparrow was probably restricted to the prairies and the Atlantic coast. It nested in native tallgrass and mixed-grass prairies in the west and low wet meadows with tall grasses. Along the Atlantic coast, it probably nested on the drier edges of salt marshes, habitat it continues to occupy. Within the eastern forest, it probably nested in prairies, savannahs, and openings created by forest fires and First Nations. It nests in cranberry bogs in New Jersey and Michigan and these habitats would have been available historically. With the arrival of Europeans, its habitat was altered drastically. Massive amounts of habitat were lost in the west as prairies were converted to agricultural land. This was partially compensated for by deforestation in the east which allowed it to colonize exotic grasslands, pastures, and old fields north and east of its original range. It began to nest in a variety of anthropogenic habitats, including CRP lands, hayfields, abandoned fields, meadow marshes, reclaimed mine surfaces, capped landfills, sphagnum bogs mined for peat, lightly grazed pastures, military training areas, and very young conifer plantations. In North Carolina, it nested in pocosins that had been clear-cut and planted with pines 0.6-2.4 m tall. Pocosins are wetlands on poorly drained fine sandy or sandy loam soils that have a seasonally high water table at or near the surface. The pattern throughout the east was similar to what occurred in Ontario: colonization in the 1880s to 1900s, growth in populations until the mid-19th century, followed by a significant decline due predominantly to habitat loss. BBS data indicates that it declined at an annual rate of 8.7% continentally 1966-2004. Its decline is the steepest of any North American grassland songbird. It is now extirpated as a breeding species in North Dakota, Texas, Quebec, most of New Jersey and Delaware, most of Virginia, and part of West Virginia. Prior to 1900, it was abundant in Illinois and among the most numerous prairie species in some areas of the state. Populations declined by as much as 94% between 1958 and 1979. This was attributed to a 65-75% decrease in grassland habitat and a 75% decline in its density in the remaining grassland. The CRP has partially slowed the decline in some areas but has not fully compensated for losses elsewhere. Many of these lands will probably be converted back to agricultural uses once the 10-year contracts expire. In Ohio, Pennsylvania, and some other states, reclaimed surface mines are providing large tracts of habitat for the Henslow's Sparrow. Unless active management is undertaken, these areas

remain suitable for only a few years due to natural succession (Askins et al. 2007; Graber in Austin 1968; Herkert 1994a, 1994b; Herkert et al. 2020b; Hyde 1939; McCracken 2005; Melde and Koford 1996; Lynch and LeGrand 1985; Pearce et al. 2010; Pruitt 1996; Swanson 1996; Wells 2007).

The Henslow's Sparrow was designated threatened nationally in 1984 and its status was upgraded to endangered in 1993. In Ontario, it was designated threatened in 1986 and endangered in 1994 (Austen 1994; Austen and Cadman 1993; Austen et al. 1995).

Four recovery strategies have been prepared for the Henslow's Sparrow, with the objectives becoming more pessimistic with time. In 1995, the recovery objectives were to prevent a further decline and establish a stable or increasing breeding population of 500 adults distributed across Ontario in 50 colonies with a minimum of 10 birds in a colony (Austen et al. 1995). In 2006, the short-term objective for the next 5 years was to create large patches of suitable secure grassland habitat at 3 locations in Ontario. The long-term objective was to increase the population to a stable annual minimum population of 50 breeding pairs among at least 3 geographically distinct nesting areas over the next 20 years (Pearce et al. 2006). In 2010, the objective over the next 5 years was to establish and secure at least 1 large patch (larger than 50 ha) of suitable grassland habitat and achieve at least 1 stable population of 5-10 pairs (Pearce et al. 2010). In 2015, no objectives for recovery were stated but suggestions for habitat regulations under Ontario's *Endangered Species Act* were recommended in the event that the species was found breeding (Kraus 2015).

POSTFLEDGING PERIOD

In Missouri during the dependent stage, all fledglings remained within 100 m of the nest for the first 2 weeks after fledging. Average movement between daily locations was 36 m. At the onset of the independent period (16-23 days postfledging, median 19 days), fledglings moved an average of 236 m from the nest with an average of 90 m between daily locations. Fledglings used an area of 1.5 ha, considerably larger than the 0.29-ha territory. Areas used during the dependent period had a lower percent cover of woody vegetation than random sites. During the independent period, fledglings used areas with shorter grass and lower percent cover of woody vegetation than occurred in random sites. Areas used during the independent period had a higher percent cover of forbs and lower percent cover of litter than areas used during the dependent period. Habitat characteristics at the territory scale (100-m radius) influenced fledgling survival. Survival decreased as shrub cover increased and as the season progressed. Survival was higher 2 and 3 years after burning than 1 year after burning (Young et al. 2019).

It appears as though adults remain in the breeding area until autumn migration. In August in Michigan, juveniles made minor movements into adjacent habitat. Some were observed in weedy vegetation along a railway right-of-way that ran between 2 breeding areas, but the adults remained in the breeding habitat (Hyde 1939).

MIGRATION

The Henslow's Sparrow is believed to migrate singly or in small groups at night over a period of 1-2 weeks (Pearce et al. 2010). Rivers may function as major migration corridors and Lake Ontario may act as a barrier to migration (Hyde 1939).

Males tend to arrive in spring earlier than females, but the interval between the sexes' arrival has not been determined in Ontario (Knapton 1984a). Spring migrants arrive in southwestern Ontario from mid-April to mid-May and arrive in the breeding areas in late April and early May (Austen et al. 1995; Black and Roy 2010; Curry 2006; Devitt 1967; Heagy 2011; LaForest 1993; Lancaster et al. 2004; Weir 2008).

The Henslow's Sparrow leaves Ontario during September or early October and probably winters along the Gulf Coast of the United States. Birds may remain on the breeding grounds until autumn departure, but autumn migrants have been seen in late July. It has been seen as late as mid-October. One seen at Luther Marsh on 8 October was in a field where breeding did not occur (personal observation), but 1 at Millgrove on 7 October appeared to be still on territory (Austen et al. 1995; Curry 2006; Devitt 1967; Heagy 2011; Hyde 1939; LaForest 1993; Weir 2008).

During migration, the Henslow's Sparrow occurs mostly in grasslands and wet meadows but may also occur in hedgerows, in small copses of trees, and forest edges. In Iowa, the first spring arrivals were in shrubs at edges of wooded areas, later moving out into prairie. A group of 3 that appeared to have just arrived in Michigan were seen around a small puddle in a heavily grazed field that offered no cover (Herkert et al. 2020b; Hyde 1939; Pearce et al. 2010). An autumn migrant at Luther Marsh was observed in a moist field dominated by reed canary grass and several at Conestogo Lake were in a 160-ha field dominated by timothy, quack grass, and orchard grass (personal observation).

Suitable habitat for migrants has decreased significantly but it is unknown if this is causing adverse effects. The Henslow's Sparrow occasionally strikes buildings, communication and television towers, and other tall structures during migration, particularly in autumn. It may also be vulnerable to adverse weather during migration. Thirty-two were killed in an April storm in Indiana in 1960 (Herkert et al. 2020b; Pruitt 1996).

James (1991) considered the Henslow's Sparrow a rare migrant and this is confirmed in all books on regional populations. At least 20 were seen at Conestogo Lake on 27 September 1973. It bred there that year so it is uncertain if these were migrants or had nested or been raised on site (personal observation). There are fewer autumn than spring records because it tends to be silent at this time. It is still found during migration almost every year, but numbers are declining. Numbers reported in the entire province during migration from 1986 to 1993 were 17, 17, 18, 0, 3, 5, 7, and 8 (Austen 1994; COSSARO 2011).

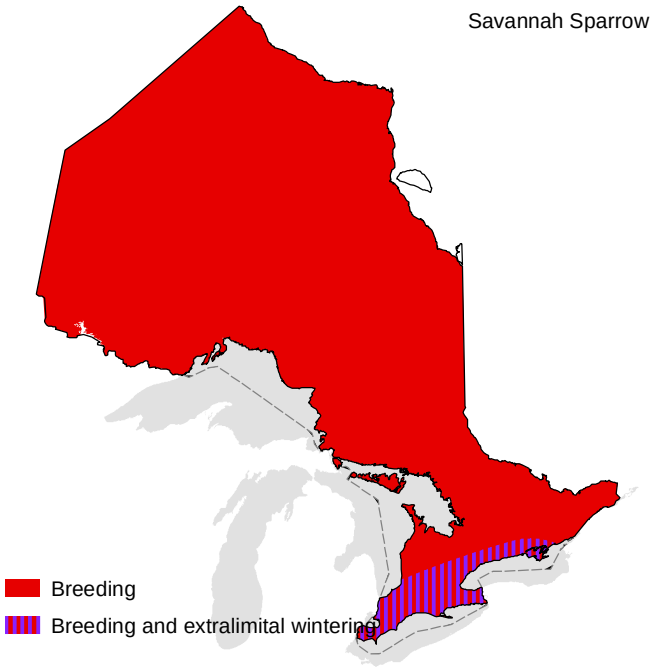
Savannah Sparrow

Passerculus sandwichensis

BREEDING SEASON

Habitat Requirements

In southern Ontario, the Savannah Sparrow nested in grassy fields, hay and clover fields, and occasionally grain fields (50.4% of southern nests); in open and overgrown pastures (34.5%); in other grassy areas such as playing fields, campgrounds, airfields, lawns, young conifer plantations, and orchards (4.3%); on grassy dunes, river banks, floodplains, and shorelines (3.6%); on roadsides, embankments, and in fencerows (3.2%); on mine tailings and in lumberyards (2.9%); on blueberry barrens (0.4%); in heath bogs (0.4%); and on a rocky island near a tern colony (0.4%). In northern Ontario, nesting occurred in sedge and grass marshes (44.6% of nests), on sedge-lichen tundra (25.0%), in bogs and fens (23.2%), and in salt marshes (7.1%). It nested in both wet and dry habitats that were open with sufficient growths of grasses, sedges, or forbs to provide nest sites and concealment (Peck and James 1987).



In the Hudson Bay Lowland, the Savannah Sparrow is most abundant along the James and Hudson bay coasts from the Moosonee area to York Factory. Highest numbers occurred in dwarf willow and birch at edges of barrens. It also occurred in the long grass of coastal barrens, occasionally in open grass or scrub areas behind the first rows of spruce, and among willows and alders at the Attawapiskat River. It was scarce or absent in deep alder thickets. Occasionally it occurred in isolated patches of spruce, but never within the main spruce forest. It was especially common at a marsh at Beacon Point in mid-July and appeared to nest in Moosonee (Manning 1952). On the Twin Islands in James Bay, it nested in dense dwarf birch and avoided the shoreline (Manning 1981). Wilson and McRae (1993) concluded that it was the most abundant nesting passerine at all the coastal stations they examined. At Moosonee, it was most abundant in extensive grassy areas such as the airport, but a few nested in a tamarack fen. There are extensive areas of bogs and fens in the southern portion of the Hudson Bay Lowland that may also support populations of the Savannah Sparrow.

Erskine (1977) considered the Savannah Sparrow characteristic of open bogs and fens with low (10-20 cm) ericaceous shrubs, sedges, and a few herbaceous species in the Boreal Forest Region. It also inhabits wetter sedge meadow bogs. It may nest in unvegetated areas in addition to natural grasslands, sand barrens, and abandoned farmland. Nesting may occur in burns or clear-cuts, but only if a ground cover of grass is present. Because it avoids forested habitat, it is associated with the tundra-forest and alpine-forest ecotones. In the Clay Belt, it was the most common sparrow around farms, lakesides, and river banks. It also nested in bogs and fens and clearings about buildings (Smith 1957). In the Clay Belt, it nested in a wet nutrient-poor stand dominated by Labrador tea, leatherleaf, and sphagnum moss (Welsh and Lougheed 1996). Near Hearst, it nested in a 3-year-old clear-cut in lowland coniferous forest (Welsh and Fillman 1980). Near Pickle Lake, it occurred regularly in large open bogs (James 1980). Between Pickle Lake and Little Sachigo Lake, highest densities were in tundra followed by heath, mixed scrub, and coniferous scrub. It was absent in deciduous scrub and all forested habitats (McLaren and McLaren 1981). Along the northeastern shore of Lake Superior, it was common in clearings around settlements and occurred in an open graminoid bog (Baillie and Hope 1943).

In Parry Sound and Muskoka Districts, the Savannah Sparrow was common where there were extensive fields and meadows (Mills 1981). In Algonquin Park, it avoided forested habitat and was restricted to grassy openings near settlements and areas cleared for log landings (MacLulich 1938). Tozer (2012) reported that most of the population in the park now breeds in sedge meadows within

large bogs and marshes. Lesser numbers breed in remnant openings such as large human-made clearings and old fields such as an old airport, former sawmill site, and farms. Small numbers probably nested in natural meadows and dry grass or sedge marshes before logging started in the 1830s. Logging resulted in marshes created by dams, large clearings, burned areas, and farm fields that provided additional habitat.

South of the Shield, the Savannah Sparrow is abundant in agricultural landscapes. Curry (2006) stated that it was found in every field in the countryside, whether cultivated or pasture. Speirs and Orenstein (1967, 1975) reported it nesting in old fields, hayfields, a very young red pine plantation where most of the trees were shorter than 0.9 m and overtopped by old-field herbaceous vegetation, and in an old-field community with scattered apple trees and hawthorns. It is abundant in hayfields, meadows, and pastures with sparse or no weedy vegetation. It occasionally nests in agricultural fields planted to row crops, but at much lower densities. At Luther Marsh, it nests within extensive bog and fen habitats (Sandilands 1984).

The Savannah Sparrow nests in a variety of open habitats throughout its range. From the Boreal Forest Region southward, it nests in habitats dominated by grasses or occasionally sedges, often with varying amounts of herbaceous species. It avoids areas with dense woody vegetation, but scattered shrubs or saplings may be included in the territory to provide singing perches. The most typical habitats consist of native grasslands, hayfields, pastures that are not excessively grazed, and old fields. Large bogs and fens may provide suitable habitat and it may inhabit cordgrass marshes on coastlines. Above the treeline, alpine meadows and tundra provide suitable high-elevation habitat. Dwarf willow and birch communities are optimal habitat in tundra regions.

In Newfoundland, the Savannah Sparrow is abundant in meadows and also occurs near tops of hills and mountains. In central Labrador, it nests in sedge bogs (Baird in Austin 1968). It is a common breeder on sand dunes on the Atlantic coast of Canada and the northeastern United States. On the mainland of Nova Scotia, it nested on beaches and dunes stabilized by dense growths of beach grass and seaside pea, with clumps of myrtle, crowberry, and American cranberry and scattered small spruce that it used as singing perches (Welsh 1975). The Ipswich Sparrow, a subspecies of the Savannah Sparrow, nests on sand dunes on Sable Island in Nova Scotia. The entire island is devoid of trees (Ross 1980). In New Brunswick on Kent Island, it nests in a grassy 10.7-ha field dominated by creeping bentgrass and red fescue (Williams 1987), with timothy, bluegrasses, reed canary grass, and some alfalfa (Nocera et al. 2007b). In Quebec, it is particularly abundant in the south in hayfields, pastures, and meadows, and in the upper drier portions of marshes, particularly those dominated by cordgrass. Its distribution in the south corresponds with open habitat found mainly in agricultural areas, near rivers and streams, and along the coast in meadows and grassy dunes. It may also frequent roadsides and transmission-line corridors. In the north, it inhabits peatlands, sedge meadows, and shrubby areas (Bonneau in Gauthier and Aubry 1996). Baird (in Austin 1968) reported that it nested on Anticosti Island in bogs, along the coast, and in drier areas surrounding muskeg. In Carleton, Quebec, 1 pair nested in a small (0.68 ha) park in the centre of the town in an area of mowed grass. Northeast of Quebec City along the St. Lawrence River, it nested in ecotones between abandoned fields and highly productive tidal marshes. The saltwater marshes were dominated by cordgrass that was regularly flooded by tides and the upland habitat consisted of old-field meadow

dominated by nonnative species such as creeping bentgrass, red fescue, timothy, and Canadian burnet. The meadows were used for nesting and the marshes provided productive foraging habitat at low tide. Habitat was patchy so most territories contained 2 or more habitats (Bédard and LaPointe 1984a; LaPointe and Bédard 1986). In California, the Savannah Sparrow nests in meadows adjacent to saltwater cordgrass marshes (Fernández-Juricic et al. 2009; Powell and Collier 1998). At Le Pérouse Bay in Manitoba, it was common in areas dominated by short-fruit willow mostly less than 0.5 m tall with a maximum height of 1 m, and a mix of hoary willow and tea-leaved willow taller than 3 m (Weatherhead 1979). Near Churchill, it is abundant in large sedge meadows near the treeline and in wet tundra (Jehl 2004; Jehl and Smith 1970). Near Winnipeg, it nested along grassy hydro transmission corridors that were a minimum of 30 m wide and at least 500 m long. It also nested in grassy rights-of-way along a provincial highway (Leston and Koper 2017). Although it occasionally nests in bogs and fens (Kirk et al. 1996), it is almost exclusively a grassland species in the Prairie Provinces and the Great Plains. It nests in native grasslands, including tallgrass prairies, mixed-grass prairies, and, in the southwest, desert grasslands. Native vegetation tends to be dominated by grama grass, wiregrass, bluestem, thickspike and western wheat grass, June grass, native forbs, and clubmosses. It is abundant in planted grasslands including grazed, ungrazed, mowed, and unmowed sites. It readily inhabits areas planted for waterfowl production, termed Dense Nesting Cover (DNC) in Canada and Conservation Reserve Program (CRP) lands in the United States. Common species in planted grasslands include crested wheat grass, wild rye, alfalfa, smooth brome, Kentucky bluegrass, timothy, and yellow sweet clover. Occasionally, it nests in row-crop fields and it may be common along roads, in or beside prairie sloughs, and in lakeside marshes (Askins et al. 2007; Davis 2004, 2005; Davis et al. 2006; Hartley 1994; Ludlow et al. 2015; Patterson and Best 1996; Sutter and Brigham 1998; Swanson 2002; Taber in Austin 1968; Wheelwright and Rising 2020; Wilson and Belcher 1989; Winter et al. 2004). It occurs throughout British Columbia, but avoids forested areas. Breeding is most concentrated where grasslands, shrublands, weedy fields, alpine meadows, and subalpine tundra are widely distributed. It nests in meadows, edges of cultivated crops and swamps, moderately grazed meadows, hay and alfalfa fields, grassy and herbaceous edges of small lakes and ponds, upland edges of riparian willow thickets, and recent clear-cuts and burns. At the northern extent of the province, it nests in areas dominated by dwarf willows and birches and in grassy flats of low subalpine vegetation (Campbell et al. 2001). It was common in northern British Columbia in alpine tundra and subalpine meadows (Martin et al. 2009). It nests in similar habitat in Wyoming, Colorado, and elsewhere. These areas may either be dominated by low shrubs or spring wildflowers (Hendricks and Pidgeon 1990; Jones and Bock 2002; Rotenberry and Wiens 1980). In the Yukon, the Savannah Sparrow is the third-most abundant species in tundra habitat where it is most common in moist to wet sedge tundra. It is also common in grassy and low shrub habitats and occurs at numerous airstrips (Sinclair et al. 2003). Similar habitats are used in Alaska and in 1 location it nested in a grassy cemetery (Taber in Austin 1968). It frequently nests in reclaimed surface mines in West Virginia and Ohio, and probably in other areas. Most of these are dominated by nonnative grasses and forbs with varying degrees of invasion by woody plants (Graves et al. 2010; Wray et al. 1982). In Wisconsin, it was rare in pine and oak barrens and occurred only in diverse barrens (Mossman et al. 1991). In Maine, it nested in areas that were or had previously been managed for commercial blueberry production. The vegetation consisted mainly of lowbush blueberry with lesser amounts of Indian grass, poverty oat grass, sedges, chokeberry, alder, and birch (Vickery et al.

1994). In Michigan, it inhabits open grasslands, bogs, and coastal marshes and occurs wherever farming has produced pastures and fallow fields (Potter 1972). In Illinois, it inhabits all types of grasslands including marshes, hay crops, and oat and soybean fields. Populations were highest in pastures and ungrazed grasslands. Alfalfa and sweet clover were poor nesting habitat (Graber and Graber 1963).

Some studies examined whether the Savannah Sparrow initially selects habitat at the landscape level before selecting a suitable nesting patch. In the Prairie Hardwood Transition Bird Conservation Region, its abundance was positively correlated with the amount of grassland in the landscape at the 800-ha scale (Murray et al. 2008). In the Prairie Provinces, it was associated with cropland, pastures, and the number of wetland basins at the 400-m scale and wetland area at the 1,600-m scale. It was negatively correlated with the amount of trees and shrubs within 400 m (Fedy et al. 2018). In Vermont and New York, its abundance was positively correlated with the proportion of open land within 500 m and 2,500 m. At initial settlement early in the year, it showed patterns of habitat use that were strongly influenced by features outside the immediate patch and was most strongly influenced by features within 250 m. It showed an affinity for hayfields that had been recently cut. Characteristics of the field were more important after cut fields had been selected. It was attracted mostly to larger fields with less wooded edges, and landscape habitat was relatively unimportant in site selection. Shustack et al. (2010) concluded that it was a generalist species that will use hayfields with grass that is only a few centimetres tall and that have a high proportion of bare ground. Habitat use patterns changed over time due to changes in habitat. In Michigan, patch variables had more influence on the Savannah Sparrow's abundance than landscape variables (Crozier and Niemi 2003). In South Dakota, its percent occurrence and density were positively correlated with the amount of grassland within 3,200 m. The probability of occurrence was 20% when the surrounding landscape contained less than 5% grassland and 40% when grassland occupied 80% of the landscape. It was selecting for large expanses of habitat rather than large patches (Greer et al. 2016). In Minnesota, local habitat variables were more important than landscape variables in habitat selection. It was positively associated with the amount of grass cover within 100 m, but negatively associated with the amount of grass cover within 500 m. Grassland area at large spatial scales was positively correlated with woody vegetation. Tree avoidance is a potentially more important driver of habitat selection than extent of grassland (Thompson et al. 2014). In Wisconsin, densities were higher in landscapes with smaller patches of residential areas and lower cover-type density within 800 m. With 2 exceptions, lower crop-type diversity was due to the dominance of hay and grassland. In 1 exception, the landscape was more than half row crops but still had a significant proportion of hay and grassland. The other exception was a dry prairie in a landscape dominated by woods, but with grassland as the other major component. The less diverse the habitat, the higher the Savannah Sparrow density was (Ribic and Sample 2001). In Illinois, its occurrence was negatively correlated with habitat heterogeneity (Herkert 1994a). Renfrew and Ribic (2008) found that its abundance was positively correlated with the amount of grass cover within 1,200 m and negatively correlated with wooded cover. In Alberta, there were no differences in its abundance in landscapes dominated by native grasslands and those dominated by cultivated areas. In cultivated areas, roadside ditches were overgrown with tall grasses and shrubs and provided suitable habitat. It was absent from large areas of cultivated land where there was no rank edge vegetation. Edge

vegetation is often lacking in native grasslands (Owens and Myers 1973). It preferred landscapes with 0-4% forest cover in North Dakota (Cunningham and Johnson 2019). At Breeding Bird Survey (BBS) stops in the Great Plains, it was associated with pastures and hay, tallgrass prairies, and CRP grasslands. It selected for mesic sites, exotic grasses, and tall dense cover (Niemuth et al. 2017).

Presence of woody vegetation often decreases habitat quality for the Savannah Sparrow. Thompson et al. (2014) determined that it avoided treed habitat at the landscape level, and its density was negatively correlated with all woody vegetation covariates. Even larger grassland patches may not be occupied if they contain trees or are close to wooded areas. They predicted that if 4.3 shrubs, 4.7 trees, and 0.06 ha of woodlot were removed from a 100-m radius, it would increase by 32%. In North Dakota, Arnold and Higgins (1986) surveyed shrub plots with 30-80% coverage by wolfberry and silverberry and shrubless plots with 10% or less shrub coverage. The Savannah Sparrow was absent on shrub plots and present at low density on shrubless plots; the differences were not significant. Also in North Dakota, it reached its maximum probability of occurrence in open treeless grasslands. Its probability of occurrence declined to 50% when 10% of the area within 500 m was treed with aspens. Where it was present, there were no shrubs taller than 1 m or aspens within 100 m, significantly different from where it was absent. It was classed as a woodland-sensitive species, decreasing with increasing tree coverage (Grant et al. 2004). In Minnesota and North Dakota, its abundance decreased as the amount of tree and shrub coverage within 200 m increased (Winter et al. 2006). In Saskatchewan, nests were negatively correlated with distance to the nearest shrub. Its presence was negatively correlated with the amount of woody vegetation within 2.8 km^2 (Davis 2005; Swanson 2002). In Maine, its abundance was negatively correlated with blueberries and tall shrubs. It preferred sites with higher graminoid cover (Vickery et al. 1994). It was negatively correlated with shrub cover in Wisconsin (Swanson 2002). In Ohio, its abundance was negatively correlated with the amount of woody vegetation within 100 m, but it did not show strong evidence of selecting nest patches with lower amounts of woody vegetation than random sites (Graves et al. 2010). In Washington, the Savannah Sparrow was most abundant in new CRP lands, about half as common in old CRP lands, and least abundant in shrubsteppe habitats. New CRP lands were vegetated predominantly with grasses and forbs; old CRP lands and shrubsteppe areas supported a shrub layer. Its abundance was negatively correlated with shrubs, but nest survival was positively correlated with shrub cover and height of herbaceous vegetation at the nest site (Vander Haegen et al. 2015). In North Dakota, the frequency of occurrence of shrubs shorter than 1.5 m within 5 m of the nest was 19.0% and the mean distance from the nest to the nearest patch of woody vegetation taller than 1.5 m was 207.5 m. Nest survival did not appear to be affected by the presence of shrubs (Murphy et al. 2017).

Some studies compared Savannah Sparrow usage of native and planted grasslands. In Saskatchewan, nonnative vegetation consisted of pure stands of crested wheat grass or crested wheat grass mixed with wild rye and alfalfa. Introduced vegetation had significantly lower plant species richness and diversity and higher evenness than prairie vegetation. Native vegetation had higher grass and sedge coverage, less bare ground, deeper litter, and more contacts with vegetation below 10 cm than introduced vegetation. Although its abundance was 2.6 times greater in native vegetation, differences were not significant. In introduced vegetation, it was positively correlated with grass and sedge coverage, maximum height of vegetation, and litter depth. In native

vegetation, it was positively correlated with litter coverage and depth, number of contacts above and below 10 cm, and grass and sedge coverage. It was negatively correlated with bare ground and forb density. It preferred dense vegetation (Sutter and Brigham 1998). In Saskatchewan, a mean of 1.82 were detected on native grassland plots and the probability of occurrence was 100%. On DNC fields, 1.14 were detected per plot with 93.7% occurrence and 0.21 were detected in plots in wheat fields with 57.9% occurrence (Hartley 1994). Another Saskatchewan study determined that its abundance increased with the amount of native grassland within 400 m, and declined with the amount of cropland (Davis et al. 2016). In Manitoba, the mean number detected along transects was 1.5 times greater in native prairie than in introduced vegetation (Wilson and Belcher 1989). In Alberta, density decreased with increasing coverage of the nonnative crested wheat grass. Density was nearly 2 times lower in areas with 60% coverage by crested wheat grass compared with areas without it, but nests in this grass had higher fledging success. Results suggested a density-dependent relationship whereby a lower density in a patch of crested wheat grass may provide increased opportunities to acquire food resources (Ludlow et al. 2015). In Wisconsin, densities in dry pastures and alfalfa fields were significantly greater than in fields with nonnative grasses and dry prairies. Pastures and alfalfa fields supported medium-height or short vegetation that is typically occupied by the Savannah Sparrow (Ribic and Sample 2001).

Numerous studies correlated vegetation parameters with Savannah Sparrow presence or abundance, and some linked nest success with vegetation characteristics. Almost all studies concluded that it is positively correlated with litter coverage and depth. In Nova Scotia, its abundance was strongly negatively associated with vegetation height and density and this was the strongest predictor of occupancy. The same relationship occurred in an Iowa prairie, but there was a positive relationship with vegetation height and density in Wisconsin. The positive relationship in Wisconsin may have been because the pastures were so open that birds used the tallest of what was otherwise very short grass or nested in isolated clumps of tall grass. In another Wisconsin study, there was a negative correlation between its abundance and forb cover (Nocera et al. 2007b; Swanson 1996). In Tennessee, portions of fields were dominated by forbs. It nested only in grassy areas with no forbs (Knight 1989). A negative correlation with forbs also occurred in Ohio (Swanson 2002). In contrast, it is highly correlated with forb density in montane meadows (Rotenberry and Wiens 1980). At 1 Saskatchewan site, nests were positively correlated with the density of dead vegetation less than 30 cm tall, and with cow dung. Areas with cow dung may be selected because of the dense vegetation patches associated with them. The Savannah Sparrow was associated with tall dense vegetation and a moderate density of forbs 10-20 cm tall. It was negatively correlated with bare ground (Davis 2005). Other studies have documented the same relationship (Vickery et al. 1994). Wheelwright and Rising (2020) concluded that it preferred dense ground vegetation, especially grasses, and moist microhabitats. In North Dakota, its abundance was correlated with grass cover (Swanson 1996) and this relationship was also observed in Saskatchewan at 1 site but the relationship was negative at an arid site in that province (Swanson 2002). In grazed mixed-grass prairie in South Dakota, it was positively correlated with percent grass cover, litter depth, visual obstruction, density of low-growing shrubs (silverberry and snowberry), vegetation density, and plant communities dominated by Kentucky bluegrass and native grasses. It was negatively correlated with percent coverage by clubmosses. The strongest predictors were decreasing

clubmoss, increasing grass cover, increasing litter depth, and decreasing visual obstruction (Swanson 2002). In North Dakota where it was absent, there was significantly more litter, Kentucky bluegrass, and brome grass than where it was present. At occupied sites, there was significantly less live vegetation, shrubs taller than 1 m, aspen within 100 and 500 m, native herbaceous vegetation, and legumes than at unoccupied sites. Its occurrence was greatest in areas dominated by Kentucky bluegrass intermingled with native grasses and forbs (Grant et al. 2004).

Although the Savannah Sparrow occasionally sings from the ground, it typically uses a perch. In the east and Midwest, sturdy emergent forbs and fence posts are most frequently used as perches. Fields where there are shrubs or small trees are not inhabited. Further west, where forb growth is not as luxuriant and fence lines are widely spaced, it may use small deciduous shrubs. In Wisconsin, 43% of territories contained posts, 38% contained a fence line, 15% contained a wire bale, and 8% contained trees (Swanson 2002; Wiens 1969). In Ontario, forbs and shrubs in fencerows may be used as perches and these may also demarcate territory boundaries (personal observation). Harrison (1977) provided artificial perches 1.5 m and 2.0 m tall in Michigan and they were used equally by the Savannah Sparrow.

Several studies compared habitat at nest sites to the remainder of the territory, or of territories to unoccupied sites. In Saskatchewan, the Savannah Sparrow nested in taller vegetation than occurred at random sites. Mean values at nest sites were 25 cm vegetation height, 11 mm litter depth, and 3.5% bare ground, significantly less than the 12% found at random sites (Davis 2005). In North Dakota, there was 5.9% bare ground at nests compared with 1.7% in general habitat. It selected nest sites with less grass cover (9.5% compared with 35.1%), less coverage by forbs (1.1% compared with 20.2%), and more litter cover (79.5% compared with 41.5%) than random sites (Winter et al. 2004). In Montana, Dieni and Jones (2003) compared nest sites with random sites. Parameters for which there were significant differences included 0.6% bare ground (significantly less than random), 1.0% cactus cover (significantly less), 4.6% clubmoss coverage (significantly less), 65.5% grass cover (significantly more), 13.4% litter cover (significantly more), 0.1% rock coverage (significantly less), 21.2 cm litter depth (significantly more), 17 cm visual obstruction (significantly more), 34.3 cm plant height (significantly taller), and 5.4 vertical density (significantly higher). Nest patches had a well-developed litter layer and little bare ground, and clubmoss was avoided. It selected several nesting habitat characteristics but showed great plasticity in their use. It tended to select western wheat grass as a nesting substrate and its presence may be an important factor in nest-site selection. In Quebec, there was no difference in vegetation height at nests and random sites but successful nests were surrounded by a significantly higher proportion of tall vegetation than unsuccessful nests (Bédard and LaPointe 1984). In Wisconsin, forb height and density were significantly greater in territories than in unoccupied areas. In occupied areas, vegetation near the ground was significantly denser, mean effective height was significantly less, more light penetrated to the ground, there was less coverage by lawn-like habitat, and litter was significantly deeper but the cover and composition of litter was similar. Parameters for territories and unoccupied areas, respectively, included 65% and 66% grass cover, 45% and 40% very narrow-leaved grass cover, 30% and 29% narrow-leaved grass cover, 1% and 2% forb coverage, 35% and 36% bare ground, 3.1 cm and 2.2 cm litter depth, 0-13 cm and 0-20 cm range of litter depth, and 81% and 67% cover. These parameters were measured in mid-June. In April, coverage by grass was much lower, vegetation

density was lower, and nearly all vegetation was less than 5 cm tall. Vegetation density and mean effective height were significantly greater near nests than in the entire area that was inhabited. Forb density in areas selected for nesting was much less than in territories, but mean forb height was significantly higher. Litter at nest sites was significantly deeper than in the entire territory and was deeper yet at nests. Light intensity in nest cups was low with 11.1% open-sky intensity (Wiens 1969).

Additional studies identified other microhabitat features of the Savannah Sparrow. In Saskatchewan, it occurred in wetlands and wetland margins within farmland of all types and within DNC. Presence within wetlands was positively correlated with the amount of water within wetlands but negatively correlated with water depth in late July, the percent coverage by woody vegetation around the wetland, and diversity of habitat around the wetland (Swanson 2002). In another Saskatchewan study, its abundance was associated with taller vegetation and reduced cover by cow dung (Davis et al. 2016). In Massachusetts, it was associated with grass 10-50 cm tall and negatively associated with litter and shrubs 2-5 m tall (Zuckerberg and Vickery 2006). In Wisconsin, mean habitat characteristics included less than 1% woody cover, 75% herbaceous cover, and 54 cm maximum vegetation height. It avoided habitats with the tallest, densest vegetation and nested predominantly in managed or disturbed areas with shorter sparser vegetation. Territories in West Virginia were characterized by 7% grass cover, 11% forb cover, 58% litter cover, 24% bare ground, 1 cm litter depth, and 66 cm vegetation height (Swanson 1996).

The Savannah Sparrow may nest in association with the Upland Sandpiper, Clay-colored Sparrow, Vesper Sparrow, Grasshopper Sparrow, Henslow's Sparrow, Dickcissel, Bobolink, and Eastern and Western meadowlarks. The 2 most common associates in Ontario are the Bobolink and Eastern Meadowlark, and the Vesper Sparrow is also a fairly common associate. The other grassland species are less common in Ontario, but the Savannah Sparrow typically breeds wherever they are present. A possible exception is the Clay-colored Sparrow, which may inhabit areas that are too shrubby to be suitable for the Savannah Sparrow. In Nova Scotia, the strongest predictor of Savannah Sparrow occupancy was its negative relationship with vegetation height, vegetation density, and forb cover. The patterns of vegetation height and density that were beneficial to the Savannah Sparrow were detrimental to the Nelson's Sparrow and Bobolink, with these species positively associated with vegetation height and density (Nocera et al. 2007b). In North Dakota tallgrass prairie, Savannah Sparrow and Bobolink nest sites were similar but differed greatly from those of the Clay-colored Sparrow. The Savannah Sparrow and Bobolink placed their nests most frequently within thick clumps of litter and less frequently in shrubs; most Clay-colored Sparrow nests were elevated in shrubs. Savannah Sparrow nests had a higher percentage of cover, shorter vegetation, and slightly more bare ground around them than Bobolink nests. Shrub removal would benefit the Savannah Sparrow and Bobolink but be detrimental to the Clay-colored Sparrow (Winter et al. 2004). Wiens (1969) compared the habitat requirements of the Vesper, Savannah, Grasshopper, and Henslow's sparrows, the Bobolink, and the 2 meadowlark species in Wisconsin. In Savannah Sparrow territories, grass and forb height was mostly 10-40 cm, similar to most other species. Forb density was intermediate in territories, with mean forb height greater than in areas occupied by the Western Meadowlark and Vesper Sparrow but less than for Bobolink, Eastern Meadowlark, and Henslow's Sparrow. The density of vegetation in Savannah Sparrow territories was intermediate among the species and was similar to those of the Grasshopper Sparrow and Eastern Meadowlark.

Total vertical vegetation density differed significantly only from the Henslow's Sparrow, being lower in Savannah Sparrow territories, but vegetation near the ground was significantly denser than in areas occupied by the Western Meadowlark and sparser than in areas occupied by the Bobolink and Henslow's Sparrow. Light penetration to the ground was somewhat greater for the Savannah Sparrow than for most species. Effective height measurements for Savannah Sparrow areas exceeded those of the Western Meadowlark and Vesper Sparrow and were lower than areas occupied by the Bobolink, Eastern Meadowlark, and Henslow's Sparrow. Savannah Sparrow territories were intermediate in litter depth, coverage, and composition. Litter depth differed significantly only from Henslow's Sparrow territories, which had greater litter depth. In April, the Savannah Sparrow selected areas with slightly less grass coverage and slightly more bare ground than the Eastern Meadowlark. The Savannah Sparrow spent less time in grass cover and more in forbs than the Bobolink and Eastern Meadowlark. Species presence could be arranged in order of increasing habitat richness (vegetation density and height, and litter coverage and depth): Western Meadowlark, Vesper Sparrow, Savannah Sparrow, Grasshopper Sparrow, Eastern Meadowlark, Bobolink, and Henslow's Sparrow. The range of difference within this ranking was low, especially among the Savannah Sparrow, Grasshopper Sparrow, and Eastern Meadowlark. In shrubsteppe vegetation, the Savannah Sparrow's niche overlapped most closely with that of the Vesper Sparrow, but also with Upland Sandpiper, Grasshopper Sparrow, Eastern Meadowlark, and Dickcissel (Rotenberry and Wiens 1980). Wiens (1973) compared territories of Savannah and Grasshopper sparrows in Wisconsin. For Savannah Sparrows, areas colonized during the early and middle portions of the season had significantly more grass cover, deeper and patchier litter, greater vertical vegetation density, and lower forb density and coverage than those that were occupied last. Grasshopper Sparrows nested in somewhat more open situations than Savannah Sparrows and had considerably less litter associated with their nest sites. Savannah Sparrows concentrated their feeding at perimeters of grass clumps. Grasshopper Sparrows foraged more frequently in open unvegetated areas. The initial territories settled by these 2 sparrows had quite different habitat but, with the growth of new vegetation, their habitat became similar by mid-June.

In many areas, the Savannah Sparrow appears to avoid edges of fields. This is not consistently the case. Edge avoidance may depend upon the type of edge, but even this varies geographically. In Vermont and New York, Keyel et al. (2013) measured openness and edge effects on nest-site selection. Openness was quantified at points by measuring the distance to edges in 4 directions and the angle to the horizon. Openness was unaffected by edge when the edge was a road, wetland, or agricultural land and was affected predominantly by trees. Nests were placed away from edges and in more open locations than expected. It avoided both edges and non-open habitat. When only nests within 50 m of edge were considered, it still selected areas that were more open. Visually open fields were more likely to be used as breeding habitat. In Wisconsin, Savannah Sparrow territories tended to be located more centrally in grassland habitat than those of other species. Few territories were located along fence lines and mean distances to adjacent cultivated fields (94.0 m, range 0-240 m) and fence lines (49.4 m, range 0-160 m) were the greatest of the species studied. Distances to adjacent woods (225.0 m, range 20-410 m) were also large (Wiens 1969). In Alberta, Sliwinski and Koper (2012) examined responses to 3 edge types: cropland or hay, roads and fences, and wetlands. Its abundance increased as distance to crop edge increased, but not significantly, suggesting that it

may not respond to crop edges. It showed no attraction to or avoidance of roads. It decreased with distance to wetlands and was therefore attracted to wetlands. In South Dakota, Vermont, and New York, its density decreased as the percentage of wooded edge increased (Greer et al. 2016; Shustack et al. 2010). In Wisconsin, the density of nests per ha increased significantly with distance from edge from 0.2 at 25 m from edge to 0.4 at 100 m and 0.8 at 200 m. Type of edge was not a significant predictor of nest density within 50 or 100 m of edge. Edge effects were unlikely to affect predation rates because the fields were small, with few areas more than 225 m from edge, and because the highly fragmented habitat was saturated with predators. Edge avoidance would not necessarily reduce predation (Renfrew et al. 2005). Perkins et al. (2013) examined the distribution of 995 nests in relation to edges, including agriculture with a management-defined boundary, forests, hedgerows, human development, roads, and wetlands. Areas within 50 m of edge were used significantly less than expected. Sixty percent of available habitat was within 50 m of edge, but only 26.6% of nests were in that area. Thirty-one percent of habitat was 50-100 m from edge and this area supported 45.5% of nests. About 1% of nests were as close as 10 m from edge. Nests were closer to forested edges than expected: 35% of available edge supported 52% of nests, but this was not statistically significant. Portions of fields near hedgerows were used significantly less than expected: 16% of habitat and less than 1% of nests. There was no avoidance of or attraction to wetlands, roads, human development, or agriculture. Later-nesting birds nested closer to edge. Dominant or older birds may force subordinate and young birds to nest closer to edge. Early colonizers may settle into sites furthest from edges and settlement gradually moves from the centre to edges of the habitat patch. Despite the exhibited edge avoidance, nesting near edges had only minor consequences for nest success. In Illinois, it tended to nest more than 50 m from a wooded edge (Swanson 2002). In Colorado and Ohio, it appears to avoid edges of large urban centres (Jones and Bock 2002; Swanson 1996). In Nova Scotia, it nested in a 1.2-ha field surrounded by spruce–balsam fir forest. Nests were found within 3 m of this forest and density of birds nesting in the field was among the highest ever recorded (Wheelwright and Mauck 1998; Wheelwright and Rising 2020; Wheelwright et al. 1994). The Savannah Sparrow avoids edges in some areas but not in others. Where edge avoidance occurred, it was predominantly treed edges that were avoided. In another study, there appeared to be an attraction to treed edges but avoidance of hedgerows.

Several studies examined area sensitivity by the Savannah Sparrow. Results are often ambiguous and conflicting, partially because it may respond differently in different landscape types, but often because of the study methods and interpretation. Many grassland-bird researchers consider a species to be area sensitive if its density increases with habitat area. Few studies considered the minimum patch size required to support the species, which is a more meaningful measure of area sensitivity. In New York, Norment et al. (2010) studied fields as small as 5 ha and found that field size had little effect on occupancy or nest survival. In California, saltwater marshes with adjacent meadows that supported the Savannah Sparrow were highly fragmented and isolated. Nine breeding territories were in a 1-ha marsh connected to other habitat, and there were 3 territories in an isolated 2.9-ha marsh completely surrounded by urban habitat. Although nesting occurred in even the smallest fragments, no successful nests occurred in patches smaller than 10 ha (Fernández-Juricic et al. 2009; Powell and Collier 1998). In Wisconsin, its density was not associated with field size (Ribic and Sample 2001). In Nova Scotia, high numbers of Savannah Sparrows nested successfully in

a 1.2-ha field (Wheelwright et al. 1994). In Michigan, Potter (1972) studied a population in a 4.74-ha field. Johnson and Igl (2001) studied CRP fields 2.2-270.5 ha in 4 states and found no relationship between its density and patch size, although positive and negative relationships were observed at 1 site each. Because they were measuring abundance, this suggests that no significant edge avoidance was occurring. In Saskatchewan, there was no relationship between patch size and its abundance. It was area insensitive, with occurrence independent of patch size. There was no edge avoidance and in 1 of 2 years it was more abundant near edge (Davis 2004; Davis et al. 2006). In South Dakota, its density was unaffected by area but was positively correlated with patch size in another study in that state (Greer et al. 2016). In Ohio, it occupied CRP fields as small as 3 ha. The minimum area to support a breeding population in Missouri was estimated at 1-10 ha (Swanson 2002). In sedge marshes in Michigan, its abundance was correlated with patch size (Crozier and Niemi 2003). Shustack et al. (2010) found a similar relationship in Vermont and New York. In Illinois, Herkert (1994a) studied fields 0.5-650 ha and determined that its occurrence was positively correlated with patch area. It occurred on approximately 10% of 1-ha patches and 20% of 10-ha patches; 50% occurrence was achieved at 40 ha. In small patches, only 33% of transects had suitable habitat, but area requirements still appeared to limit its distribution within small fragments. He concluded that it was area sensitive, with its distribution affected by both habitat availability and patch size. In another Illinois study, Walk and Warner (1999) studied grasslands 7-120 ha in area. It was rare and occurred on only 3 of 9 sites and only on tracts larger than 40 ha. They concluded that the minimum area required to support a population was 65 ha. In Maine, Vickery et al. (1994) studied grassland barrens dominated by blueberries that were 0.3-404 ha. Percent occurrence was 10-20% on plots smaller than 1 ha, 30% at 1 ha, and 50% at 10 ha. Area sensitivity of the Savannah Sparrow may be affected by landscape features and it may only be area sensitive in regions where grasslands are scarce (Dornak 2010; Ribic and Sample 2001) or at the periphery of its range. In Minnesota and North Dakota, its density was influenced by patch area, but the magnitude and direction of the response varied annually. Field size had no influence on nesting success. The fields studied were fairly large, averaging 226.1 ha (range 2.4-1,245.6 ha; Winter et al. 2006). Coleman et al. (2000) concluded that it was area sensitive in Ontario and required a minimum of 50 ha of grassland. Rising (in Cadman et al. 2007) stated that it can use small areas of suitable habitat in the province. Given the abundance of the Savannah Sparrow in Ontario, it is unlikely that it is area sensitive. It commonly nests in fields much smaller than 50 ha. Most studies that found evidence of edge avoidance or area sensitivity were conducted in western grasslands, and these results may not be transferable to other locations.

Adults roost on the ground at night but the female spends the night on the nest while she is incubating or brooding (Wheelwright and Rising 2020).

One Ontario nest was 0.3 m from the ground in a cedar, but all others were on or very close to the ground. Most were in small depressions (one was in the side of a mossy hummock) and concealed in grasses, sedges, forbs, cattails, and occasionally shrub stems. Some were at or under bases of shrubs, seedlings, and clumps of forbs or grasses. One was in a clump of willows standing in 15 cm of water. Several were partially or completely arched over with vegetation, but 3 nests were fully exposed (Peck and James 1987). A nest on South Limestone Island in Georgian Bay was within a Common Tern colony (Mills 1981).

Almost all nests are on the ground. A few British Columbia nests were in low vegetation as high as 0.5 m from the ground. Nests at a California site averaged 3.3 cm from the ground. Typical nests are in shallow depressions in the ground that may be either natural or formed by the female. They are often within clumps of grasses, sedges, mosses, or herbaceous plants or at the base of low woody shrubs, with the rim of the nest flush with the ground; some may extend slightly above ground. Many nests are concealed by overhanging grasses or other vegetation that may form a partial dome. Others are fully exposed. In Wisconsin, 70.4% of nests were either partially domed or under overhanging litter. One nest had a 1.2-m long tunnel leading to it under long matted grass. Yearlings orient their nests in random directions. Older females preferentially construct nest entrances away from the prevailing winds. There is no evidence of nests being reused (Baird in Austin 1968; Campbell et al. 2001; Hendricks and Pidgeon 1990; Jehl and Hussell 1966a; Mousley 1916a; Powell and Collier 1998; Shields 1935; Swanson 1996; Taber in Austin 1968; Welsh 1975; Wheelwright and Rising 2020; Wheelwright and Schultz 1994; Wiens 1969).

In most areas, males establish territories shortly after their arrival. In Nova Scotia, territories in the shelter of woodlands were established first. Nests in these territories had full clutches while territorial boundaries were still being adjusted in other portions of the field. In Wisconsin, a portion of a field that had been mowed the previous autumn was settled first in several clusters of 2 or 3 contiguous territories. Territorial birds may continue to arrive into early June and new territories are wedged among existing ones. Boundary fluctuations may be extensive and are frequently demarcated by a singing perch such as a sturdy forb, a fence post or wire, or a shrub or small sapling. Perches at boundaries may be shared, with 2 males both singing from the top and the opposite side of a shrub or sapling, but at different times. In Wisconsin, 1 tall heavy-stemmed forb that was frequently used as a singing perch was in 3 different territories. Once territory boundaries are established, there are few conflicts. Some males may reduce the size of their territories while they are feeding nestlings, but reclaim any area lost to neighbours as soon as the young fledge. Bigamous males may be the only ones that do not reduce the size of their territory during the nestling period. Territorial defence wanes by late July and adults with fledglings may wander on to neighbours' territories without conflict. Territories vary in shape from almost square to long and rectangular, but territory shape has no effect on mating success. There is very little overlap in territories once boundaries are established. Females are aggressive toward other females within 20 m of the nest. Successful nests in adjacent territories have been as close together as 2.2-10 m. In New Brunswick, there was strong evidence that juveniles selected a territory and began defending it within a month of hatching. Adult males frequently defended their territories against juveniles in July and early August. Individuals located their first nest closer to the location of their last sighting as a juvenile than to their natal nest. Some territory holders are unsuccessful in obtaining a mate. In Michigan, only 1 of 9 territories as small as 0.06 ha contained a nest; territories this small may not be attractive to females. In Quebec, the distribution of territories of unmated males tended to be clumped rather than regularly dispersed. The location of unmated male territories shifted each year suggesting that failure to obtain a mate was not related to habitat quality. In some locations, the territory and home range are the same, with all activities occurring within the territory. In other areas, adults regularly leave the territory to forage in undefended areas. Where the habitat is homogeneous, feeding tends to occur within the territory. Where there is adjacent habitat that is unsuitable for breeding but offers rich food

resources, it often forages outside the territory. Birds nesting near saltwater tidal marshes, freshwater marshes, and margins of lakes and wetlands may forage outside their territories. Territories tend to be quite small, typically considerably less than 1 ha. Reported territory sizes include 0.11 ha on an island in New Brunswick, 0.01-0.29 ha (average 0.10 ha) in Michigan, 0.1-0.47 ha in Quebec, 0.09-0.33 ha (average 0.17 ha) in Nova Scotia, 0.008 to 0.10 ha (average 0.04 ha) in California, 0.16-1.74 ha (average 0.69 ha) in Wisconsin, and 0.38-0.53 ha in densely vegetated habitat and 1.09-1.25 ha in sparse habitat on Sable Island. In Wisconsin, centrally located territories were significantly smaller (0.45 ha) than those at the periphery of the field (0.65 ha) where there were no neighbours on some sides. Polygynous males have larger territories than monogamous males (0.28 ha compared with 0.19 ha). In Quebec, successful territories in fields were significantly larger (0.28-0.34 ha) than unsuccessful territories (0.28-0.30), but the relationship was the opposite in marsh habitat. Successful territories in marshes were 0.18 ha compared with 0.19-0.30 ha for unsuccessful territories. At this site, yearlings defended significantly smaller territories of 0.19-0.27 ha than the 0.47 ha defended by older males in 1 year but not in another (Bédard and LaPointe 1984a; Potter 1972; Powell and Collier 1998; Welsh 1975; Wheelwright and Mauck 1998; Wheelwright and Rising 2020; Wheelwright et al. 1992; Wiens 1969, 1973).

Natal philopatry rates vary throughout the Savannah Sparrow's range, but are consistent within a given area. High return rates are associated with areas where the habitat is isolated, such as islands or mountains above the treeline. In Montana, 3 of 193 nestlings (1.6%) returned to breed; 1 bred at its natal site and another bred 4.8 km distant (S.L. Jones et al. 2007). In Michigan, 1 of 130 juveniles (0.8%) returned to breed in a subsequent year (Wheelwright and Rising 2020). On Sable Island, 18 of 455 nestlings (4.0%) and 26 of 227 fledglings (11.5%) returned. Most yearlings settled 500-1,000 m from where they were raised but one nested 7.5 km from its natal territory. Survival rates were higher among birds from larger broods, among those hatched earlier in the year, and among those reared in dense habitat. It was concluded that all surviving individuals returned to the island (Ross and McLaren 1982). In New York and Vermont, Perlut et al. (2014) reported a natal philopatry rate of 7.5%; the survival rate of juvenile males was higher than for females. Also in New York and Vermont, 36 of 883 juveniles (4.1%) returned. The median dispersal distance was 885 m (mean 913 m, maximum 2,825 m). Of the 36 returning birds, 27.8% were detected in the same field and 72.2% in a different field. Most yearlings either dispersed less than 300 m or more than 900 m. Returning yearlings showed no propensity to select fields under the same management treatment as their natal field. They were equally likely to make favourable or unfavourable decisions regarding habitat quality (Fajardo et al. 2009). Perlut and Strong (2016) recaptured 62 of 865 nestlings (7.2%) in Vermont. The mean dispersal distance was 1,426.2 m (median 1,001.3 m). In British Columbia montane meadows, an average of 17% of juveniles returned annually (Martin et al. 2009). On Kent Island in New Brunswick, 11% of nestlings and 26% of fledglings returned to breed (Wheelwright and Schultz 1994; Wheelwright et al. 1994). At the same study area, Wheelwright and Mauck (1998) studied distances of first nests of yearlings from their natal sites and proximity of their close kin. Of 1,615 nestlings whose parentage was known, 11.2% returned to breed the following year. Of more than 7,000 Savannah Sparrows recovered during the breeding season, none were found more than 3 km from the original banding location. One nested as a yearling 3 km from its natal area, the only bird that dispersed more than 1 km. Two other islands within a few 100 m were accessible by foot during low

tide. Birds banded on Kent Island never accounted for more than 2% of the breeding birds on these islands in any given year. On 3 other islands 3-7 km distant, recruits from Kent Island accounted for 0-1% of breeding birds. Over a 6-year period, an average of 73% of newly breeding males and 71% of newly breeding females had been raised in or adjacent to the study area the previous year. Yearlings appeared to disperse random distances from their natal nests and, in some cases, avoided the natal area. The median dispersal distance between the natal site and the first nest was 228.5 m (range 0-1,400 m for males and 0-1,600 m for females), a distance of approximately 6 territories. Yearling males and females returned in approximately the same numbers and dispersal distances were not significantly different: 202.8 m for males and 248.4 m for females. Females were more likely to remain in their natal fields than males. If a female changed fields, she tended to move further than males that changed fields. Natal dispersal was unaffected by population density (and therefore competition for territories), the date that an individual hatched, or its mass at age 7 days. There was no significant relationship between dispersal distances of yearlings and those of its biological mother or father, suggesting that dispersal distance was not a heritable feature. Yearlings were more than twice as likely to nest in a field other than their natal field if their opposite-sex parent returned, but the probability of changing fields was unaffected by whether the same-sex parent returned. Birds nested significantly further from siblings raised in the same year than expected by chance. Distances between a yearling's first nest and the nearest nest of a sibling of either sex were: median of 327.9 m and mean of 399.8 m for birds raised in the same nest in the same year; median of 338.5 m and mean of 332.4 m for birds raised in a different nest in the same year; and median of 129.9 m and mean of 281.2 m for birds raised in different nests and different years. Siblings raised in different years that were therefore unfamiliar with each other nested closer to each other than by chance. The mean distance of first nests of siblings of the same sex (274.3 m) was significantly less than that of siblings of the opposite sex (517.6 m). Of 1,073 breeding attempts, no cases of pairing between full siblings, parent and offspring, half siblings, uncles and nieces, or grandparents and grand-offspring occurred, even though 20% of adults had one or more close relatives breeding in the population at the same time. Birds actively avoided breeding with close relatives, partially by dispersal from the natal area. Returning juveniles were not relegated to inferior habitat and their territories were dispersed among those of older birds. Returning yearling males produced significantly more offspring than those that had been raised outside the study area. Brewer et al. (2018) reported that a juvenile banded near Bewdley was recaptured at the same site 5 years later.

Site fidelity by adults is high and distances between nesting areas in subsequent years are usually negligible. In Michigan, 20 of 22 males (90.9%) returned the next year and 16 of 18 (88.9%) returned the following year (Potter 1972). Near Quebec City, 167 of 344 breeding adults (48.5%) returned for at least 1 and a maximum of 4 breeding seasons. There was a slight tendency for males to return at a higher rate. Distances moved by returning birds were small, with 80% of interyear movements less than 60 m, the average diameter of 1 territory. There was no significant difference in the distance moved by the sexes. Some moved further than 140 m. There were no significant differences in distances moved by birds that had been successful or unsuccessful the previous year, or if mates were changed between years. Moves that took place between 2 successive nesting attempts within a year were always shorter than moves between seasons. Males tend to return to the same territory each year even if it is of poor quality. Yearling males that have to squeeze in

between other territories do not attempt to upgrade in subsequent years. One male returned to the same territory for 5 years even though he never managed to attract a female, and males that failed to raise young in several successive years also did not move (Bédard and LaPointe 1984b). In Montana, S.L. Jones et al. (2007) reported an adult return rate of 5.4%, with 2 of 37 returning. Both returning adults occupied the same territory as the previous year. In an alpine meadow in British Columbia, 68% of adults returned (Martin et al. 2009). On Kent Island, 51% of adults returned after their first year of breeding and 47% returned after their second year of breeding. Birds that nested later in the season were more likely to return than those that nested earlier. Dispersal by adults was negligible once they established a territory. The median distance between nests within breeding seasons was 16.9 m and the distance between nests in different breeding seasons was 31.8 m. No females moved more than 0.5 km between seasons (G.W. Mitchell et al. 2012; Wheelwright and Mauck 1998; Wheelwright and Schultz 1994). In Vermont and New York, 226 of 553 adults (40.9%) returned. The mean dispersal distance between years was 113 m (median 63 m, maximum 2,009 m). Males moved significantly further than females, with a median of 78 m for males and 50 m for females. Results may have been biased because females were more difficult to detect. Birds that dispersed between years exhibited a strong selection for sites under the same management practices as the site used the previous year. Only 6 of 226 breeding dispersal events (2.7%) were to fields under different management practices. The Savannah Sparrow was more likely than expected to make unfavourable decisions regarding management practices, with 53.0% remaining in or moving to low-quality habitat. Birds that were unsuccessful the previous year were equally likely to breed in the same location as the previous year as birds that had been successful. It exhibited high site fidelity regardless of habitat quality (Fajardo et al. 2009). In California, no movement of 277 adults was detected among habitat patches within seasons and between years (Powell and Collier 1998). A Michigan adult was captured at the same site where it had been banded 6 years previously (Swanson 2002).

Limiting Factors

Eggs have been reported in Ontario nests from the last week of April until mid-August, with most present from the last week of May until the last week of June (Peck and James 1987). In Algonquin Park, eggs are present from late May to mid-June, nestlings are present from mid-June to late July, and dependent fledglings have been observed from late June to early August (Tozer 2012). The mean dates of clutch completion were 14 June at Moosonee (range 6-20 June), 17 June at Attawapiskat (range 6-25 June), and 21 June at Winisk (range 11-30 June; Schueler et al. 1974). Manning (1952) observed the first volant juveniles along the Hudson and James bay coasts on 19 July.

First nests take 4-5 days to complete but replacement nests are usually built in 2 days, typically within 20 m of the original nest. An average of 3 days elapses between nest completion and when the first egg is laid. Eggs are laid at the rate of 1 a day but a day may rarely be missed. In 1 Nova Scotia nest, 1 egg was laid in the morning and another was laid in the afternoon. It was uncertain if both eggs were laid by the same female or if this was a case of intraspecific nest parasitism. At high elevations and latitudes, egg laying within populations tends to be synchronized within a short period. Egg laying may be spread throughout the season in more temperate areas. At Churchill, more than 65% of all clutches were initiated within a 3-day period. In New Brunswick, clutch

initiation extended over 52 days. The timing of clutch initiation may vary annually depending upon weather conditions. Full-time incubation does not start until the penultimate egg is laid. The incubation period has been reported as 10-13 days, but mostly 12 days. At 1 closely monitored Ontario nest, the incubation period was only 9 days. Hatching may be asynchronous due to initiation of incubation before the clutch is complete. The nestling period is 7-14 days, with most young fledging in 9-11 days. Near Quebec City, nestlings from early nests (12 June or earlier) fledged significantly later (10.4 days) than those from later nests (9.8 days) in 1 year. In another year, young fledged in 10.0 days from early nests and in 9.0 days from later nests (Baird in Austin 1968; Baptista 1984; Bédard and LaPointe 1985; Bédard and Meunier 1983; Dixon 1978; Hendricks and Pidgeon 1990; Martin et al. 2009; Peck and James 1998b; Ross 1980; Weatherhead 1979; Welsh 1975; Wheelwright and Mauck 1998; Wheelwright and Rising 2020; Wheelwright and Schultz 1994; Wheelwright et al. 1992; Wiens 1969; Winter et al. 2004).

The Savannah Sparrow has been documented raising 1-4 broods annually. A number of factors affect how many broods can be reared, especially the length of the breeding season and nest success rates. Populations at high altitudes and latitudes typically raise only a single brood. On Sable Island, 3 or 4 broods are often raised annually because the nesting season is long and there are few predators. In other areas, only 1 or 2 broods are raised. Over several years of study in New Brunswick, only 1 bird raised 3 broods. The number of broods raised may vary even among areas that are close together. In West Virginia, almost all birds were double brooded. At another site in the same state, all were single brooded and birds left the area by mid-July. Ontario egg dates suggest that double broods occur, but this has yet to be confirmed. In southern coastal British Columbia, it is double brooded but presumably single brooded in much of the remainder of the province. In Wisconsin, most birds were double brooded but a few raised only a single brood. Single broods are raised near Churchill, Quebec City, and in alpine meadows in British Columbia. When another brood is attempted after raising the first brood, a new nest is built in the same territory. There is no difference in the vegetation in the vicinity of subsequent nests. On Sable Island, yearlings averaged 2.4 clutches per year compared with 3.0 for older birds. The female may begin or even complete the second clutch before the young of the first brood fledge. Renesting is common if a nest is lost or abandoned. In some areas where losses are high due to predation or agricultural activities, females may lay 3 or 4 clutches in an attempt to raise a single brood. Replacement nests are close to the original nest. Successive nests have been as close together as 0.5 m. In New Brunswick, replacement nests averaged 17 m from the original nest (range 3-31 m). Distances between successive nests in Nova Scotia were 6-38 m. Within 2-8 days of nest loss, females construct new nests and begin to lay the replacement clutch. Yearlings take significantly longer to replace their clutches, with an average of 4.9 days for yearlings and 3.0 days for older females. When adverse weather late in the season resulted in the loss of most nests near Churchill, no renesting occurred (Bédard and Meunier 1983; Dixon 1978; Jehl and Hussell 1966a; S.L. Jones et al. 2010; LaPointe and Bédard 1986; Martin et al. 2009; G.W. Mitchell et al. 2012; Peck and James 1987; Ross 1980; Shields 1935; Swanson 1996; Weatherhead and Robertson 1980; Welsh 1975; Wheelwright and Rising 2020; Wheelwright and Schultz 1994; Wheelwright et al. 1992; Wiens 1969; Winter et al. 2004; Wray et al. 1982).

Clutches of 3-5 eggs have been reported in Ontario (average 4.05 eggs). Most (59.5%) clutches contained 4 eggs. Throughout its range, the Savannah Sparrow lays 2-6 eggs, with 4-egg clutches

most frequent. Clutch size increases with latitude, with a mean of 5.0 in Alaska and 3.2 in California. Within a given area, other factors may affect clutch size such as habitat type, whether it is early or late in the season, and age of the female. At La Pérouse Bay, clutch size was significantly higher in short willows (4.78 eggs) than in tall willows (4.17 eggs). Either food availability was lower or predation pressure was more intense in tall willows. There was no difference in nestling growth rates in the 2 habitats suggesting that reduced food availability may have been compensated for by smaller clutch sizes in tall willows. Significant clutch size declines with season are often associated with more northern populations where clutch initiation is highly synchronous. In these areas, replacement clutches tend to be significantly smaller than initial clutches and clutches laid outside the peak of clutch initiation are smaller. Near Quebec City, clutch sizes by the same female were 4.1 eggs for first clutches and 3.8 eggs for replacement clutches. In British Columbia alpine meadows, first clutches averaged 4.65 eggs and replacement clutches averaged 4.00 eggs. In most areas, there is a decline in clutch size as the season progresses, consistent with the waning abundance of food resources. An exception is in New Brunswick and Nova Scotia where replacement clutches are larger than initial clutches. In Nova Scotia, clutches averaged 4.0 eggs in May, 4.5 in June, and 3.6 in July and a similar trend occurred in New Brunswick. Both sites were on the Atlantic Ocean coast and cool, wet, foggy weather early in the year depressed insect availability. More food resources were available for nests initiated slightly after the initial peak of nesting. Older females consistently lay larger initial and replacement clutches than yearlings, but both age classes lay similar-sized second clutches. In Quebec, individual females laid similar-sized clutches as yearlings (4.2 eggs) and in their second (4.2) and third (3.8) years. Despite this, older birds consistently fledged more young than yearlings. On Sable Island, adult females had larger clutches (4.54 eggs) than yearlings (4.16 eggs). In New Brunswick, 24.1% of females increased their first clutch size between ages 1 and 2 years, 69.0% had the same clutch size, and 6.9% had a smaller clutch. Clutch size of individuals increases between ages 1 and 2 years and then declines each year to age 6 years. As females age, they nest progressively earlier each season. In New Brunswick, a greater percentage of eggs in 4-egg clutches fledged young (40.4%) than other clutch sizes: 25.0% of 2-egg clutches, 32.5% of 3-egg clutches, and 19.7% of 5-egg clutches. In normal food years, adults may not be able to feed 5 nestlings adequately. During a year with prolonged cold, foggy, wet weather, 3-egg clutches were most successful. Mean clutch sizes are available from several locations: 11 clutches at Moosonee all contained 4 eggs, mean size of 29 clutches at Attawapiskat was 4.1 eggs (range 4-5), 12 clutches at Winisk averaged 4.5 eggs (range 4-5), 4.20 eggs in New York, 5.00 in a year of high grasshopper abundance and 4.60 in a year of low grasshopper abundance in Alaska, 3.9-4.2 in West Virginia over 3 years, 4.17 and 4.02 in New Brunswick, 4.0 in mid-May and 3.5 at the end of July in North Dakota, 4.4 and 4.8 in Saskatchewan, 4.5 in Alberta, 4.3 in Montana, 4.1 in Wisconsin, 3.97 near Quebec City, 4.2 on the Nova Scotia mainland, 52% of clutches with 4 eggs in British Columbia, and 4.65 for initial nests and 4.0 for replacement nests in British Columbia alpine meadows (Baird in Austin 1968; Bédard and LaPointe 1985; Bédard and Meunier 1983; Campbell et al. 2001; Davis 2003; Dixon 1978; Gaudet et al. 2020; S.L. Jones et al. 2010; LaPointe and Bédard 1986; Ludlow et al. 2014; Martin et al. 2009; Miller et al. 1994; G.W. Mitchell et al. 2012; Norment et al. 2010; Ross 1980; Schueler et al. 1974; Weatherhead 1979; Welsh 1975; Wheelwright and Rising 2020; Wheelwright and Schultz 1994; Wiens 1969; Winter et al. 2004; Wray et al. 1982).

Both sexes are capable of breeding when they are yearlings and breeding occurs annually thereafter. Some yearling males are unsuccessful in obtaining a mate. Near Quebec City, 20%, 40%, and 35% of males failed to attract a female over 3 years. Failure to mate was unrelated to habitat quality because the same area was often defended by a mated male in different years. In southwestern Ontario, 7-13% of territorial males failed to mate. Some populations are entirely monogamous but some polygyny may occur in other populations, particularly those in the Maritime Provinces. Monogamy is the rule in northern and high-altitude populations where the breeding season is short and a single brood is raised. Nesting is highly synchronous in these populations, giving males limited opportunities to acquire a second mate. Polygyny opportunities arise in populations where nest initiation occurs over an extended period due to multiple broods, renesting, later nesting by younger birds, and a long breeding season. In New Brunswick, 15-43% of males were polygynous, depending upon the year. Females were rarely synchronous in their breeding attempts, allowing the male to provision the young of both females if he chose to do so. Polygyny occurred as a result of 4 situations: younger females often returned from spring migration several days later than older females and chose to mate with a male who was already mated; territorial males sometimes vanished and neighbouring males expanded their territories and mated with the resident female; new females occasionally appeared as much as 6 weeks after the first eggs were laid; and females occasionally returned to their territory to find it already occupied by another female. The quality and size of a male's territory was unrelated to the probability of his attracting more than 1 mate. Polygynous males fledged 32% more young than monogamous males, but there were no differences in productivity of females mated to monogamous or polygynous males. In the event of nest loss, secondary females in polygynous relationships were more likely to leave the territory and move to a new one 100-500 m distant. Females mated to polygynous males incur higher mortality and appear to be in poorer condition than those mated monogamously. The pair bond typically persists throughout the breeding season. Divorce is rare but mates are replaced if one is lost. Both sexes exhibit high site fidelity and frequently reunite in subsequent years (Bédard and LaPointe 1984; Martin et al. 2009; Powell and Collier 1998; Ross 1980; Weatherhead 1979; Weatherhead and Robertson 1980; Welsh 1975; Wheelwright and Mauck 1998; Wheelwright and Rising 2020; Wheelwright and Schultz 1994; Wheelwright et al. 1992, 1994; Wiens 1969).

Extra-pair copulations may be common. In New Brunswick, 14 of 24 nests (58.3%) contained at least 1 extra-pair offspring and 31 of 92 first-brood offspring (33.7%) were a result of extra-pair fertilizations. Females mated to a polygynously mated male were more faithful than those mated to monogamous males. Extra-pair fertilizations accounted for 62% of offspring for monogamously mated females, 24% for primary females in a polygynous relationship, and 20% for secondary females. All monogamous females produced at least 1 extra-pair young; 54.5% of primary polygynous females and 33.3% of secondary females produced extra-pair young. Seventy-five percent of young in nests of polygynous males were due to in-pair fertilizations compared with 40% for monogamous males. In 95% of cases, extra-pair sires were neighbours whose nests were within 88 m of another female's nest. Thirty percent of young were extra-pair in first broods but only 16.3% of young in second broods were extra-pair. Males that provided more care to the nestlings were less likely to have extra-pair young in their broods (Freeman-Gallant 1996, 1997; Welsh 1975; Wheelwright and Mauck 1998; Wheelwright and Rising 2020). Intraspecific nest parasitism appears

to be rare. Weatherhead and Robertson (1978) reported a nest at La Pérouse Bay that contained 10 eggs. Eight eggs were readily separated into 2 groups by appearance indicating that they had been laid by different females. Hatching sequence suggested that the eggs were laid simultaneously.

The Savannah Sparrow forages mostly on the ground in open areas, avoiding dense vegetation. Foraging occurs in short vegetation in pastures, hayfields, roadsides, sedge bogs, tundra, beach wrack, mudflats near cover, and in tidal marshes and pools during low tide. It hunts for insects and other arthropods while walking on the ground, peering around bases of grasses or herbaceous plants, or searching seaweed and beach wrack. On Kent Island, it gleans flies and caterpillars from tips of white spruce branches. Males forage higher than females when this technique is used. Occasionally it leaps from the ground to make short sallies to capture butterflies or flies in flight. It captures spittle bugs by stabbing into the spittle mass on vegetation. Seeds are consumed by picking them off the ground after they have fallen or by stripping them from grasses. This latter method is used mostly when snow or freezing rain covers seeds on the ground. Less frequently, it double scratches with both feet in the litter to uncover seeds and invertebrates (Baird in Austin 1968; Bédard and LaPointe 1984a; Wheelwright and Rising 2020; Wheelwright and Schultz 1994; Wiens 1969; Williams 1987). In Nova Scotia, its abundance was positively correlated with the abundance of flies and beetles (mostly ground beetles) which are prey items. Abundance was negatively correlated with abundance of centipedes (Nocera et al. 2007b).

In Nova Scotia, caterpillars formed a significant proportion of the food brought to young nestlings. Later, adult lepidopterans formed the bulk of the diet. Only very small insects were fed to the young in the first 2 days, with the size and amount of food increasing as they grew (Welsh 1975). In Saskatchewan, nestlings were fed spittle bugs, wasps, spiders, flies, bugs, and beetles. Birds breeding near marine shores may feed young amphipods and seaweed fly larvae. Less commonly, nestlings are fed fruits of strawberries and blueberries (Wheelwright and Rising 2020). Near Quebec City, the diet of nestlings consisted entirely of arthropods. Major food items in decreasing order of numerical importance included caterpillars and sawfly larvae, fly larvae and adults (predominantly flower flies and picture-winged flies), and bugs (mainly froghoppers and leafhoppers). Groups of secondary importance included adult lepidopterans, orthopterans, spiders, and beetles. Caterpillars and sawfly larvae constituted 27% of prey items and the consumption of these remained constant throughout the sampling period. There was an abrupt increase in the use of soft-winged bugs during the week of 27 June to 3 July when they comprised 38% of the diet. Adult lepidopterans were seldom consumed until after 18 July when they constituted 20% of the diet. Nonstaple items such as orthopterans, spiders, and beetles were always of minor importance in the diet even though they were abundant. Adult lepidopterans and beetles were disregarded despite their abundance at times. Caterpillars and sawfly larvae were selected even when they were scarce. There was a tendency for adults to collect a greater diversity of prey items as the season progressed. Soft-winged bugs constituted 38% of prey items brought to nestlings 1-3 days old but only 10% for 7-9-day-old nestlings. Adult lepidopterans were seldom brought to 1-3-day olds but represented 18% of the diet of older nestlings. Caterpillars and sawfly larvae increased from 24% at age 1-6 days to 30% during the final 3 days in the nest. Nestlings in broods of 2 received significantly more adult lepidopterans and adult flies than broods of 3 and 4. Both sexes brought all types of prey, but males brought significantly more caterpillars, sawfly larvae, and adult flies than females, and females brought

significantly more soft-winged bugs than males. Adults brought adult lepidopterans and fly larvae in equal proportions. Sexes may bring different prey because males can forage over larger areas. Females are more likely to forage near the nest. Although adults prefer certain prey, they are opportunistic and can respond to temporary increases in palatable prey. There was no indication that food abundance was a limiting factor (Meunier and Bédard 1984). In Alaska, Miller et al. (1994) compared the diet of nestlings during periods of grasshopper high abundance and rarity. During the year of abundance, significantly more grasshoppers were fed to nestlings and in the year of scarcity, nestlings were fed significantly more caterpillars and flies. In the year of abundance and scarcity, respectively, the nestling diet consisted of 25.2% and 25.2% spiders, 60.8% and 0% grasshoppers, 0% and 0.1% neuropterans, 0% and 5.9% adult beetles, 0% and 3.7% beetle larvae, 1.4% and 2.2% adult lepidopterans, 5.6% and 25.2% caterpillars, 2.1% and 11.9% flies, 4.9% and 4.4% crane flies, and 0% and 20.7% hymenopterans.

Adult Savannah Sparrows subsist predominantly on seeds in early spring, late autumn, and winter, and feed mostly on insects during the breeding season. Judd (1901) analyzed the contents of 119 stomachs. The diet consisted of 46% animal material and 54% vegetable material. The animal matter consisted of 15% beetles, 9% lepidopterans, 8% orthopterans, 5% hymenopterans, 2% true bugs, 4% flies and miscellaneous insects, and 3% spiders with a few snails. It consumed more beetles than other sparrow species and ate them every month, but in lesser quantities in winter. Beetles comprised a third of the diet in May and June, particularly weevils and leaf and ground beetles, but it also ate fireflies and click, dung, rove, and pill beetles. It preferred weevils and they constituted 11% of the August diet. The lepidopterans that were consumed were mostly owlet moth caterpillars. Grasshoppers were common in the diet from June to August and comprised 34% of the July diet. The hymenopterans were mostly ants and the flies consisted of crane flies and horse flies. The vegetable matter that was consumed was almost entirely seeds. Foxtails and panic grasses comprised 31% of the diet; 22% of food items were seeds of herbaceous species. In Utah, 14 stomachs contained 136 unidentified seeds and numerous invertebrates. These included 1 grasshopper nymph; 50 soft-winged bugs including leafhoppers and aphids; 39 true bugs including plant and seed bugs; 28 beetles including larvae, leaf beetles, and weevils; 8 caterpillars and 17 lepidopteran eggs; 15 flies that were mostly midges; and 4 hymenopterans including ants (Knowlton 1950). At La Pérouse Bay, birds collected prior to 11 June had a diet of 45% seeds by volume. Birds collected later had not eaten any seeds. It has eaten odonates, small insects, crustaceans, and aquatic insect larvae and nymphs. Birds nesting on marine shores may eat crabs, isopods, and amphipods. It consumes a wide range of sizes of prey, from 3-mm long midges to 4-cm caterpillars. Seeds consumed include those of foxtails, crabgrasses, ragweed, panic grasses, amaranths, knotweeds, oats, nightshade, barley, and sorghums. Foxtails, crabgrasses, and panic grasses are particularly important in the diet. It occasionally eats fruits of blueberries and strawberries. At any given time, it may feed almost exclusively on 1-4 types of seeds (Baird in Austin 1968; Wheelwright and Rising 2020). During years of high grasshopper abundance in Alaska, grasshoppers constituted 45.8% and 56.2% of the diet compared with 8.2% in a low grasshopper population year. Beetles comprised 14.7% and 17.2% of the diet in high years and 47.6% in years of low grasshopper abundance. There was no significant difference among years for other taxa: 1.9-18.0% for true bugs, 5.2-7.4% for soft-winged bugs, 0.6-14.5% for beetle larvae, 0-0.2% for adult

lepidopterans, 1.3-2.5% for caterpillars, 0.4-1.4% for flies, 0-8.2% for hymenopterans, 4.7-13.8% for spiders, and 0-2.7% for molluscs. The Savannah Sparrow exhibited a high degree of dietary flexibility in response to fluctuating prey (Miller and McEwan 1995). In California, de Rivera (2000) observed adults chasing fiddler crabs, which carry their eggs ventrally. On 18 of 49 chases (36.7%) sparrows successfully ate eggs from crabs without otherwise harming them. Birds never chased male crabs or females without eggs. Adults also fed crab eggs to fledglings which later started chasing crabs. The Savannah Sparrow is very flexible in its diet and food availability is not a limiting factor for it (Wheelwright et al. 1992).

The Savannah Sparrow is commonly parasitized by the Brown-headed Cowbird. In grassland landscapes, the rate of parasitism may be influenced by tree cover. In North Dakota, there was a significant negative relationship between parasitism rates and the amount of tree cover within 2 km. The probability of parasitism was 90% when there was 2% tree cover within 2 km, dropping to 0% at 3-5% tree cover and remaining at 0% with increasing tree cover. All nests were in areas with 2-15% tree cover and 92% of parasitism occurred in areas with 2-3% tree cover. Woodlands support higher densities of breeding birds and a greater diversity of potential hosts for cowbirds (Pietz et al. 2009). In Saskatchewan, there were no significant differences in distances to potential cowbird perches or amount of concealment for parasitized and unparasitized nests. In Minnesota, parasitism rates decreased with increasing distances to wooded edges (Swanson 2002). Klippenstine and Sealy (2008) artificially parasitized Savannah Sparrow nests with natural and artificial cowbird eggs and blue eggs. Some nests were naturally parasitized by cowbirds. Sparrows successfully ejected 1 real cowbird egg and were unsuccessful in ejecting another resulting from natural parasitism. For artificially parasitized nests, 11.1% of artificial and 0% of natural cowbird eggs were rejected and 13.3% of blue eggs were rejected. Puncture ejection was used to expel eggs from nests. It appeared to be reluctant to eject cowbird eggs, possibly due to their similarity to their own eggs which increases the risk of ejecting their own eggs. Although the Savannah Sparrow may successfully fledge both its own young and cowbirds from parasitized nests, parasitism decreases reproductive productivity. Parasitized nests have smaller clutches and fledge fewer young. In Saskatchewan, clutch size was 2.9 eggs in parasitized nests and 4.4 in unparasitized nests; 0.1 fledgling was produced in parasitized nests compared with 1.1 in unparasitized nests, and 2.0 fledglings were produced in successful parasitized nests compared with 3.5 in successful unparasitized nests. In Alberta, clutch size was 1.6 eggs in parasitized nests and 3.1 in unparasitized nests. Successful nests produced 1.9 fledglings in parasitized nests and 3.6 in unparasitized nests. Predation rates did not differ between parasitized and unparasitized nests (Davis 2003; Ludlow et al. 2014; Winter et al. 2004). Cowbirds may further reduce productivity by attacking nestlings or destroying eggs in unparasitized nests. This may result in renesting which potentially provides additional opportunities for parasitism (Granfors et al. 2001). In Ontario, 44 of 607 nests (7.2%) were parasitized. Parasitism rates from other locations include 0 of 41 nests in West Virginia; 45 of 675 nests (6.7%), 31 of 150 nests (20.7%), and 13 of 83 nests (15.7%) in North Dakota; 24 of 83 nests (28.9%) and 2 of 27 nests (7.4%) in Saskatchewan; 11% of nests in Alberta; 34 of 160 nests (13.1%) in Montana; 4 of 405 nests (1.0%) in Wisconsin; 5 of 398 nests (1.3%) in New Brunswick; 0 of 479 nests in Michigan; 1 of 128 nests (0.8%) in New York; 2 of 232 nests (1.3%) on Sable Island; 46 of 687 nests (6.7%) in Minnesota and North Dakota; and 2 of 203 nests (1.0%) in British Columbia (Campbell et al. 2001; Davis 2003; Dixon 1978;

Gaudet et al. 2020; Granfors et al. 2001; S.L. Jones et al. 2010; Ludlow et al. 2014; Norment et al. 2010; Peck and James 1998b; Pietz et al. 2009; Renfrew et al. 2005; Wheelwright and Rising 2020; Winter et al. 2004; Wray et al. 1982).

Habitat loss and degradation is occurring in southern Ontario due to natural succession, reforestation, urbanization, and changes in agricultural practices. Marginal farmlands have been abandoned and allowed to succeed into forest and other areas have been actively planted with trees. Natural succession is the most important factor affecting habitat on the southern Canadian Shield and the area immediately south of it. Natural succession is less of an issue in southern Ontario agricultural landscapes, where changes in agricultural practices are a more important source of habitat loss and degradation. These include reductions in the amount of pastureland and hayfields and conversion to cash crops such as soybeans and corn. Although the Savannah Sparrow may nest in row crops, it does so at much lower densities than in grasslands, hayfields, and pastures. Declines in the Carden Plain between the 2 atlases were a result of conversion of pastures and hayfields to row crops and invasion of shrubs in grasslands (Merondun et al. 2024). Similar results have been documented in most areas (Bonneau in Gauthier and Aubry 1996; Wheelwright and Rising 2020).

Another significant factor affecting habitat quality for the Savannah Sparrow is the change in composition of hayfields. Ontario hayfields were originally dominated by grasses and clovers in the genus *Trifolium*. They are now dominated by alfalfa. Alfalfa grows much denser than other hay types and is less appealing to Savannah Sparrows. Alfalfa grows more quickly and can be cut earlier and more frequently than other hay crops. This results in hay being cut before young can fledge from nests. Numerous studies examined the effects of mowing on the Savannah Sparrow, but there is no consistent pattern of response. Shustack et al. (2010) studied hayfields that were mowed 1-4 times annually in Vermont and New York. It had an affinity for recently cut fields and was negatively correlated with the amount of time since cutting and fields with taller vegetation. It was positively correlated with fields that were cut more often. Seventy-one percent of fields that were cut retained the same number or gained Savannah Sparrows. It appeared to be attracted to mowed fields and may have immigrated into them. Most birds renested in New York and Vermont hayfields after mowing and successfully fledged young after both the first and second cuts (Fajardo et al. 2009). In the same area, fields cut before 11 June and again in early to mid-July resulted in 99% nest failure. After haying, sparrows immediately renested but fledging success was low. Reproductive success was greater in fields cut once between 21 June and 10 July and in those cut after 1 August (Perlut et al. 2006). Densities increased in Wisconsin hayfields after mowing (Swanson 2002). Norment et al. (2010) studied pastures, hayfields, and fallow fields in New York. Fallow fields were left undisturbed. Pastures or hayfields were lightly grazed or mowed after 1 August. Nest survival was higher in pastures and hayfields than in fallow fields. In Vermont and New York, Perlut et al. (2008) compared Savannah Sparrow survival rates in hayfields cut before 11 June and again in early to mid-July, hayfields cut once between 21 June and 10 July, hayfields cut after 1 August, and rotationally grazed pastures. Survival on late-hayed fields was more than 25% higher than for all other treatments. Male survival rates were 35% higher than for females. Recruitment was higher in more intensively managed fields than in late-hayed fields, indicating a greater turnover of individuals in more disturbed areas. In Nova Scotia, Nocera et al. (2007b) concluded that third hay cuts after August could be beneficial. This potentially delays the first harvest in the following year. In Massachusetts, it

was equally abundant in grasslands that had been mowed and those that had been left undisturbed (Zuckerberg and Vickery 2006). Zalik and Strong (2008) studied the effects of hay cropping in Vermont on invertebrate biomass and Savannah Sparrow productivity. In control fields, invertebrate biomass increased throughout the season. Biomass declined 28-82% after cutting in treatment fields. As vegetation height increased, invertebrate biomass quickly recovered. There were no differences in clutch sizes for either first or second broods in control or treatment fields. The number of young fledged per successful nest where clutches were completed after 24 June was lower on cut fields (2.2) than uncut fields (3.2), but not significantly. Adults brought 48% more food mass per trip on uncut than cut fields and the number of trips made was similar in both habitats. In both Saskatchewan and Alberta, the Savannah Sparrow was more abundant in grasslands and tame hayfields that had not been cut for 3 or more years, although it did nest in fields that had been cut the previous summer. In another Alberta study, it occurred significantly more on undisturbed plots than those that had been mowed or grazed. In Illinois, it was more common in recently mowed grasslands (within 4 months of 1 May) than in unmowed grasslands. These provided the low and medium height vegetation that it prefers. In North Dakota, it was more abundant in CRP lands that had been mowed the previous year than in undisturbed areas (Owens and Myers 1973; Swanson 2002). Wheelwright and Rising (2020) concluded that earlier and more frequent harvest in agricultural grasslands was a major cause of decline for the Savannah Sparrow. Tews et al. (2013) considered it to be at high risk due to haying operations in Canada. It had the highest annual mortality of any species, in part due to its high density and broad geographic range. They estimated direct mortality of 940,697 eggs and nestlings; 75,094 of these were estimated to occur in the Carolinian Forest Region of Ontario and an additional 187,737 mortalities were estimated for Bird Conservation Region 12 which includes the remainder of the area in Ontario south of the Shield as well as portions of Manitoba and Quebec. Wolcott et al. (2023) recommended that grassland management be deferred until August to protect both nests and fledglings.

van Vleit et al. (2019) compared nesting success and fledgling survival of the Savannah Sparrow in southwestern Ontario in agricultural and non-agricultural habitats. Agricultural sites were monocultures of corn, soybeans, or winter wheat. Non-agricultural sites were open areas dominated by nonnative grasses and herbaceous species. In agricultural lands, all nests were in grassy laneways and margins between crops. The daily survival rate of nests was negatively influenced by intensive agriculture, with 11% probability of nest survival in agricultural land compared with 27% in non-agricultural land. Land use did not affect fledgling survival, clutch or brood size, arthropod abundance, or condition of adults or nestlings.

In Manitoba, the Savannah Sparrow nested on transmission line and highway rights-of-way. It was less abundant on rights-of-way surrounded by more wooded lands or more urban lands. Numbers on plots were 4-6 at 0% wooded lands (trees and shrubs) within 100 m, declining to 1 at 50% wooded lands. Numbers were 5.8 when there was no urban land within 100 m, declining to 1.3 at 50%. Densities increased along rights-of-way that were mowed more frequently and were higher within hayed than unhayed rights-of-way. Occupancy decreased as the percent bare ground increased (Leston and Koper 2017).

In Alberta, abundance and productivity increased when winter and spring wheat crops were managed with minimal tillage practices rather than conventional tillage. In Iowa, the Savannah Sparrow nested at low density in untilled corn and soybean fields that were idle in spring and autumn and contained crop residue year-round. Conservation tillage may create an ecological trap. Birds may be attracted to the habitat but have low nesting success (Swanson 2002).

Grazing may be detrimental or beneficial depending upon the intensity of grazing and the initial density of the vegetation. Light to moderate grazing in dense vegetation may make it more suitable for the Savannah Sparrow. Intensive grazing or grazing where vegetation is initially sparse may be detrimental. In short and mixed-grass prairies, moderately and heavily grazed areas do not provide the dense ground cover it requires. In the Great Plains, there were higher densities on idle or lightly grazed grasslands than on moderately or heavily grazed grasslands. In Saskatchewan, densities were more than 25 times higher in ungrazed than grazed grasslands. It foraged there most frequently in grazed grasslands but nesting density was consistently lower in grazed than ungrazed grasslands (Swanson 2002). In addition to altering the habitat by grazing, cattle can have direct impacts on nesting success. Cattle may trample nests or lie on them and even actively depredate eggs and nestlings (Nack and Ribic (2005). Campomizzi and LeBrun-Southcott (2022) studied the effects of rotational grazing in Grey County on a 234-ha pasture subdivided into 21 2.6-20.5-ha fields by temporary fencing. Grazing was initiated in late May for 1-12 days and rested 4-7 weeks before being grazed again. The Savannah Sparrow was resilient to grazing, but nested more frequently in ungrazed grasslands. It renested after nest loss and continued to nest throughout the season.

The impacts of fire on the Savannah Sparrow vary depending upon the initial structure of the habitat and intensity of the fire. In Saskatchewan, it was adversely affected by an autumn burn in fescue prairie. Density in the burn was 48% of that in the control area the first year postfire, 36% in the second year, and 68% in the third year. This population used shrubs for nesting cover and song perches and fire greatly reduced the density of shrubs. The response in the third year may have been related to recovery of snowberry, the dominant shrub (Pylypec 1991). In Massachusetts, there was no difference in its abundance in burned and unburned native grasslands (Zuckerberg and Vickery 2006). In Illinois, densities were highest in grasslands during the first season postfire and it was absent by the third season postfire. It preferred recently burned grasslands for nesting. In Wisconsin, highest densities occurred in recently burned restored tallgrass prairie. In Minnesota, Wisconsin, and South Dakota, highest densities occurred in grasslands that had not been burned for a year or more. At other sites, it was concluded that 2 or more years were required for sufficient litter to accumulate to provide suitable nesting habitat. At 2 sites in North Dakota, highest densities were attained 1-5 and 6-8 years postfire (Madden et al. 1999; Swanson 1996, 2002).

In tundra areas, Savannah Sparrow habitat may be lost or degraded due to excessive browsing by Snow Geese. Grubbing by geese removes graminoid species, resulting in higher soil temperatures, higher evapotranspiration rates, and increased soil salinity. Sites may take decades to recover even after goose grazing has ceased. Near Cape Churchill, the Savannah Sparrow nested in freshwater sedge meadows dominated mostly by water sedge. Areas that had not been grazed by geese supported 1.85 times higher density of sparrows than grazed areas. At La Pérouse Bay, grubbing by geese affected the dwarf willow and birch habitat that it favoured. Density of sparrows

in 1965-67 was 6 times greater than in 2000 and 4 times greater than in 2011. There was no change in density during 1977-2012 on a BBS route 30 km distant where there was no goose damage. It was estimated that the Savannah Sparrow population in the Churchill region declined about 50% from 1965-67 to 1991 as a result of goose grazing, and there was an 80% decline over 36 years at La Pérouse Bay (Jehl 2004; Peterson et al. 2014; Sammler et al. 2008).

Shaffer and Buhl (2015) studied the reactions of the Savannah Sparrow to wind turbines in North Dakota and South Dakota. There was a significant and immediate displacement behaviour, with lower density 100-300 m from turbines than at reference sites. Displacement was observed at 200-300 m at 1 site and 100-300 m at another. Hamilton et al. (2011) and Ludlow et al. (2015) studied responses to facilities associated with oil and gas extraction in Alberta. These include wells, roads, trails, and a network of pipelines. Areas near these sites had a higher proportion of nonnative plant species, particularly crested wheat grass, and the vegetation is often taller in these areas. At 1 study area, the Savannah Sparrow was significantly more abundant with higher occurrence in disturbed areas, particularly in areas of high well density. It preferred taller vegetation and disturbed areas where there was more crested wheat grass. In the other location, nest locations relative to wells, roads, and trails did not differ from random and proximity to these features did not affect nest success. Sparrows fledged more young closer to wells than distant from them and the number of young fledged per successful nest increased as the percent coverage by crested wheat grass increased. Despite the higher success rate in crested wheat grass, density was lower in this grass. In Alberta, its abundance, clutch size, and nesting success were affected by distance to infrastructure and by gas well density. Infrastructure seemed to positively affect clutch size with largest clutches adjacent to oil wells, roads, and shallow gas wells. Abundance declined with increasing gas well density, suggesting that these affected a very large area for this sparrow. Clutch sizes declined with increased density of gas wells. Noise did not appear to be a factor because results were similar at quiet gas wells and noisy oil wells (Daniel and Koper 2019). In Alberta, Warrington et al. (2018) studied the effects of noise from 4 types of oil and gas extraction infrastructures on the Savannah Sparrow's song. There was no effect on its entire song, but song minimum frequency increased with ambient background noise. Most effects occurred at generator-powered oil well pumps, the loudest type of infrastructure which measured 80-88 dB within the frequency range of the Savannah Sparrow's song.

Severe weather and catastrophic events may affect reproductive success of entire populations in certain years. In more northern areas and at high altitudes, cold and wet weather can cause widespread nest losses that may affect annual production. Such events have been documented near Churchill, Quebec City, and in British Columbia alpine meadows (Jehl and Hussell 1966a; LaPointe and Bédard 1986; Martin et al. 2009). In British Columbia alpine habitat, nest survival was lower in colder years and was negatively correlated with cumulative precipitation. Nest mortality was approximately 4.6 times greater after 2 or more days with rain than following days without rain (Martin et al. 2017). Birds nesting near saltwater marshes may have their nests inundated by spring tides, which are higher during full and new moons. Birds can still nest successfully if they squeeze the nesting cycle between 2 high tides and situate the nest above the upper level of the neap tide (Bédard and LaPointe 1984).

Certain herbicides and pesticides may have adverse effects on the Savannah Sparrow. In Wyoming, mortality was observed after fenthion was sprayed to control mosquitoes. In Maine, density decreased for 2-6 years following application of the herbicide hexazinone on lowbush blueberry. In Ontario corn fields, there was no significant difference in its abundance before and after application of fonofos and tertbufos to control corn rootworm, or between treated and control fields (Swanson 2002).

Niemuth et al. (2008) concluded that the Savannah Sparrow was adversely affected by drought in North Dakota. Densities were lower in drought than wet years and its abundance was significantly correlated with the number of ponds present in May in the same and previous years.

Nixon et al. (2016) used climate models to predict the change in area of suitable climate in Alberta for the Savannah Sparrow. They predicted that there would be a 10% decline in area of suitable habitat by the 2050s and a decline of about 24% by the 2080s. It was anticipated that it would experience declines in suitable land cover within its projected suitable climate of 28% by the 2050s and 60% by the 2080s.

Wheelwright et al. (1997) studied nesting of the Savannah Sparrow in relation to an American Herring Gull colony in New Brunswick. The American Herring Gull is a potential predator of eggs and nestlings, but may also help to defend nests against the American Crow, a more efficient predator. Density was almost 2 times higher where gulls were absent than where they were present. Those nesting near gulls disproportionately selected nest sites with dense patches of lowbush blueberry and goldenrods. Vegetation surrounding their nests was 4.5 times taller than those nesting in areas of low gull density. Gulls were ineffective in finding Savannah Sparrow nests and typically found them only when females flushed from the nests. Gulls reacted strongly to crow models and attacked them. Where gull densities were intermediate or high, 70.7% of sparrow nests fledged at least 1 young, significantly more than in areas of low or no gull densities (55.7%). Despite the apparent advantage of nesting among gulls due to protection from crows, Savannah Sparrows avoided gulls.

Miller and Fair (1997) concluded that parasitism by blow flies did not have an impact on Savannah Sparrow reproductive success.

Swanson (2002) provided management recommendations for the Savannah Sparrow: remove woody vegetation within and along the periphery of grassland patches to discourage predators and enlarge the amount of interior habitat; grassland restoration areas should be 50 ha or larger and preferably 100 ha or larger; avoid burning, mowing, and moderate-to-heavy grazing in suitable habitat from 1 May to 1 August; burn grasslands in early spring or late autumn; in grasslands 50 ha or larger, burn 25-30% annually and burn every 5-7 years in mixed-grass prairies; where possible, delay mowing hayfields until mid-July; when mowing must be done during the breeding season, mow only half per year; and grazing that leaves 40% of vegetation cover 25 cm or more tall can be used to create the intermediate vegetation height and density that it prefers.

Price (2004) predicted that the Savannah Sparrow might not continue to breed in southern Ontario if the average summer temperature increased by 2°C.

Status

McIlwraith (1894) stated that the Savannah Sparrow was not plentiful. By the 1940s, it was common in Hamilton and could be found in almost all cultivated and pasture lands in rural areas in the 2000s (Curry 2006). It was scarce on the mainland near Kingston in the early 1900s, but common on Simcoe Island where the forest cover had already been cut. It was rare inland from Kingston and Lake Ontario in 1859 but a very common summer resident in the 2000s (Weir 1989). In Elgin County, it was common in 1891 and 1954. In 2000, it was still common but local in distribution, with considerable habitat loss in the previous 50 years due to cash cropping (Lancaster et al. 2004). Baillie and Harrington (1937) considered it one of the most common sparrows that bred in suitable habitat throughout the province. Manning (1952) concluded that it was the most common nesting passerine along the Hudson Bay and James Bay coasts and Peck (1972) stated that it was probably the most common species at Cape Henrietta Maria. During the first atlas, Rising (in Cadman et al. 1987) concluded that it was the most common species nesting in fields and meadows throughout the province. Its range covered the entire province except for notable gaps in the heavily forested areas in the northern portion of the Boreal Forest Region and in the Algonquin Park area. Although it occurred in the southern portion of the Shield, it was not very common in this largely forested habitat. Highest densities occurred along the Hudson Bay and James Bay coasts and in agricultural landscapes south and east of the Shield. James (1991) considered it an abundant summer resident throughout the province.

The second atlas revealed no significant change in the distribution of the Savannah Sparrow. It was found in more blocks within the Boreal Forest Region but continued to be relatively scarce in this area. There was no change in its probability of observation except in the Hudson Bay Lowland, where it increased significantly. It experienced a nonsignificant increase in the province. It was most abundant along the Hudson Bay coast, at the northern extent of the James Bay coast, and in portions of the agricultural landscape south of the Shield. In this region, highest densities occurred in agricultural areas in Lambton, Huron, Bruce, Dufferin and Wellington counties; on the Carden Plain; in the Haldimand Clay Plain; and in the extreme southeast of the province. It remained scarce in the Algonquin Park area and the Shield, where it is restricted to the Clay Belt, pastureland, airports, and natural forest openings (Rising in Cadman et al. 2007).

BBS results indicate that the Savannah Sparrow decreased at annual rates of 2.11% in Canada and 4.05% in Ontario 1970-2021, and 3.93% in Canada and 5.35% in Ontario 2011-21. Results were highly reliable except that the long-term trend for Ontario was of medium reliability (A.C. Smith et al. 2023). The BBS method is a bit deficient because it does not sample northern populations where there are no roads.

POSTFLEDGING PERIOD

Adults divide the brood shortly after the young fledge. Males are most likely to care for the smallest fledglings, perhaps because they remain closer to the nest and the centre of the male's territory. Males contribute most of the care to first broods if the female is incubating a second clutch. Females tend to care for more fledglings from late broods. The sexes contribute equally to fledgling care and fledgling survivorship is not affected by the sex of the adult that cares for them (G.W. Mitchell et al. 2012; Wheelwright and Rising 2020; Wheelwright et al. 2000).

On Sable Island, young hide in the grass after leaving the nest until they are about 3 weeks old. On the mainland of Nova Scotia, fledglings concentrated in an area along the shoreline that was outside any territory. As many as 6 females attended their young there. This was the most luxuriant growth in the study area, being covered by a dense growth of seaside pea and beach grass. The highest concentration of midges and flies occurred there, offering an abundance of food for fledglings. Fledglings that are still being cared for by adults often wait to be fed in nest-like tunnels in the grass. Young are able to fly 1-5 m about 3 days after leaving the nest or when they are 13-15 days old and are erratic but proficient fliers by age 20 days. In New Brunswick, fledglings remained with a single parent a median of 15 days and a maximum of more than 40 days. Young became independent at age 22-24 days and gradually started to disperse from each other. The wings are fully developed by age 27 days (Ross 1980; Weatherhead 1979; Welsh 1975; Wheelwright and Rising 2020; Wheelwright et al. 1992, 1994, 2000). On Kent Island, some fledglings remained near their natal territories throughout the postfledging period whereas others travelled distances of 200 m or more shortly after fledging. Fledglings from second broods travelled further than those from first broods. Male fledglings travelled further than female fledglings. Birds from areas with high nest densities travelled further than those from areas with low or moderate nest densities. The distance fledglings moved between consecutive days increased with age, peaking around day 20-30 and then levelling off. Some individuals moved greater distances again between days late in the postfledging period, around day 70-80 (Mueller et al. 2025).

Independent juveniles 26 or more days old begin to congregate in monospecific flocks that may swell to more than 100 birds in late summer. These are often found in grassy areas and saltwater marshes. Juvenile flocks may wander distances of 0.5-1 km daily, but delay migration until 2-3 months after fledging (Baird in Austin 1968; Wheelwright and Mauck 1998; Wheelwright and Rising 2020). McIlwraith (1894) reported that the Savannah Sparrow became abundant along the marshy shores of Hamilton Bay in late summer. In Saskatchewan, juveniles and adults flock together and with other sparrow species. At first, they mix mostly with Vesper and Clay-colored sparrows but are later seen in the company of Song, Swamp, White-throated and other sparrows. These flocks tend to inhabit trees and shrubs bordering pastures and cultivated fields (Leighton et al. 2002).

In Michigan, females left the breeding grounds before initiating the moult. They usually left within 2 weeks of completing their last nest regardless of whether it failed or successfully produced young. Females left gradually through June and July. Males stayed an average of about a month later and occasionally 1.5 month later, with most leaving in the last 2 weeks of July (Potter 1972).

MIGRATION

All populations of the Savannah Sparrow migrate except those that are resident along the California coast or breed in Mexico. It is predominantly a nocturnal migrant but migration may continue into the morning either as a continuation of migration or as redirected movement. In autumn, it may occur in flocks of conspecifics or in mixed-species flocks of sparrows. Autumn migration is stimulated by cold fronts associated with high pressure that causes a sharp drop in temperature, clear skies, and strong winds from the north or northwest. Acoustical surveys conducted during spring migration on the shoreline and in Lake Erie demonstrated that the Savannah Sparrow readily crossed the lake, but fewer crossed in the central basin. The central basin of Lake Erie may act as a

partial barrier during spring migration (Baird in Austin 1968; Gesicki et al. 2016; Wheelwright and Rising 2020).

Arrival of males usually spans several days. In Michigan, all males arrived within a 10-day period in both of 2 years. Near Quebec City, males arrived over periods of 16, 19, and 24 days in 3 years. Returning males do not have to rush back in spring to claim territories because of the very high site fidelity to territories and the later arrival of yearling males. Although the first females may occasionally arrive as soon as the first males, females tend to arrive a minimum of a week later than males. In Michigan, the first females arrived 15 and 21 days after the first males in 2 years, and the intervals between male and female arrivals near Quebec City were 12, 18, and 20 days in 3 years. Females do not need to rush to acquire a mate and territory because of high site fidelity (Bédard and LaPointe 1984; Potter 1972; Wheelwright and Rising 2020).

In Ontario, the Savannah Sparrow arrives in early to mid-April with most birds passing through from late April to mid-May. Some arrive in late March or rarely in early March (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

In New Jersey, the average autumn stopover period for the Savannah Sparrow was 7.3 days (maximum 28 days; Seewagen and Newhouse 2018). In the southern Shield, autumn migration begins in August, peaks in September, and continues until mid-October, with some remaining until late October (Mills 1981; Tozer 2012). In southern Ontario, autumn migration occurs from mid-September to late October, but there are occasional sightings into mid-November and rarely until early December (Black and Roy 2010; LaForest 1993; Lancaster et al. 2004; Weir 2008). Near Guelph, juveniles migrated earlier than adults. The first detection of migrant juveniles away from the site was on 14 September compared with 14 October for adults. Both age classes moved in a southwest direction but 2 juveniles made northward movements (Horn et al. 2022).

In Algonquin Park, the Savannah Sparrow is first observed in spring on patches of bare ground along roadsides and in clearings and fields (Tozer 2012). It may be observed in open fields, roadsides, dune vegetation, coastal marshes, edges of sewage lagoons, and other ponds in open areas. It rarely occurs in open woodlands (Wheelwright and Rising 2020). In British Columbia, migrants occur in cultivated fields, farmsteads, airports, log-littered beaches with vegetation, along dykes, adjacent to tidal marshes, rocky islets on the ocean coast where gullies are well vegetated and support abundant invertebrates, logging clear-cuts, subalpine tundra, timberline shrubbery of dwarf birch and willow, and edges of alpine meadows (Campbell et al. 2001). In the Yukon, migrants occur in shrubby wetlands, on open mudflats, and in weedy patches near settlements and along roads (Sinclair et al. 2003). On 2 islands in the Gulf of Maine during spring migration, it was significantly more abundant on the shrubby island than the treed island (Suomala et al. 2010).

Sinclair et al. (2003) reported that the Savannah Sparrow frequented bird feeders during migration in the Yukon. During migration, it feeds predominantly on seeds and some fruits, and also consumes some invertebrates where they are available (Wheelwright and Rising 2020).

In Arizona, Bock and Bock (1992) studied the response of autumn migrant Savannah Sparrows to a wildfire. The fire burned native and nonnative grasslands, eliminating litter cover and reducing grass cover, except for an invasive love grass that covered approximately 90% of both burned and

unburned nonnative grasslands. It was absent or very rare in unburned grasslands of both types. It responded positively to fire, but only in the year of the fire. Burning increased seed production of grasses and the reduction of litter made them more available. Its abundance was negatively correlated with grass cover.

The Savannah Sparrow is frequently killed during migration by striking communication towers, tall buildings, and other structures. Severe snowstorms during migration may cause mortality (Baird in Austin 1968).

James (1991) considered the Savannah Sparrow a common migrant in the province.

Hussell et al. (1992) reported a 1.1% nonsignificant annual decline in the number of Savannah Sparrows banded at Long Point 1961-88. Trends by period were: 1961-70, −3.0%; 1970-79, −3.2%; and 1979-88, +4.4%.

WINTER

In the east, the Savannah Sparrow winters predominantly where the average minimum January temperature is higher than −1°C (Root 1988). Males winter further north than females and both sexes may move even further south later in winter in response to adverse weather. In the east, it typically winters only as far north as Delaware (Baird in Austin 1968; Wheelwright and Rising 2020). Birds observed in Ontario are far north of their normal wintering range.

In winter, the Savannah Sparrow inhabits open areas that provide an abundance of food and have a mix of sparse and dense habitats. Suitable areas may include recently fallow fields dominated by annual plants such as horseweed, fields with heavy crops of crabgrass or other suitable plants for foraging, agricultural fields with fencerows and drainage ditches, undisturbed native prairies, native prairies disturbed by mowing or fire, nonnative grasslands, pastures, golf courses, roadsides, landfill sites, salt marshes, shrub thickets, and vegetated beaches. It prefers areas with bare soil or light litter cover where it can easily move and forage, an abundance of small seeds, and an overhead cover of low- to medium-height grasses. Where habitat is uniform, birds are distributed evenly. In fields of dense horseweed where some plots were mowed to a height of 15 cm, birds were evenly distributed in unmowed areas. Those in mowed plots concentrated around edges of plots adjacent to unmowed areas. Density within 22 m of the edge of mowed plots was 3.1 times greater than in central portions. During clear and overcast days with no rain, most birds on mowed plots were within 7.5 m of the taller edge vegetation. Density on mowed plots was 3 times higher on rainy days than on clear days. Densities remained constant in unmowed areas. The usage pattern in the mowed plots appeared to be related to the potential for predation by the Northern Harrier which foraged more frequently on clear and overcast days than on rainy days. In Arkansas, Kentucky, and Mississippi, density of the Savannah Sparrow was more than 2 times greater in fields with buffers of warm-season grasses and forbs than in fields without buffers. It exhibited higher densities in buffers wider than 23 m than in narrower buffers (Baird in Austin 1968; Campbell et al. 2001; Evans et al. 2015; Gordon 2000; Saafeld et al. 2016; Smith et al. 2005; Watts 1990; Wheelwright and Rising 2020). In South Carolina, it was more aggregated where crabgrass was common (Norris 1960).

During winter, the Savannah Sparrow roosts on the ground, either solitarily or in loose aggregations of as many as 30 birds. Texas roost sites had greater total cover and grass cover than

random sites, and roosts were interspersed within or around foraging sites. The greater horizontal vegetation depth at roosts may be important because it provides space for birds to roost and move under the vegetation without being exposed. It roosted in areas that provided better protection from weather. Those foraging on the coast travelled further inland to roost. The distribution of foraging and roosting areas influences movement patterns and overall home range size. It often roosts outside its foraging range and has specific habitat requirements for foraging and roosting areas (Baird in Austin 1968; Ginter and Desmond 2005).

Although large numbers of birds may occur together, birds act as individuals most of the time. At any given time 10-15% of birds are likely to be in small flocks of 2 or 3 but the composition of these flocks constantly changes. In Texas, each individual foraged within a small flock on at least 1 occasion, always with conspecifics in loose aggregations. In Georgia, the proportion of birds was influenced by the openness of the habitat. In habitat mowed to a height of 15 cm, 17% and 20% of birds in 2 plots were individual compared with 52% and 62% in unmowed plots. Large flocks were significantly more common in open than weedy plots. Fifty percent of birds in flocks in open areas were in flocks larger than 3 compared with 25% in weedy plots. The greater tendency to flock in open habitat was probably related to predator detection (Baird in Austin 1968; Ginter and Desmond 2005; Norris 1960; Watts 1996; Wheelwright and Rising 2020).

The Savannah Sparrow is not territorial in winter but it maintains a home range. In Arizona, birds at 1 site were highly sedentary; the average net movement at another site was 186 m over 40 days. In South Carolina, birds ranged over a maximum of 5.7 ha within a week (average 3.4 ha, minimum 0.8 ha). Winter home ranges in Georgia were 6-60 ha. Movement patterns are variable and probably related to the distribution of food, predator avoidance, and the distribution of suitable foraging and roosting habitat. Birds in Texas had a mean winter home range of 9.1 ha, a mean foraging area of 5.6 ha, and a mean roosting area of 6.6 ha. The mean core foraging area (50% of activity) was 0.9 ha (range 0.15-31.7 ha). One bird moved 2 km before returning 5 days later and subsequently disappearing; another moved 800 m. Many birds occupied small areas for 1-2 months but some may wander long distances. The mean distance moved from the centre of foraging areas to roosting sites was 165 m, with some birds travelling 400-600 m (Ginter and Desmond 2005; Gordon 2000; Norris 1960).

The Savannah Sparrow may exhibit winter site fidelity. In South Carolina, 33 of 453 (7.3%) returned in subsequent years and return rates of 38% and 41% occurred in other areas. There was little evidence of winter site fidelity in Texas (Baird in Austin 1968; Ginter and Desmond 2005).

In winter, the Savannah Sparrow forages in areas that provide a mix of open and dense cover. Foraging areas had more bare ground, less visual obstruction, and less horizontal depth than random sites. Seed biomass did not differ between foraging areas and random sites. The most common food seeds of little bluestem, spikerushes, panic grass, paspalum, and crabgrass were universally present. It foraged in areas of higher seed abundance suggesting that it is attracted to areas of high resource abundance. It forages almost exclusively on the ground in winter (Ginter and Desmond 2005). The winter diet consists of about 90% seeds of grasses and forbs, with those of crabgrass, ragweed, and sorghum important. It consumes insects and spiders where they are available. In California, where invertebrates are still available in winter, the winter diet consisted of

39.2% animal and 60.8% vegetable matter. Animal food consisted of 22.7% crustaceans (10.7% crabs), 8.4% insects (4.7% beetles, plus ants and lepidopteran cocoons), and 0.4% spiders. Much of the plant material was unidentified, but 12.3% consisted of wild oats and oats, 4% stork's-bill, and 4% nightshade. At another site, 10 of 11 birds had eaten snails. These comprised 18.5% of the diet for these birds but only 7.3% for the entire sample of 28 birds (Taber in Austin 1968; Wheelwright and Rising 2020).

James (1991) considered the Savannah Sparrow rare in winter in the extreme south, north to Peterborough and Kingston. In the Kingston area, it is seen on average 1 in 4 winters (Weir 2008). In the Hamilton area, a few have overwintered since 1960, and it occurred almost annually beginning in the mid-1990s (Curry 2006).

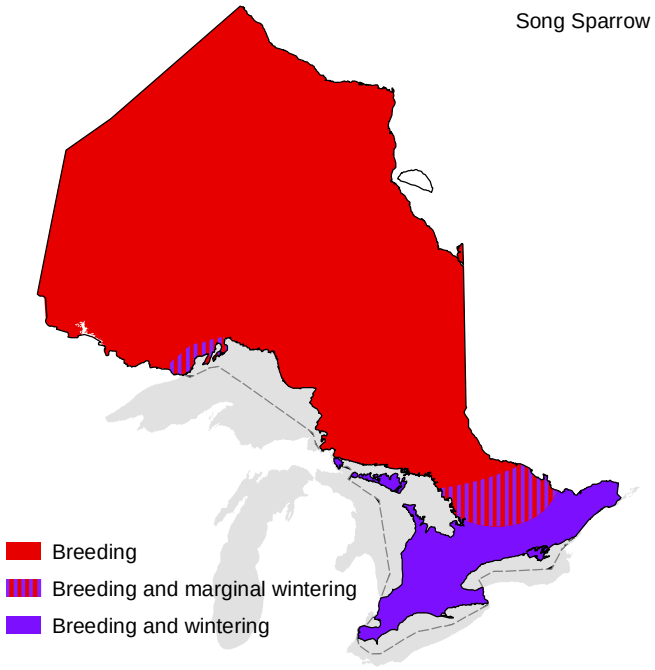
Song Sparrow

Melospiza melodia

BREEDING SEASON

Habitat Requirements

The Song Sparrow is an open-country species that nests in a wide variety of habitats, but it typically requires some shrubby areas within its territory. Of 655 Ontario nests, 40.5% were in farmland, including fields, conifer plantations, pastures, willow swales, wet meadows, orchards, vineyards, raspberry patches, hedgerows, and gravel pits; 16.9% were in woodlands including bogs, swamps, beaver ponds, and burns; 13.9% were in rural and urban areas including gardens, cemeteries, campgrounds, and cottage lots; 12.7% were in river valleys and shorelines of lakes, rivers, ponds, and marshes; 8.7% were on road, railway, or hydro transmission line rights-of-way; 5.8% were on rocky islands and outcrops; and 1.5% were in sand dunes. Nests in wooded areas were either at their edges



or where the canopy was open. Most nesting habitats were dry, but 31.3% were near water or in wet areas (Peck and James 1987).

In the Hudson Bay Lowland, Wilson and McRae (1993) found several territories at Moosonee. Most were within the town site and all were along creeks bordered with shrubs.

From Pickle Lake northward in the Boreal Forest Region, the Song Sparrow was most abundant in deciduous scrub followed by heath habitat, coniferous scrub, and mixed scrub. It was absent in all types of forest and tundra (McLaren and McLaren 1981). Near Pickle Lake, it occurred in small numbers in bogs and at lake edges (James 1980). In the Clay Belt, it was common in farms, natural clearings, lakeshore thickets, along river banks, and in old burns and similar habitats. It was common in alder thickets on rocky islands or points in rivers (Smith 1957). Near Hearst, Welsh and Fillman (1980) reported it in 3- and 6-year-old clear-cuts in lowland coniferous forests. Erskine (1977) considered it characteristic of prairie-forest ecotones where it occurred in early shrubby stages of succession and in various edge situations. It was characteristic of swamp and floodplain forests and numerous in wetter areas dominated by sedges and low shrubs such as sweet gale and willow. It is also common in northern urban areas.

In the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, the Song Sparrow was rare in jack pine stands near Gogama. It occurred predominantly at forest edges and near water where deciduous shrubbery was present among small jack pines. It was also present in low density in a 7-year-old jack pine stand (James and Peck 1995a). In Algonquin Park, it seldom occurred within dense forests but was abundant in shrubbery, at edges of woods, and along banks of streams and lakes (MacLulich 1938). Tozer (2012) noted that it bred mostly along lakeshores or rivers, but also in other edge habitats such as margins of bogs, edges of gravel pits, and shrubby borders of fields, clearings, and log landings. Also in Algonquin Park, it was common in both wet and dry bogs where it was the third-most abundant species (Martin 1960). In Algonquin Park white pine stands, it occurred in 8.3% of cuts that were 2-9 years old. It was absent in cuts 10-16 years old and in uncut forests (Kingsley and Nol 1999). In Muskoka and Haliburton, it was associated with low canopy volume and tree density, shrubby areas, and lawns. It was associated predominantly with mixed conifers and a reduced understory and was typically found in cottage areas where much of the vegetation had been removed (Clark et al. 1983). In Muskoka and Parry Sound districts, it was abundant in all areas except deep forest; it occurred in roadsides, gardens, farmlands, and margins of streams, ponds, bogs, and lakes (Mills 1981).

South of the Shield in the Great Lakes–St. Lawrence Forest Region near Ottawa, the Song Sparrow bred in hedgerows and fence lines predominantly in corn and soybean fields, but also in hay and wheat fields. The hedgerows it inhabited varied from grassy strips with occasional shrubs to fully treed (Girard et al. 2012). In Durham Region, it occurred in old fields, hayfields, gravel pits, woodlot edges, pastures, and stream sides. It showed a strong preference for old-field habitat with very few in pastures (Speirs and Orenstein 1967). It also occurred in very young pine plantations, old orchards, open-canopy forests, woodlots grazed by cattle, and small remnant woodlands including those that were mature. It was associated with early stages of forest succession and reached its greatest abundance in young seral stages, but occurred in all stages (Speirs and Orenstein 1975).

At the landscape level in southern Ontario, Austen et al. (2001) considered the Song Sparrow an edge species. Its abundance was positively correlated with the amount of forest cover within 2 km and the amount of forest cover in the region but was negatively correlated with woodlot size and the amount of forested habitat more than 100 m from edge. These relationships were not significant. In farmland, it was equally abundant on organic and conventional farms. It was positively associated with hedgerows, woods, trees, and pastures. It was negatively correlated with use of herbicides, farmsteads, grassy strips between fields with a fence, and railway, road, and hydro corridors (Kirk et al. 2011). In Oxford and Elgin counties, it was abundant in some fields, using shrub habitats for nesting and agricultural crops for foraging (Knapton 1990). In the Hamilton area, it was found wherever there was human habitation. It commonly nests along streams that run through suburbs (Curry 2006; McIlwraith 1894).

The Song Sparrow is a generalist species that occupies several habitats. In Ontario, it is absent from only tundra, deep forests, and the interior of grasslands and agricultural fields where there are no shrubs. Despite its adaptability, it has specific habitat requirements that include some shrubs or tall herbaceous vegetation for perching and dense nesting cover but with patches where sunlight can penetrate to the ground. It is most abundant in shrubbery bordering watercourses, water bodies, and wetlands and often attains very high densities on islands. It tends to be more abundant in landscapes altered by humans where woodlands are fragmented. Shrubbery around fields, pastures, and human dwellings provides good nesting habitat. In many areas, it appears to require wet or moist soils and is usually associated with water, but this is not the case in Ontario (Arcese et al. 2020; Bonneau in Gauthier and Aubry 1996). In Ohio, some territories consisted solely of herbaceous species with no trees or shrubs (Nice 1943).

Song Sparrow breeding habitat includes thickets of willows, alders, and similar shrubs along watercourses, lakeshores, pond margins, and in and at edges of wetlands; bogs and fens; open or forested islands of all sizes; woodland edges and openings; riparian woodlands; urban parks; suburban and rural residential lots; farmsteads; native and planted grasslands where it occurs in very low densities; clear-cuts; very young plantations; old fields and pastures; shelterbelts; subalpine and alpine shrubby areas; Great Lakes and marine coastal meadows; hedgerows; roadsides; along logging roads in forests; in recent forest burns; along drainage ditches; in marshes; in unmanicured orchards; in hayfields and occasionally row-crop fields; in fields managed for biofuel production by grasses; in areas managed for blueberry production; along pipeline and hydro transmission line corridors; along railway rights-of-way; and near brush piles. In British Columbia, 30% of nests were

near the edge of a forest, 24% were in wetlands, 22% were in clear-cuts, 21% were in shrublands, 2% were in grasslands, and 1% were in miscellaneous habitats (Arcese et al. 2020; Burhans et al. 2010; Campbell et al. 2001; Dawson 1979; DeGraaf 1989; Finch 1989b, 1991a; Graber and Graber 1963; Hartley 1994; Hoffman 1989b; Howe 1979; Keller et al. 2003; Judd 1901; Morse 1977; Mossman et al. 1991; Nice in Austin 1968; Nolan in Austin 1968; Patterson and Best 1996; Renken and Dinsmore 1987; Riffell et al. 2001; Robertson et al. 2012; Taylor and Taylor 1979; Vickery et al. 1994; Wilson and Arcese 2006; Yahner et al. 2002). The Song Sparrow frequents all these habitat types in Ontario and is found essentially wherever there are at least scattered shrubs. It may be found in almost all edges between habitat types.

At the landscape level, the Song Sparrow greatly prefers open or fragmented landscapes to forested areas. In Quebec, its frequency of occurrence is highest in the highly disturbed south with its abundance of abandoned fields and edge habitat resulting from forest fragmentation. It is less abundant in the north where the landscape is dominated by coniferous forest. There it is confined to disturbed areas and openings such as clearings, logging roads, and margins of lakes, rivers, streams, and wetlands (Bonneau in Gauthier and Aubry 1996). Its relative abundance is similar in Ontario. In Saskatchewan, it was significantly more abundant in small forest fragments or in landscapes with low local forest cover (Hobson and Bayne 2000). In North Carolina, it was negatively correlated with the amount of tree canopy coverage at the 200-m scale. As tree cover increases, shrub coverage decreases. It was positively correlated with habitat heterogeneity at the 200-m scale. Heterogeneous landscapes consisted of a mosaic of forest patches, lawns, and pastures. Homogeneous landscapes consisted of unbroken forest tracts (Gilbert and Ferguson 2019). It preferred areas with 51-75% forest cover in North Dakota and 23-45% tree cover in New York (Cunningham and Johnson 2019).

Several studies identified microhabitat preferences of the Song Sparrow in open habitats or compared its usage of shrubby and forested habitats. In riparian willow habitat in Colorado, it was equally abundant in short dense willows and tall sparser willows (Olechnowski and Debinski 2008). In Massachusetts grasslands interspersed with shrubs, it was positively associated with grasses 0.1-0.5 m tall and shrubs of the same height but negatively correlated with litter 0-0.1 m from the ground (Zuckerberg and Vickery 2006). In Massachusetts, DeGraaf (1989) compared territories in suburban and rural areas, which consisted mostly of country roadsides with scattered houses. The size of rural territories was significantly correlated with the amount of herbaceous vegetation. Suburban territories were significantly associated with the number of adjacent territorial males, shrub density, and shrub crown volume. All territories contained at least 70 shrubs per ha. Territory size was smallest where herbaceous vegetation and shrub cover were low. Territories that were not bordered by other territories appeared to be marginal but acceptable habitat. There may be a requirement for some openness in territories because territories were larger when both shrub numbers and volumes were greater. Habitats consisting entirely of shrubs may be marginal. In suburban areas of Massachusetts, its abundance was positively correlated with the volume of deciduous vegetation 1.8-3 m from the ground and herbaceous vegetation, and negatively correlated with the volume of deciduous vegetation 7.9-9.1 m from the ground. It preferred open situations and open shrub-herbaceous areas provided optimum habitat (Thomas et al. 1977). In Utah, Arizona, and Nevada, it occurred in areas of high shrub density with little canopy cover and

moderate ground cover (Whitmore 1977). In Michigan Great Lakes coastal marshes, its abundance was positively associated with increasing frequency of bulrushes and negatively correlated with tall dense grass (Riffell et al. 2001). In Iowa riparian habitat, its abundance decreased with sapling and tree richness and density, shrub density, and number of trees (Stauffer and Best 1980). In Pennsylvania, Smith and Hatch (2008) compared Song Sparrow usage of forested and shrubby habitat. The number detected per 100 m of transect was 0.07 in forest and 0.35 in shrubs. The number captured per 1,000 hours of netting was 0.2 in forest and 0.35 in shrubs. Usage of shrubs was significantly greater for both survey techniques. In British Columbia, it was significantly more abundant in riparian vegetation consisting of a dense understorey of deciduous vegetation than in adjacent coniferous forest (Wiebe and Martin 1998). In Illinois, it was most abundant in early shrub habitat where the oldest trees were 10 years old, followed by late shrub habitat where the oldest trees were 37 years old, and in areas dominated by bare soil. It was not detected in bottomland forest or upland maple-oak forest (Karr 1968). On hydro corridors in Pennsylvania, it was absent where shrubs were cut and more abundant where low basal area was retained and where foliage had been sprayed (Yahner et al. 2002). In Indiana, its abundance was almost 0 where there was 0-85% low ground vegetation, increasing abruptly as ground cover increased to 95% (Grundel and Pavlovic 2007a).

In forests, the Song Sparrow prefers very young stands, stands dominated by early successional species such as aspens, forests with very low canopy cover or with large openings where shrubs can grow, or riparian forests rather than upland forests. In Nova Scotia northern hardwoods, it was most common in stands 1-2 years old, uncommon in stands 5-12 years old, and absent in stands 20 or more years old. It was characteristic of young stands and one of the more abundant species. Also in Nova Scotia, it was absent in uncut forests, abundant in clear-cuts, uncommon in thinned forests, and absent in strip-cuts and shelterwood cuts. In New Brunswick spruce plantations, it was common in stands 3-8 years old and absent in stands 13 or more years old (Freedman and Johnson 1999; Freedman et al. 1981). In Quebec, it was common in clear-cuts in both deciduous and mixed stands, slightly less common in final cuts using the strip-cut method, and absent in young, medium-aged, and old strip-cuts (Falardeau et al. 1999). In Minnesota, it was associated with harvested areas but not forested plots (Hanowski et al. 2003). In the Prairie Provinces, it was associated with mixed-wood or deciduous forests that tended to be nutrient-poor and slightly damper than average. It was a very early successional species associated mostly with stands 0-9 years old (Kirk et al. 1996). In green ash woodlands in South Dakota, it occurred in low densities in young stands and was absent in old stands. Young stands had less overhead tree cover and small trees and shrubs in the understorey, and some had grass in the understorey (Rumble and Gobeille 1998). In Wisconsin upland deciduous forests, it was associated with young dense forests occasionally interspersed with snags after clear-cutting, but did not occur in more mature stands (Hoffman 1989a). In northern hardwoods in the northeast, it occurred in 20% of plots in mature undisturbed habitat and 47% of disturbed and early successional forests (Noon et al. 1979). In poplar-birch stands in the northeast, it was the fourth most abundant species. It was common in sapling-pole-stage forests but absent in pole-stage and mature stands (Back 1979). In pine forests in the northeast, it was common in seedling-sapling-stage forests, less common in pole-stage forests, and absent in older stands. After fire in pitch pine stands, it was absent 0-1 years after fire and present at low density 2-20 years after fire (Capen 1979). In

northeastern mixed forests, it was associated with increasing abundance of aspens (Temple et al. 1979). In clear-cuts in Minnesota, the Song Sparrow was the fourth most abundant species. It was negatively correlated with the density of both dead and live trees and the basal area of live trees. It occurred in open habitats dominated by shrub patches (Niemi and Hanowski 1984a). In North Dakota, it occurred in all forested habitats but was most abundant in willow shrub communities (Faanes and Andrew 1983). In California, Larison et al. (2001) examined Song Sparrow usage of natural and restored cottonwood-willow riparian habitats. Restored areas were not underplanted and were occasionally grazed in winter. The probability of a site being selected for nesting increased as foliage cover 0-1 m from the ground increased. In restored areas, it was increasingly likely to nest as foliage cover 2-3 m from the ground increased but this was not the case in natural areas. At the nest-patch scale of 5 m, the probability of nesting increased as lateral cover increased. The probability of nesting decreased with increasing foliage height in natural stands and increased in restored habitats. Nest-scale variables were much more important than nest-patch variables in selecting nest sites. The mean foliage cover was 67.8% at 0-1 m and 13.1% at 1-2 m from the nest. Restored stands had significantly fewer plots with above-average foliage cover at 0-1 m and 2-3 m than natural stands. Nests with higher forb cover were less likely to be depredated. Although forb cover was important in determining predation rates, it was not important in nest-site selection. Restored sites had low foliage cover and provided poorer nesting habitat. Birds that nested in restored areas had lower reproductive success. On islands in Wisconsin, the Song Sparrow occurred in red pine and poplar stands. It was significantly associated with aspen and appeared to prefer pioneer forests and pine to some extent (Beals 1960). In Illinois forests, its abundance was significantly correlated with shrub density and mean litter depth (Herkert 1994a). In Wisconsin and Minnesota, it occurred significantly more often in floodplain than upland forests (Kirsch et al. 2013). In North Carolina, forest-breeding Song Sparrows were positively correlated with the number of buildings within 200 m and negatively correlated with forest canopy closure (Lumpkin and Pearson 2013). In Wisconsin floodplain forests, it demonstrated a slight preference for wet forests (Mossman 1988). In aspen forests in western North America, highest densities occurred where large well-spaced trees with moderate shrub coverage were present. Where it occurred, there was always surface water present nearby (Flack 1976).

In Pennsylvania, the habitat of Song and Swamp sparrows differed considerably with the greatest difference being the amount of water cover in the territories: 92% for the Swamp Sparrow and 13% for the Song Sparrow. The distinction was even greater if a single Song Sparrow territory was removed from the analysis: 92% compared with 8%. There were significant differences in certain habitat characteristics in Song and Swamp sparrow territories respectively: forb cover, 59.4% compared with 34.4%; rush cover, 7.1% compared with 25.0%; raspberry cover, 2.7% compared with 0.1%; water cover, 13.2% compared with 92.2%; and water cover and moist areas, 15.9% compared with 97.0%. Other average characteristics of Song Sparrow territories that did not differ from Swamp Sparrow territories included 22.8% grass cover, 92.1% total ground cover, 0.75 m ground cover height, 0.59 shrubs per 3.14 m^2, and 5.5 cm water depth. Whether a particular area was defended by a Song or Swamp sparrow could be predicted with 90% accuracy based solely upon whether there was standing water or saturated soils. A beaver pond was defended by 5 Swamp Sparrows in a year prior to its drainage. The following year, it was defended by 5 Song Sparrows. Extensive rains resulted

in reflooding and Swamp Sparrows moved 50-300 m into Song Sparrow territories, but the Song Sparrows did not abandon their territories. The earlier-arriving and dominant Song Sparrow did not attempt to colonize marsh habitat and left it for the Swamp Sparrow. The Song Sparrow is incapable of moving through water and searching for food on its surface as the Swamp Sparrow does (Greenberg 1988). In Wyoming, Salt (1957) examined habitat partitioning by the Song, Lincoln's, and Fox sparrows in willow thickets and marshes. The Song Sparrow inhabited stream margins and open water where willow formed a dense thicket 1.8-3 m tall. The Lincoln's Sparrow inhabited drier areas with clumps of willow 0.6-1.2 m tall. The Fox Sparrow frequented grassy glades surrounded by willows 3-3.6 m tall. The Song Sparrow occurred wherever there was open water, typically along streams and willows. In Maine in large mainland forests and deciduous edge areas, the Song Sparrow coexisted with the White-throated Sparrow and Dark-eyed Junco. The junco did not nest on adjacent small islands and the White-throated Sparrow did so only sporadically and did not nest on islands where there was a high density of Song Sparrows. On islands, the Song Sparrow foraged regularly in the interior of spruce forests and, on small islands, it foraged in the low live foliage of spruce, a foraging technique not observed elsewhere. There was a competitive release for the Song Sparrow on small islands (Morse 1977). On very small islands in Minnesota, the Song Sparrow spent considerable time on the forest floor and also in dense shrubs, along rocky shorelines, amongst fallen trees, and near the top of the canopy. It used a wider diversity of habitats on islands with fewer regularly occurring species (Howe 1979).

The Song Sparrow is not an area-sensitive species. In areas of suitable habitat, area has either no effect on its abundance or it may be negatively correlated with larger patch sizes. In forested habitats, it tends to decrease with increasing patch size. It may inhabit very small areas, particularly on islands. In Michigan, it nested on 7 small islands ranging from 0.04 to 1.1 ha. It remained on the island where it nested and did not visit adjacent islands or the mainland (Howe 1979). In Maine, Morse (1977) studied islands 0.1-4.0 ha in area and it nested on every island every year including the 2 smallest islands (0.10 and 0.11 ha). Two pairs nested on an island that was only 0.16 ha. In Illinois grasslands, it occurred in all sizes of grasslands; the smallest field was 7 ha (Walk and Warner 1999). In Michigan Great Lakes coastal marshes, its abundance was significantly associated with the perimeter-to-area ratio but patch size had no effect on its abundance (Riffell et al. 2001). In Illinois grasslands, it was negatively correlated with patch size (Herkert 1994a). In pure grasslands, there may be few or no shrubs in the interior of the patch and it may be confined to edges. In Maine grasslands managed for blueberry production, its abundance was negatively correlated with patch area but positively correlated with shrubs 0.6-2.0 m tall and with forbs. Larger sites were more intensively managed and supported a lower proportion of tall shrubs. The probability of occurrence of the Song Sparrow was 80% in 0.5-ha patches, 40% in 1-ha patches, 10% in 10-ha patches, 0.2% in 100-ha patches, and 0% in 1,000-ha patches (Vickery et al. 1994).

At night, the Song Sparrow roosts in dense herbaceous vegetation and shrub thickets, usually close to the ground. It also frequently roosts in hedges and conifers. One nest was constructed for a night roost. In Maryland, a Northern Mockingbird constructed a nest 1.8 m up in a white cedar against the wall of a house. After the mockingbird abandoned the nest, a Song Sparrow immediately adopted it as a night roost (Arcese et al. 2020; Brackbill 1976; Nice 1943).

Most (61.0%) Ontario nests were on the ground but the remainder were elevated in shrubs, trees, vines, and herbaceous plants; on human-made objects and buildings; and on muskrat houses and brush piles. Ground nests were usually well concealed in or under clumps of grasses, ferns, mosses, and other plants; under trees, shrubs, and vines; under fallen branches, brush piles, dead leaves and litter, logs, and roots; under sandbank overhangs; at bases of stumps, fence posts, and boulders; and on an anthill. Twenty-nine nests (3.7%) were on bare ground with 9 in depressions in the ground. One ground nest was under a piece of plywood imbedded obliquely in a sand beach. Elevated nests were in coniferous trees and shrubs (7 species, 55.0% of elevated nests) or in deciduous trees, shrubs, and vines (21 species, 45.0% of elevated nests). The most frequently selected species were juniper (48 nests), white cedar (34), spruce (29), hawthorn (27), pine (25), and raspberries (20). Elevated nests were in tufts of grass (17 nests); cattails, sedges, or rushes (7); goldenrods (4); vetch (3); ferns (2); 1 nest each in artichoke, purple loosestrife, and daisy; in cavities in stumps and trees; and 1 each in a roll of fence wire, on a low fence wire in a grass clump, in weeds left in a wheelbarrow, on a ledge in a boathouse, in a mound of hay, in a bed of plants in a greenhouse, in a tin can, and in a depression in mosses and grasses covering a stump and roots. Elevated nests in trees and shrubs were 0.08-3.7 m from the ground with most 0.3-0.9 m up. One nest was built on top of an old Red-winged Blackbird nest (Peck and James 1987, 1998b). In Willowdale, first nests were usually on the ground and second nests were about 0.5 m above ground. If a third nest was built, it was usually about 0.9 m from the ground, often in a thorny shrub. One nest was 2.9 m from the ground in a horizontal hole in a willow (Nice in Austin 1968).

Most early nests are on or near the ground in grasses or forbs. Later nests may be higher once leaf cover is available in shrubs and saplings. Nests may rarely be as high as 10 m from the ground, but almost all are less than 4 m up; most are less than 1 m from the ground. Most nests are low in grasses and shrubs, predominantly on the ground under tufts of grass or shrubs, but they may also be in sedges and cattails, trees, and over water. Nests may rarely be in tree cavities, hollow logs, rails, woodsheds, or nest boxes. The Song Sparrow often nests close to houses in flowerbeds or other areas that provide sufficient cover. In Alaska, most nests are about 1 m from the ground in conifers. In tidal marshes, it nests as high as possible while maintaining overhead cover. Lower nests are at risk of flooding. Most elevated nests are woven onto branches but some may be wedged among erect branches. Elevated nests are typically deep within the nest plant on the leeward side to provide optimal protection from the wind. In British Columbia, 61% of nests were in low vegetation and attached to plant stems, 19% were in tall grasses, and 9% were in shrubs or low trees. Red elderberries were avoided as a nest substrate, with only 1 of 1,051 nests (0.1%) in this species. It nested preferentially in blackberries and in rose and snowberry as often as expected by their occurrence. In Michigan, 11 consecutive nests by 1 female averaged 87.8 m apart (range 18-160 m). Ten were on the ground and 1 was 50 cm above ground in a blackberry thicket. Seven successive nests of a Maryland female were all in backyard hedges of barberry 1.1-1.8 m from the ground. Nests are rarely reused with only 4 reports of reuse out of thousands of nests. One pair raised 4 broods within a single nest in a season, relining it between each use. In Ontario, 1 pair raised 3 broods and used the same nest for the second and third broods, and both nests were in the same tree (Arcese et al. 2020; Berger 1951; Brackbill 1950a; Campbell et al. 2001; Crombie et al. 2017; Flaspohler and Matteson 1994; Larison et al. 2001; Nice in Austin 1968; Nolan in Austin 1968; Peck and James 1998b).

The Song Sparrow defends an area that normally includes mating, nesting, and feeding areas. In Ohio, most activities took place within the territory except that birds left their territories several times a day to drink water and bathe. On a small island in British Columbia, adults foraged within the territory when they were feeding nestlings. When they were foraging for themselves, they frequently entered grassland habitat adjacent to the territory and occasionally the tidal zone that functioned as a common feeding area. Territories within shrubs were well defined by obvious perching trees and singing perches. Territory boundaries in meadows were difficult to define and overlapped. Meadows appeared to be part of the home range rather than the territory. On this island, all available habitat was occupied and territoriality limited population levels. Both males and females defend territories and unmated males may also defend territories. Males vigorously defend their territories against floaters to prevent losing a portion of or all their territory, and females defend against floaters to prevent polygyny. Intrusion pressure declined slightly over the season, probably because some floaters were successful in procuring a territory. Territories overlapped with a mean of 5.4 floaters (range 0-10). Of successful settlement attempts by floaters, 52.6% resulted in partial acquisition of the owner's territory and 47.4% resulted in the eviction of the owner. Males that were evicted from their territory lost weight after eviction. Other birds did not, suggesting that evicted males were in poor condition. Floaters most often intruded upon males that were least able to defend themselves: the young, old, and handicapped. Intrusion pressure was unrelated to territory size, density of floaters, fertility of females, or whether a female was present in the territory. Territory boundaries remain remarkably stable from year to year even if different birds are defending the territory. If a male disappears and is not replaced, neighbours may annex part of his territory. On a British Columbia island, birds of both sexes that were removed were rapidly replaced. Where birds were simultaneously removed, the number of occupied territories increased 40% with a significant decline in average territory size. There was a total reorganization of territorial boundaries after simultaneous removal and replacement. Where birds were successively removed, replacement birds settled on a 1-to-1 basis and territorial boundaries remained constant except for some minor modifications. All but 1 of the replacement birds were juveniles. Those juveniles that failed to establish a territory in October either dispersed or remained overwinter, attempting to establish dominance in winter flocks to obtain a territory the following spring. In habitat patches, territories may be contiguous and have several abutting territories. In other areas, territories may be arranged linearly, such as along hedgerows, roadsides, streams, and lakesides (Arcese 1987; Arcese et al. 2020; Knapton and Krebs 1974; Nice 1937; Nice in Austin 1968; Nolan in Austin 1968; Tompa 1962, 1971).

Territory size may be affected by population density, settling patterns, habitat quality, and the mating status of the owner. The extent of the male's singing repertoire and the number of neighbours may also influence territory size. With higher breeding density, territory size shrinks. This is accompanied by increasing resistance by territory holders until a point is reached where no further decrease in territory size can be tolerated. Territories are smaller when habitats are settled simultaneously instead of gradually. This may be correlated with density because density was higher in areas settled simultaneously. In Massachusetts, territory size in rural areas was significantly correlated with the area of herbaceous vegetation. Suburban territories were significantly correlated with both shrub density and crown volume. On a British Columbia island, differences in territory sizes between areas were related to differences in the density and species of shrubs present. On

another British Columbia island, unmated males had territories that averaged 82 m^2 (range 65-105 m^2) and a home range of 120 m^2 (range 98-135 m^2). Mated males had territories that averaged 288 m^2 (range 110-400 m^2) with a home range of 473 m^2 (range 167-822 m^2). Island territories may be only 10% of the size of those in mainland habitats. In Ohio, the minimum territory size was 0.2 ha, the average was 0.27 ha in well populated areas, and the maximum was 0.61 ha. Birds nesting on small Minnesota islands defend territories as small as 0.016 ha. Linear lakeshore territories in the same state average 0.19 ha (range 0.14-0.28 ha). In Maine, territories averaged 0.49 ha on the mainland and 0.18 ha on small islands; 2 pairs nested on a 0.16-ha island. In Algonquin Park, territories averaged 0.43 ha (range 0.06-1.03 ha). Territories extended from the ground to the top of the canopy (6 m), but not to the top of dead snags (9 m). Territories in urban habitat in California were 0.1-0.4 ha. Territories on university campuses and near freeways averaged 47.9 m from a road, 491.6 m from a major freeway, and 36.3 m from a building. Those in urban parks had territories averaging 262.0 m from a road, 2,628.3 m from a major freeway, and 261.5 m from a building. In anthropogenic habitats, 29.6% of the area within 50 m of a male's capture site consisted of impervious surfaces compared with 1.0% in parks. In Massachusetts, there were no differences in territory sizes between birds nesting along country roads (0.21 ha) and those nesting in suburban habitat (0.26 ha). The number of neighbours and shrubs combined to account for 51% of the variability in territory size. Although unmated males may have territories as small as 0.0065 ha on islands, territories may be as large as 0.65 ha in habitat consisting of a mix of shrubs and forest. On a British Columbia island, territories were as small as 0.02 ha at a density of 2,500 pairs per km^2 compared with 0.5 ha at a density of 200 per km^2 on the mainland. On a California island, territories averaged 0.07-0.23 ha. They were smaller in dense shrubs (0.15-0.25 ha) than in open areas (0.28-0.42 ha) and in territories held by newly settled (0.18 ha) than established (0.23 ha) males. Other reported territory sizes include 0.038-0.050 ha in tidal marshes, 0.11 ha along a Minnesota lakeshore, and 0.09-0.57 ha in rural Massachusetts (Arcese et al. 2020; Bonneau in Gauthier and Aubry 1996; DeGraaf 1989; Grunst et al. 2014; Knapton and Krebs 1974; Martin 1960; Morse 1977; Nice 1943; Nice in Austin 1968; Nolan in Austin 1968; Tompa 1962). Territory size may be affected by the number of competing species present. On Pacific Coast islands, territory size was unaffected by insect abundance and amount of dense shrub vegetation 0.6-1.2 m tall. Territory size increased with the number of competitive species and was about 0.32 ha in complex communities with 10-15 species and 0.06 ha in simple communities of 1-2 species (Yeaton and Cody 1974).

The rate of natal philopatry depends upon whether the population is migratory or resident. Near Kingston, 1 of 146 nestlings (0.7%) returned to breed. It was a male that nested 5 territories from its natal site. In Ohio, where some birds are migratory and others are resident, yearling males took up territories 90 m to 1.6 km from their natal site. Females settled 45 m to 1.6 km from their natal territory. Of 317 fledglings, 26 males and 14 females (total of 12.6%) returned to breed, an estimated 50-60% of young that survived; 4.5% of eggs laid produced young that returned to breed. In resident island populations in British Columbia and California, natal philopatry was very high. It is possible that philopatry rates are lower in mainland areas. On British Columbia islands, very few yearlings immigrated. Juveniles remained in the breeding area until territoriality peaked again in October. At this time, some successfully obtained a territory and remained for the winter; approximately 20% emigrated. In spring, unmated juveniles that overwintered attempted to establish a territory. Those

that failed either left the island or remained as nonterritorial floaters. Of 112 young on 1 island, 21 (18.6%) were recovered the following year. These included 6 breeding males and females and 2 unmated males. Median distances of settlement from the natal territory were 200-240 m for males and 150-200 m for females in California, 280 m for males and 270 m for females in Ohio, and 185 m for the sexes pooled at San Francisco. At this site, 42% of birds settled within 150 m of the natal territory and 81% settled within 360 m (Arcese et al. 2020; Keller and Arcese 1998; Knapton and Krebs 1974; Nice 1937; Nice in Austin 1968; Schlossberg 2009; Tompa 1962; Weatherhead and Boak 1986).

In a migratory population near Kingston, adult site fidelity was low; 53 of 77 males (68.8%) on territories at the beginning of the breeding season abandoned them by the end of the season and 83.2% were not seen again. Males exhibited a similar lack of fidelity between years but returned more frequently to territories that had been successful the previous year. Thirty of 152 males (19.7%) returned and 21 (70.0%) retained their original territory. Four males were seen in all 4 years of the study. Three retained the same territory in all 4 years but the fourth bird occupied more than 1 territory in 3 of the 4 years. Females showed little site fidelity between and within years. Only 3 of 23 females (13.0%) remained in their original territory for the entire breeding season. In another Ontario population, returning females moved an average of 180 m from their previous year's territory, significantly further than males (90 m). Males with larger song repertoires either retained their original territory or bred significantly closer to their previous territory than males with smaller repertoires. In 2 studies with 442 adults in migratory populations, 25% were site faithful. In Ohio where there is a mix of resident and migratory birds, some males retained their territory in successive years; others made slight changes. Females returned to their former territory in 20 of 54 cases (37.0%), settled on the adjacent territory in 19 cases (35.2%), or settled at distances of 90-730 m. In resident populations, both sexes exhibit extremely high site fidelity, usually remaining in the same territory in successive breeding seasons and even in nonbreeding seasons. Changes in territory holders are most often due to mortality. On a British Columbia island, 29 of 55 adults (52.7%) survived over winter. With 1 exception, all kept their old territories except for minor boundary adjustments. A male that was unmated the previous year moved to a neighbouring territory where the owner had died overwinter. On the same island, only 9% of surviving females had a territory that did not overlap with the previous year's territory (Arcese et al. 2020; Hochachka 1993; Keller and Arcese 1998; Nice 1937, 1943; Nice in Austin 1968; Potvin et al. 2015; Schlossberg 2009; Tompa 1962; Weatherhead and Boak 1986).

Limiting Factors

Nests with eggs have been reported in Ontario from mid-April until the first week of September, with most present from the last week of May until the last week of June (Peck and James 1987). In Algonquin Park, eggs are present from mid-May to early August, nestlings are present from late May to late August, and fledglings have been observed from mid-July to late August (Tozer 2012). Nice (in Austin 1968) reported that nesting began around 20 April in Willowdale.

The female may build 1, 2, or rarely 3 nests and abandon them before finally building the nest that receives the eggs. Nest-building activity is stimulated by high temperatures and inhibited by low temperatures. As many as 5-10 days may be required to complete a nest depending upon weather, the time of the year, and which nest of the season it is. The first egg is usually laid the day

after the nest lining is complete but as many as 13 days may elapse between nest completion and egg laying if the weather is inclement. Eggs are laid at the rate of 1 a day. In 1 Ontario nest, there was a 3-day delay between laying of the second and third eggs. In clutches with 3 or fewer eggs, incubation begins with the laying of the last egg; in larger clutches, incubation begins with the laying of the penultimate egg. The incubation period of 18 Ontario nests was 11-15 days, mostly 11-12 days. At London, the incubation period averaged 12.6 days. Overall, incubation periods of 10-15 days have been reported. In Ohio, most eggs hatched in 12 or 13 days (mean 12.6 days, range 12-15 days). The incubation period was 12-14 days on a British Columbia island and averaged 13.0 days on a California island. Hatching is usually synchronous in 3-egg clutches and asynchronous in larger clutches. Young may leave the nest when they are 7-15 days old but leave at age 7 and 8 days only when they are disturbed or if other siblings have left the nest. Most leave when they are 10-12 days old (Arcese et al. 2020; Berger 1951; Campbell et al. 2001; Nice 1937; Nice in Austin 1968; Nolan in Austin 1968; Peck and James 1987, 1998b; Scott and Lemon 1996; Smith 1978a; Smith and Merkt 1980; Smith and Roff 1980).

The Song Sparrow normally raises 2 broods per season, but may occasionally rear 3 or rarely 4 broods. There is 1 confirmed case of a pair raising 3 broods in Ontario. Two cases of 4 broods have been reported: one from British Columbia and the other from Ohio. Its ability to raise more than 2 broods is dependent upon the length of the breeding season and how many fledglings there are in early broods. Third and fourth broods can only be raised in years of early springs and when there is no autumn drought. On a British Columbia island, no third broods were raised in a year when the egg-laying season was 75 days, but 1 pair raised 3 broods in a year when the egg-laying season was 98 days. Those that successfully raise 3 broods overlap successive broods more and raise more young per year. At London, 16.7% of pairs raised 0 broods, 59.5% raised 2 broods, and 23.8% raised 3 broods (average 1.07 broods). The interval between fledging of 1 brood and initiation of the next clutch increases by approximately 3.3 days for each extra young in the brood. The interbrood intervals are approximately 9.5 days for a brood of 1 fledgling, 12.5 days for 2 fledglings, 15 days for 3 fledglings, and 17 days for 4 fledglings. The interbrood interval is not consistent year to year and birds may adjust it depending upon the length of the breeding season. In most cases, the female begins incubating the next clutch before the fledglings of the previous brood are independent. A brood size of 1 fledgling is the only size that allows the Song Sparrow to raise 4 broods (Arcese et al. 2020; Nolan in Austin 1968; Peck and James 1998b; Scott and Lemon 1996; Smith 1982; Smith and Roff 1980; Tompa 1962). Failed nests are typically replaced and as many as 7 nests may be attempted to raise 1 or 2 broods. The interval between nest loss and initiation of the replacement clutch is 5-8 days, seldom as long as 12 days. In Ohio, replacement nests averaged 23 m from the previous nest (range 9-50 m). In California, the internest distance averaged 17 m (range 5-49 m). The female may occasionally renest outside her mate's territory which leads to vigorous conflicts with the neighbours (Arcese et al. 2020; Berger 1951; Nice in Austin 1968; Smith and Roff 1980). Clutches of 2-7 eggs have been reported in Ontario. Two nests in Prince Edward County in 2 different years contained 8 eggs. It is possible that more than 1 female contributed to these clutches. Most clutches contained 5 eggs, followed closely by 4-egg clutches. Two- and 7-egg clutches were rare; the normal clutch range was 3-6 eggs. Excluding the 8-egg clutch, the mean clutch size of 499 Ontario nests was 4.43 eggs. Nests had smaller clutches later in the season, and all August clutches

contained 3 or 4 eggs (Peck and James 1987). Most London clutches contained 5 eggs (Scott and Lemon 1996). Elsewhere, clutches of 3-5 eggs are typical, with 6-egg clutches rare to uncommon. Clutches of 1 and 2 eggs occur, but are likely due to egg losses. Largest clutches occur in migratory populations, but clutch size also increases with latitude and altitude. Individual females usually have larger second than first clutches, but the overall average clutch size declines with the season because younger birds lay later and have smaller clutches. In North Carolina, 175 nests had predominantly 4 eggs, with only 1 5-egg clutch but several 2-egg clutches and a single 1-egg clutch. Average clutch sizes reported elsewhere include 3.05 eggs in Baja California, 3.69 in southern California, 3.28-3.31 in southcentral California, 3.71 in San Francisco Bay, 3.53 in northcentral California, 3.81 in Washington and Oregon, 3.99 in the Sierra Nevada, 4.17 in Alaska, and 3.1 for first clutches and 3.6 for second clutches on a California island (Arcese et al. 2020; Campbell et al. 2001; Nice in Austin 1968; Nolan in Austin 1968; Smith and Roff 1980).

Both sexes are capable of breeding in their first year and all females breed in their first year and annually thereafter. Some yearling males may be unsuccessful in defending a territory and attracting a female. Some males may not breed until they are 2 or 3 years old. Some nonbreeding yearlings remain as floaters within defended territories, waiting to supplant a male that dies or actively challenging territory holders for a portion or all their territory. Other nonbreeding yearling males remain in loose groups in unsuitable nesting habitat that offers rich food resources. On a British Columbia island, 27.9% of males were floaters in 1 year and 17.0% were floaters in another year. The success of a male in obtaining a mate was dependent upon the amount of shrubbery he defended (Arcese 1987; Arcese et al. 2020; Knapton and Krebs 1974; Tompa 1971). All populations with high proportions of nonbreeding yearling males were residents living on small British Columbia islands. In these areas, all suitable habitat is occupied and defended by year-round residents. The incidence of nonbreeding yearling males is probably much lower in mainland areas and in migratory populations. Migratory populations are more flexible in their selection of territories and may use ephemeral habitats such as clear-cuts and temporary openings in forests. Mainland yearlings have the option of settling in suboptimal habitat; the islands that were studied were either good or unsuitable nesting habitat.

The mating system is predominantly monogamous, but the Song Sparrow is adaptable and may adopt a variety of reproductive strategies. These may include polygyny, polyandry, extra-pair copulations, and intraspecific parasitism. Inbreeding may also occur in resident populations. Both sexes are more faithful to their territories than they are to each other. Often there is no attempt by the female to maintain the same pair bond even between broods. Near Kingston, 3 females that remained in the same territory all season retained their mates, but those that switched territories within seasons also switched mates, with the male remaining in the original territory. Zero to 25% of pair bonds remain intact in resident populations from year to year, with many mate changes due to mortality of one of the mates. In Ohio, 8 of 30 possible pairs (26.7%) reunited in a subsequent year. The low proportion is likely due to the many opportunities that a male has of acquiring a mate before his former partner returns. A female that returns to find her former mate already mated joins with another male (Arcese 1987; Arcese et al. 2020; Berger 1951; Hochachka 1993; Nice 1937, 1943; Nice in Austin 1968; Weatherhead and Boak 1986).

The sex ratio often defines the dominant mating strategy of the Song Sparrow. If the male to female ratio is less than 1, polygyny may occur; if the ratio is near 1, monogamy is favoured; and if the ratio is greater than 1, polyandry may occur. Over 3 years on a British Columbia island, 7 of 213 pairings (3.3%) were polygynous. In all cases, the mates consisted of a single male and 2 females. In 4 cases, polygyny followed the death of a neighbouring male. In the remaining cases, 2 females were paired with a male from the beginning of the breeding season. All polygynous mating occurred within the only year when the number of breeding females exceeded the number of males. Territories of males with 2 females were larger than those of monogamous males because they were often a combination of 2 territories. Nestling survival was good in all polygynous nestings. Polygyny was disadvantageous to females only if the male did not feed the young (Smith et al. 1982). In Ohio over a 6-year period, 4 of 173 males (2.3%) were in polygynous relationships. These all occurred when an incubating female lost her mate and mated with the neighbouring male (Nice in Austin 1968). Twenty-one percent of females and 13% of males engage in a polygynous relationship at least once in their lifetime. One male was mated to 4 females on a tiny island in British Columbia, but only those 5 birds were present. Although the incidence of polygyny is positively related to a female-biased sex ratio, polygyny has occurred when territorial males outnumbered females by 1.4 to 1 (Arcese et al. 2020). In British Columbia, when males were experimentally removed, most widowed females elected to mate with neighbours rather than waiting until an unmated male was available (Smith et al. 1982).

Polyandry occurs when 2 or more males mate with a female and contribute care to a single brood. Cooperative polyandry is where a female receives parental care from more than 1 male and maintains social contact with them. Sequential polyandry occurs when 2 males care sequentially for a brood, such as after a territory takeover. At a British Columbia site, an average of 16% of females (range 0-37%) occupied territories with 2 or more social mates over an 11-year period. Females gained new social mates by forming social bonds with replacement mates after a territory takeover (111 cases) or by occupying 2 or more territories within a season (55 cases). Cooperative polyandry was confirmed once and suspected twice and there were 7 confirmed and 8 suspected cases of sequential polyandry. Overall, 18 of 492 females (3.7%) and 33 of 505 males (6.5%) bred at least once in a polyandrous group; 3 males occurred in polyandrous groups twice in their lifetime. The percentage of females in polyandrous relationships was unrelated to the sex ratio but was significantly related to the number of females that had more than 1 social mate in a season and the percentage of females that mated with replacement males while still caring for the young of a previous mate. Fifteen of 18 males (83.3%) that fed their new mate′s young were previous neighbours but 3 were formerly nonterritorial floaters (Janssen et al. 2008).

Extra-pair copulation may be a common reproductive strategy. Arcese (1987) observed 3 cases of extra-pair copulations involving neighbours. In this population, 15-27% of nestlings were fathered by a male other than the social mate. Most extra-pair sires were neighbours (Arcese et al. 2020; Janssen et al. 2008). Near Newboro, 8-15% of nestlings were a result of extra-pair paternity (Potvin et al. 2015).

In both California and New York, Latif et al. (2006) confirmed intraspecific parasitism. At 1 California nest, a second female entered the nest and laid another egg in the nest. Two days later,

the first female ejected an egg out of the nest but it was one of her own eggs. Two of 14 nests (14.3%) had 2 eggs laid in them in a single day. In New York, 2 eggs were laid in a nest within 2 hours and 1 was ejected. At another nest on 2 different days, a marked egg disappeared and was replaced by 2 new eggs. At another California site, no intraspecific parasitism occurred. Parasitism occurred in both the west and east but not in all populations. When parasitism occurs, an egg may be removed by the host, not the parasite. Females appear unable to recognize parasitic eggs and may eject their own eggs.

In a resident British Columbia population on a 6-ha island, there was no evidence of inbreeding avoidance and no preference or avoidance of relatives as mates. The Song Sparrow may not be able to recognize relatives. Inbreeding occurred regularly with 283 of 479 matings (59.1%) occurring between relatives; 18 matings (3.8%) were between full siblings or parents and their offspring. Inbreeding depression was significant with eggs produced by full-sibling matings suffering a 49% reduction in survival to breeding age. The occurrence of inbreeding is probably less frequent in mainland populations and may be rare to absent in migratory populations (Keller and Arcese 1998).

The Song Sparrow forages mostly on the ground where it may run under the vegetation in a mouse-like manner. It forages for seeds on the ground by scratching with both feet, takes seeds from plants by reaching up from the ground or perching in the plant, occasionally picks fruit up from the ground but more frequently takes it from the plant, and eats flower parts of blue-eyed grass by reaching from branches of an adjacent shrub. It commonly feeds on foliage and bark in shrubs and saplings but also on the ground and in herbaceous vegetation. In freshwater marshes, it often forages at the edge of water, occasionally with its feet in the water. In intertidal areas, it eats small snails or flips over vegetation to find amphipods. It may make short jerky runs or hops to capture salt-marsh flies and cling to steep dirt or rock slopes partially supported by its tail to capture insects. It tears rolled leaves open to extract leafroller moth caterpillars and catches winged termites as they emerge from their colony. It occasionally flies high into the air to capture insects. Flights are usually from a perch atop a 1-3 m shrub and may extend 10 m into the air. On a British Columbia island, adults foraged outside their territories in grassland for lacewings and other insects later in the breeding season when caterpillars became scarce. It may forage for insects in foliage and on the bark of conifers at heights as high as 9 m. On the lower Colorado River, 50% of foraging occurred on the ground, 40% in shallow water, and 10% on bark and leaves. It has been documented seizing and devouring small minnows (Arcese et al. 2020; Girard et al. 2012; Hailman 1960b; Judd 1901; Nolan in Austin 1968; Salt 1957; Smith 1978b; Tompa 1962).

Males may engage in anticipatory feeding by offering food to eggs. In the Ottawa area, the diet of nestlings in 3 nests was highly variable and included hoppers (leafhoppers, planthoppers, and froghoppers), spiders, caterpillars, beetles, hymenopterans, true bugs, flies, and unidentified larvae. The mean proportion of the diet from seminatural habitats was significantly greater than the proportion of seminatural habitat within 100 and 35 m of the nest. Hoppers had the highest mean contribution to the nestling diet but the proportion of hoppers in the diet was not significantly greater than caterpillars. Taxa making the lowest contributions to the diet included picnic beetles, ground beetles, and spiders. Invertebrate biomass was higher in hedgerows and hayfields than in cropland. Song Sparrows may select hedgerows and hayfields as foraging habitat because they

support the highest biomass of insects. At nests with less than 7% seminatural cover, hedgerows provided at least 90% of the seminatural habitat and the majority of nestling food. Hoppers are pests of alfalfa and soybean crops and may be more prevalent in the diet of nestlings in farm habitats than other areas (Girard et al. 2012). Elsewhere nestlings have eaten spiders, beetles, grubs, flies, caterpillars (especially leafrollers), grasshoppers, worms, crane flies, and aphids. Young may also be fed seeds from feeders. Nestlings are fed smaller items for their first 2 days, particularly aphids, spiders, leafrollers, and flies. Food items brought to older nestlings are identical to those consumed by adults, including caterpillars longer than 4 cm (Arcese et al. 2020; Nolan in Austin 1968). Juveniles on a British Columbia island foraged extensively on leafrollers, slow-flying flies, and hymenopterans (Arcese 1987).

Judd (1901) analyzed 401 adult stomachs collected throughout the year from 26 states and British Columbia. The diet consisted of 66% vegetation (mostly seeds) and 34% animal matter (mostly insects with occasional spiders and snails). That the Song Sparrow often inhabits damp habitats was indicated by some of the food items such as seeds of wild rice, sedges, smartweeds, amphipods, aquatic snails, tiger beetles, mayflies, and dragonflies. Foraging in upland with other bird species also occurs: picking up seeds of crabgrass and ragweed with the Dark-eyed Junco and American Tree Sparrow in winter; eating earthworms on lawns with the American Robin; fighting for bread crumbs with the House Sparrow in cities; eating raspberries with Gray Catbirds and Brown Thrashers; and feeding on honeysuckle berries with the White-throated Sparrow. Of the vegetable diet, 24% of the entire diet consisted of grasses, 16% smartweeds, 3% ragweeds, and 18% miscellaneous seeds of wild sunflowers, amaranths, lamb's-quarters, clovers, gromwell, plantains, nightshade, purslane, spurges, wood sorrel, dandelions, duckweed, docks, and sheep sorrel. More than 50% of the grass seeds consumed were those of crabgrass and foxtails, but it also ate timothy, paspalum, old witch grass, barnyard grass, bluestems, orchard grass, and wild rye. Fruits comprised 8% of the July diet, especially those of blackberries, strawberries, raspberries, blueberries, mulberries, and black cherry. It also eats fruit of elderberries, wild grape, pokeweed, and bayberry. Fruit is largely ignored once grasses and weedy herbaceous species seed. Insects comprise about 33% of the annual diet and more than 50% from May to August. These include 9% beetles, 7% orthopterans, 6% lepidopterans, 4% hymenopterans, 3% bugs, 2% flies, and 1% miscellaneous taxa such as neuropterans, stoneflies, and mayflies. Beetles were eaten year-round, but especially in late spring and early summer. Leaf beetles comprised 5% of the July diet and weevils comprised 11% of the June and 4% of the annual diet. In addition to these beetles, it ate ground, click, clown, scarab, long-horned, tiger, and tumbling flower beetles and fireflies. Orthopterans were important in the August diet when they comprised 28% of all food items. These were mostly short-horned grasshoppers but it ate some long-horned grasshoppers and crickets. The lepidopterans that it consumed were all moths, mostly geometer and owlet moth caterpillars. Twenty-five percent of the May and June diet consisted of caterpillars; it captured cutworms on the ground and ate some cankerworms and gypsy moth larvae. More than 50% of the hymenopterans were ants; other prey in this order included braconid and scoliid wasps, sawflies, ichneumonid wasps, and small bees. The flies that it consumed were mostly larval and adult midges and crane flies and it sometimes ate adult deer flies. The diet included 2% miscellaneous animals that were mostly aquatic snails, but it also ate spiders and millipedes. Arcese et al. (2020) summarized the contents of 342 stomachs from the northeast and

354 from the Pacific region. Plant material accounted for 54% of the spring diet, 60% in summer, 92% in autumn, and 86% in winter. The most important plants in the diet were smartweeds, foxtails, ragweeds, and amaranths (each 10-25% of the diet), and 5-10% knotweeds in the Pacific region. The most important animal foods included beetles, caterpillars, crickets, ants and other hymenopterans, and bugs. A sample of stomachs of 222 breeding and 99 wintering birds demonstrated that females ate 42% animal food compared with 39% for males. Diet in saltmarsh habitat was high in animal matter. This material was mostly snails but it also ate polychaetes, insects, and other invertebrates. In Illinois, it ate 8-10-mm-long gizzard shad. On a British Columbia island, it ate berries of Saskatoon, red elderberry, and raspberries and rarely those of snowberry. It also fed on flies and amphipods in tidal areas. Other breeding season food items include brown-tailed moths, northern corn rootworms, tarnished plant bugs, gull feces, apical buds of spring-beauty, and crowberries (Arcese et al. 2020; Garfinkel et al. 2020; Nolan in Austin 1968). In British Columbia, most prey captured while flycatching consisted of robber flies (Smith 1978b). The Song Sparrow regularly drinks fresh water and may leave its territory to drink. In areas without water, it relies on rain water, dew, and condensed fog (Arcese et al. 2020).

Arcese and Smith (1988) provided supplemental food in 16 territories of a British Columbia island population. Sixteen neighbours had some access to the food and the remaining 40 pairs were considered controls. Pairs with supplemental food began laying an average of 18 days earlier than control birds, laid 3.31 eggs compared with 2.77 eggs, and 60% of fed adults successfully raised young compared with 45% of controls. Experimental females initiated more clutches (2.81) than control females (2.24) and raised almost 4 times as many young. Parasitism rates by the Brown-headed Cowbird were significantly less for experimental (18.4%) than control (44.7%) nests, probably because fed females spent less time foraging and could defend their nests more diligently. Food availability was an important stimulus for the onset of breeding. The amount of food available per pair decreases as the number of pairs increases. They acknowledged that effects would be less striking in lower density populations; density of their study population was approximately 1,200 pairs per km^2.

Hipfner et al. (2013) compared the diets of the Song and Fox sparrows in British Columbia. The Song Sparrow ate more animal material and less plant material than the Fox Sparrow. These dietary differences probably allow the species to coexist.

The Song Sparrow is one of the most common hosts of the parasitic Brown-headed Cowbird, but also one of the species least harmed by parasitism. Cowbird eggs are typically accepted but nests may be deserted if egg removal by cowbirds lowers the clutch size below an acceptable threshold. In a British Columbia population, desertion rates due to parasitism were 8.9-16.5%. In Ontario south of the French River, 27% of parasitized nests were deserted compared with 2% of unparasitized nests. No cases of cowbird egg ejection occurred. Acceptance rates were similar before and after the peak of nest initiation, and in singly and multiply parasitized nests. In southern Ontario, desertion appears to be an adaptive response to parasitism. Cowbird eggs laid before the first sparrow egg is laid may be buried in the nest. This is unlikely to be an adaptation to avoid parasitism but rather a continuation of nest building (Arcese et al. 2020; Graham 1988; Nolan in Austin 1968; Rothstein 1975; Smith and Arcese 1994; Smith et al. 2003). The Song Sparrow is capable

of raising its own young in parasitized nests and there tends to be no difference in nestling growth rates in parasitized and unparasitized nests. The number of young fledged in parasitized nests is lower, usually a result of the cowbird removing sparrow eggs from the nest. In Ohio, parasitized nests fledged an average of 1.0 young less than unparasitized nests. In British Columbia, the loss was 0.3-0.5 young per nest. Greatest losses occur when female cowbirds remove entire clutches or broods from nests in an endeavour to induce renesting and create additional opportunities for parasitism. Young were found dead in or near 4.7% of nests in British Columbia. Presence of cowbird young in the nest may increase the probability of nests being depredated (Arcese et al. 2020; Nice 1937; Nice in Austin 1968; Smith 1981; Smith and Arcese 1994; Smith et al. 2003; Zanette et al. 2007).

The probability of parasitism may be affected by cowbird abundance, increasing density of Song Sparrow populations (at least on islands), distance of islands from the mainland or a large island such as Vancouver Island, age of the female Song Sparrow, percent forest cover in the landscape, percent pasture and rangeland, presence of suitable perches for cowbirds, and nest concealment. Parasitism rates are higher where cowbirds are more abundant. On British Columbia islands, parasitism rates were higher in years of higher sparrow densities. When sparrows were abundant, the probability of a cowbird successfully finding a nest to parasitize was higher. When sparrows were scarce, cowbirds did not expend the energy required to visit the island. Nests on islands closer to the mainland are more likely to be parasitized than those on distant islands; cowbirds are less likely to visit islands far from shore. Females that are 3 or 4 years old are more likely to have their nests parasitized than yearlings and 2-year-olds. Older females initiate more nests per season which increases their probability of being parasitized. The rate of parasitism decreases as forest cover in the landscape increases but increases with increasing coverage by pasture and rangeland. In New York, parasitized nests were significantly closer to trees and permanent objects at least 2 m tall than unparasitized nests. Overhead visibility of the nest did not affect parasitism rates. In California, the probability of parasitism increased as foliage cover at 2-3 m increased and decreased as lateral cover below 1 m increased. When foliage cover 2-3 m from the ground reached 20%, the parasitism rate was 88.9%. Foliage at this height may enhance a cowbird's ability to find the nest. Parasitism was significantly reduced when lateral cover below 1 m reached 90%. Dense cover may conceal the host's activities and make it more difficult to find the nest (Hauber and Russo 2000; Larison et al. 1998; Saunders et al. 2003; Smith 1981; Smith and Arcese 1994; Wilson and Arcese 2006).

The rate of parasitism varies greatly geographically and even annually at given sites. In Ontario, 457 of 2,032 nests (22.5%) were parasitized. In the 1990s, only 37 of 220 nests (16.8%) were parasitized, thereby slightly lowering the overall rate (Peck and James 1998b). McLaren et al. (2006) analyzed parasitism rates in Ontario in the previous 130 years using Ontario Nest Record Scheme data. The first cowbird was reported in the province in 1870. Of nests with sufficient data, 230 of 484 (47.5%) were multiply parasitized and 484 of 2,177 (22.2%) were parasitized. There was a significant increase in multiple parasitism until 1970 followed by a nonsignificant decline. For the entire period and separately for pre- and post-1970, the overall frequency of parasitism did not change significantly. The significant increase in multiple parasitism prior to 1970 supports the hypothesis that the intensity of parasitism is related to cowbird density. The post-1970 trend may have reflected declines in the cowbird population. At the University of Western Ontario campus in London, 46 of 54 nests (85.2%) were parasitized. This appears to be the highest rate of parasitism ever

documented. Both the Song Sparrow and cowbird began laying in late April but the cowbird completed its egg-laying period well before the sparrow. The chronology of cowbird laying relative to that of the Song Sparrow was 4% during the prelaying period, 8% with 1 egg in the nest, 28% with 2 eggs, 24% with 3 eggs, 4% with 4 eggs, 8% with 5 eggs, and 24% later in the nesting period (Scott and Lemon 1996). In British Columbia, 53 of 753 nests (7.0%) were parasitized (Campbell et al. 2001). On 1 island in British Columbia, 332 of 1,509 nests (22.0%) were parasitized and annual parasitism rates ranged from 0 to 46%. The frequency of parasitism varied seasonally, rising to a peak in early June and declining thereafter. On 11 other small British Columbia islands, 29 of 64 nests (45.3%) were parasitized (Arcese et al. 2020; Saunders et al. 2003; Smith and Arcese 1994; Smith et al. 2003). At Delta Marsh, the Song Sparrow was the most frequently parasitized species and was consistently multiply parasitized. The parasitism rate was 30% (McLaren et al. 2003). Other parasitism rates include 65% in the Sierra Nevada and 28% in New York (Latif et al. 2006); 9 of 28 nests (32.1%) in New York (Hauber and Russo 2000), 1 of 29 nests (3.4%) in Missouri (Burhans et al. 2010), 5 of 11 nests (45.5%) in North Dakota (Granfors et al. 2001); 9.5% in the United States, with greater than 20% in the upper Midwest, 15-19.9% in the Rocky Mountain states, 10-14.9% in the Pacific region, 5.99% in Kansas, Missouri, and Tennessee; and less than 5% in the east and northeast (Arcese et al. 2020); 2 of 50 nests (4.0%) in New York (Hahn and Hatfield 1995); 1 of 10 nests (10.0%) in a forested landscape in Minnesota (Hanski et al. 1996); 135 of 398 nests (33.9%); 98 of 223 nests (43.9%, 24.6-77.7% annually) in Ohio (Nice in Austin 1968; Nolan in Austin 1968); and 9 of 1,168 nests (0.8%) in California (Chase et al. 2005).

Habitat for the Song Sparrow remains abundant, particularly south of the Canadian Shield, but habitat loss is occurring. The original deforestation for forest resources and agriculture was beneficial and created much habitat where little previously existed. Although it nests in urban habitats, it does so at much lower densities than in agricultural landscapes. Modern subdivisions, where the lots are very small and houses are very closely spaced, provide little to no habitat. In farmlands, hedgerows which are prime habitat continue to be regularly removed to create larger fields. Pesticides used on farms may also depress food resources for the Song Sparrow. In the Canadian Shield, habitat loss has occurred due to natural regeneration, with abandoned farmland reverting to forest (Arcese et al. 2020; Bonneau in Gauthier and Aubry 1996; Girard et al. 2012; Tozer 2012).

Where the habitat is suitable, the Song Sparrow is well adapted to urban life. Grunst et al. (2014) compared the adrenocortical stress responses of urban sparrows living in activity centres where there was noise from air conditioners, traffic, and humans to those dwelling in parks. Males in activity centres had lower stress responses than those in parks indicating that they were not pathologically affected by human disturbance. They also had better quality feathers suggesting that activity centres may be superior habitat. In Virginia, urban birds had significantly shorter flight initiation distances from approaching humans than rural birds, suggesting that urban birds are habituated to humans (Battle et al. 2016). In Oregon, urban Song Sparrows altered their songs in response to anthropogenic noise. Those singing in noisier environments had higher-frequency low notes and less amplitude in the low-frequency range of their songs. There was no difference in high frequency, maximum amplitude, number of notes, or frequency of the buzz note. Songs in noisy and quiet areas differed only in those aspects that were masked by the prevailing noise (Wood and Yezerinac 2006).

Predation may be the greatest limiting factor to the Song Sparrow. Populations that suffer a 50% or higher rate of predation tend to be sink populations that are replenished by immigration. On islands, predation is lowest on smaller islands and those more distant from the mainland. In urban and agricultural landscapes, cats may be a significant predator (Arcese et al. 2020; Wilson and Arcese 2006). In Seattle, Marzluff et al. (2007) studied the distribution of the Song Sparrow in relation to the presence of predators. It was most abundant in forests rather than edges or open habitat. Its abundance was significantly negatively correlated with the American Crow at the 1-km^2 scale but nonsignificantly associated with it at the forest-patch and within-patch scales. It was negatively associated with squirrels and chipmunks at the forest-patch scale and the Steller's Jay within patches. The Song Sparrow appeared to avoid areas where corvids and scuirids were abundant but was rarely able to avoid specific habitat patches with predators. It strongly avoided areas within forest patches that were rich in a single predator or all predators combined. It managed this despite co-occurring with nest predators at larger scales.

Weather can affect the reproductive success of the Song Sparrow. On a British Columbia island, a late spring snowstorm eliminated about a third of the adult population, but the young surplus population was left fairly intact. About 60% of pairs were either partially or completely eliminated. Yearling unmated birds filled the vacancies and the number of breeding pairs increased. The population showed signs of stress such as a 1-week delay in the onset of nesting, more frequent fights among neighbours, and a hatching failure rate of 13.7% compared with 3.8% in previous years (Tompa 1971). The effects of this storm were not overly devastating because it was a resident population with a surplus of nonterritorial birds that were able to occupy vacancies. Storms that affect migratory populations and those without many nonterritorial birds may result in greater losses of reproductive effort. Chase et al. (2005) conducted a 21-year study in California that included an 8-year dry period and 2 years of very high precipitation. The number of young fledged per female was greater in wet years, with rainfall accounting for 30% of the variation in the number of fledglings produced. Daily nest survival was significantly lower during the dry period and was significantly correlated with precipitation but negatively correlated with May rainfall. Nesting occurred over a longer period in years of high precipitation, starting earlier in spring and extending later into autumn. Nesting ended significantly earlier in years with high summer temperatures. In wetter years, the availability of annual grasses and other dense vegetation may be greater. This may reduce predation and increase insect populations. Wet weather in May has the potential to lower nest survival by causing exposure, starvation, and parental neglect or desertion. Egg addling is an important cause of hatch and nest failure where cover is sparse and the heat is extreme. Inclement weather, particularly continuous rain and cool temperatures lasting 3 or more days, often causes nest neglect (Arcese et al. 2020). In British Columbia, the length of the breeding season is determined by the onset of the summer dry season. It breeds later in wet summers there, with more adults breeding into late July and early August (Campbell et al. 2001). Nice (in Austin 1968) observed the same phenomenon in Ohio.

Knapton (1990) studied the effects of application of terbufos and fonofos in Oxford and Elgin county cornfields on Song Sparrows nesting in margins of fields. There was no difference in the disappearance rates of birds in control and treatment areas, and no differences in clutch size, number of unhatched eggs, or number of young fledged per nest. He concluded that the Song

Sparrow was not taking up the pellets as food or grit, at least not in sufficient quantities to kill it, and there were no apparent sublethal effects.

Grazing has the potential to cause adverse impacts on the Song Sparrow. In Wyoming, it was significantly more abundant in areas distant from elk feeding areas (Anderson 2007). In Oregon, its abundance increased significantly after livestock grazing was terminated in riparian aspen stands (Earnst et al. 2012). Livestock grazing in Ontario is usually at a high intensity so that all or most shrubs are eliminated. This renders the habitat marginal or unsuitable for the Song Sparrow. High populations of white-tailed deer also have the potential to degrade habitat.

Forest management may be beneficial to the Song Sparrow. Clear-cuts create temporary habitat for 4-10 years depending upon the rate of natural succession. In New York, it was common 2 years after clear-cutting and uncommon by 6 years after cutting. The sparrow-dominated guild declined as leaf area increased and the shrub-opening edges used by this group disappeared with natural succession. This guild represented 37% of the total avian population in 2-year-old cuts and only 9% in 6-year-old cuts (Keller et al. 2003). In Maine, clear-cuts were sprayed with glyphosate. This reduced vegetation structural and species diversity. It is likely that spraying young clear-cuts would be detrimental because this would kill the shrub layer. Spraying older clear-cuts may be beneficial because natural succession would be retarded and dead saplings could provide cover until new woody growth became established. In southern Ontario, the Song Sparrow was absent in uncut woodlots and occurred in low density in those that had been selectively thinned or where diameter-limit cuts had been made. These types of harvests do not create conditions that are very favourable for it and any openings that are created are very ephemeral (Arcese et al. 2020; Holmes et al. 2004; Santillo et al. 1989). In the Canadian Shield in Ontario, there was no difference in its abundance in burned and logged forests in either early successional stands or mid-successional stands. It was significantly more abundant in early successional stands than in mature stands but significantly more abundant in mature stands than in mid-successional stands (Zimmerling et al. 2017).

The effect that mowing and burning have on the Song Sparrow depends on the density of shrubs when the management is undertaken. In Massachusetts, unmanaged grasslands eventually become invaded with shrubs. Habitat quality declines if shrub density becomes too high. Management that substantially reduces shrub cover decreases Song Sparrow abundance. Grasslands that were burned and mowed supported similar populations of sparrows. Populations were significantly lower than in unmanaged grasslands, so the management was detrimental (Zuckerberg and Vickery 2006). In Indiana savannahs and oak woodlands, the Song Sparrow responded positively to fire. It reached its greatest abundance with the maximum frequency of fire: 7.3 fires per 15 years (Grundel and Pavlovic 2007a).

Price (2004) predicted that the breeding range of the Song Sparrow might contract in southern Ontario if the average summer temperature increased by 2°C.

Status

McIlwraith (1894) considered the Song Sparrow an abundant breeder in Ontario. It was probably at its peak population then, shortly after deforestation by European settlers and before intensive farming and agriculture occurred. Baillie and Harrington (1937) considered it a very common summer resident north to northern James Bay and west to Lake of the Woods and probably

northward from there. It was common in 1930 between latitudes 53°N and 54°N along the Manitoba border. They concluded that it bred everywhere within this range. The first atlas demonstrated that its range included the entire province except for an area in the extreme northeast including Cape Henrietta Maria and areas south and west of there. It was scarce in the Hudson Bay Lowland and common to abundant south of James Bay. Highest densities were in the south from Brantford east along the north shore of Lake Ontario to Brockville. On the Breeding Bird Survey (BBS) at that time, highest densities occurred south of the Shield and in western Rainy River District (Rising in Cadman et al. 1987). Weir (2008) reported that it was the third most abundant species in the Kingston area. James (1991) considered the Song Sparrow abundant in the south, common in the north to the north shore of Lake Superior, and rare in the Boreal Forest Region north to the Hudson Bay coast.

The second atlas confirmed that the Song Sparrow bred throughout the province, including the area in the northeast where it was not documented during the first atlas. It occurred in every square south of the Shield, in most squares in the Shield portion of the Great Lakes–St. Lawrence Forest Region, and in most blocks in the north. There was no difference in its province-wide probability of observation between atlases, but the probability increased significantly in the Shield portion of the Great Lakes–St. Lawrence Forest Region and in the Hudson Bay Lowland. It was most abundant south of the Shield, except for small pockets of lower density in the Toronto area and in the intensively farmed areas of Essex and Chatham-Kent. Abundance declined northward, except that it was locally common in western Rainy River District (Rising in Cadman et al. 2007).

BBS data indicate that the Song Sparrow decreased at annual rates of 0.923% 1970-2021 in Canada and 0.928% in Ontario. For 2011-21, it decreased at annual rates of 0.227% in Canada and 1.21% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young are unable to fly when they leave the nest and remain hidden in plant cover. A few may be able to fly weakly when they are 10-11 days old but they are not proficient until they are 17-18 days old. Young disperse in different directions from the nest and emerge from dense vegetation when they are about 17 days old and able to fly (Nice 1943; Nolan in Austin 1968). In British Columbia, young that left the nest a day before the other young moved about 10 m in the first 4 hours and remained there for the next day. Young remained near the nest in dense shrub coverage but some dispersed as far as 30 m within 3 days. Most young were separated by several metres, but some were as close together as 2 m. Fledglings that were 23 days old were much more mobile and followed their parents, begging persistently and sometimes feeding independently. By age 31 days, most fledglings were independent although birds in second broods may be fed a little longer. All fledglings as young as 13 days remained within the breeding territory but some older young cared for by females were fed in neighbouring territories. The presence of these birds was not contested by neighbouring birds (Smith 1978a; Smith and Merkt 1980; Smith and Roff 1980).

It appears as though brood division occurs, with each individual being fed largely or exclusively by a single parent. By age 13, young in British Columbia were not fed randomly by both parents. In only 2 of 68 cases (2.9%) was a fledgling fed by both adults, and there was a significant division of labour in 53 of 68 broods (77.9%). In 4 cases when there was only 1 young in the brood, it was fed by the female. In broods of 2, 11 of 14 (78.6%) were split evenly, in 2 cases (14.3%) the female fed

both young, and in 1 case the male fed both young. In broods with 3 young, females fed 2 young and the male fed the other in 23 of 35 cases (65.7%); in the other cases, the male fed the extra young. Five of 6 broods (83.3%) of 4 young were divided equally and in the sixth case, the female fed 3 young and the male fed 1. In all cases of unequal parental investment, females were significantly more likely to care for the extra young. By age 23, there was still a significant division of broods in 6 of 11 cases (54.5%). At this age, there were some cases where both adults fed a young. This was associated with males making a higher proportion of provisioning trips, increasing from 42% to 66%. At this time, females were often incubating their next clutch and fed young only when they were off the nest. In 4 cases, a fledgling was fed solely by the female at age 13 days and only by the male at age 23 days. The tendency for males to increase care for older fledglings occurs even when the female does not initiate another clutch. If a first brood contains only a single fledgling, the female may continue to feed it while she incubates her next clutch (Smith 1978a; Smith and Roff 1980). Reed (1981) concluded that there was no evidence that parents partitioned the brood. His study was conducted on nestlings and was not relevant to brood partitioning of fledglings.

The dense shrubbery required by young fledglings can be provided by numerous habitats and most territories contain at least patches of shrubs. At the landscape level in Seattle, Song Sparrows used forested and urban landscapes to an equal extent during the postfledging period. Probability of survival increased as the amount of forest cover at the 4,000-m scale increased. Despite a high occurrence of residential areas, 13 of 16 birds (81.3%) had no commercial, industrial, institutional, parking lots, or roads within their home ranges. Use of residential housing areas was significantly higher where this habitat was least common, possibly because of the presence of feeders. Its mean home range size was 8 ha, which comprised 51% forest cover, 26% residential areas, and 15% nonresidential built areas. Differences in its use of land cover were not significantly different from what was available (Whittaker and Marzluff 2009). Fledglings, adults, and family groups may be common in regenerating clear-cuts during the postfledging period. In such habitat in Pennsylvania, the Song Sparrow was the third most abundant species. It was rare in adjacent mature forest that had similar coverage by shrubs: 69 adults and 95 juveniles were captured in clear-cuts compared with 0 adult and 2 juveniles in forest (Stoleson 2013). It also inhabits clear-cuts in Ohio and Minnesota during the postfledging period (Streby et al. 2011b; Vitz and Rodewald 2006). In Pennsylvania, family groups and all age classes of birds were common on hydro corridors but absent in the adjacent forests that they passed through (Yahner et al. 2002). In Michigan, Akresh et al. (2009) studied its usage of riparian and upland forests during the postfledging period. The capture rate per 100 net-hours was 0.1 in upland forest and 7.0 in riparian forest. All juveniles were captured in riparian forest. In riparian habitat, trees and shrubs formed an open canopy with a structurally dense understorey. Upland habitat consisted of 100-year-old stands of large-toothed and trembling aspens.

When the young become independent, family units break up and juveniles form loose flocks and congregate in good foraging areas such as where there are shrubs with ripening berries. They may also frequent bathing sites with fresh water. In resident populations, juveniles may attempt to establish territories after completion of the prebasic moult in August, emigrate to other areas to obtain a territory, migrate, or wait until February to attempt to attain a territory. Those that remain through the winter and fail to establish a territory by early spring either emigrate or persist as nonterritorial floaters. In British Columbia, young float among territories for about 7 months after

reaching independence, maintaining a home range that encompasses 3-25 territories and nonbreeding habitat (Arcese et al. 2020; Nice 1937, 1943; Nice in Austin 1968; Tompa 1962).

MIGRATION

Song Sparrow populations may either be resident, completely migratory, or a mix of resident and migratory birds. Although some birds overwinter in Ontario, it is probable that all birds are migratory, with wintering birds representing birds that bred further north. In Ohio, about 50% of males and 20% of females were residents. Ninety percent of males and 98% of females remained either migratory or sedentary without changing their migration strategy. Cold weather in October stimulated migration in most birds and warm weather inhibited it in some. Banding of 2-3 successive generations gave no evidence of a hereditary tendency to either migrate or be a resident (Arcese et al. 2020; Nice 1937; Nice in Austin 1958). Migration occurs at night but there is some northward movement during the day in spring. Birds breeding the furthest north are most likely to migrate and those wintering the furthest south are most likely to have migrated from the far north. The mean distance migrated for birds travelling more than 250 km was 850 km for adults and 885 km for juveniles. Spring migration is leisurely with British Columbia birds taking nearly 2 months to travel the length of the province. This may be due to different subspecies following different timetables. In Ohio, there were 2 peaks of spring migration, with an early migration of breeding males in late February or early March and the main flight of breeding males, females, and transients in mid-March. Early migrants were dependent on a warm spell in late February or early March; severe cold weather stopped migration during this period. Early males moved at significantly higher temperatures (average 10°C) than later males (6.1°C). The migration of early males appeared to follow the 7°C isotherm. The main migrants were only dependent on a moderate rise in temperature. Of 22 males, 5 arrived consistently early, 6 were consistently late, and the others varied their timing depending upon weather and their age. Older birds arrived sooner than yearlings and adult males arrived before adult females. Autumn migration takes place in late September and throughout October and can be hastened by cool, wet weather. Mild weather may delay or suppress autumn migration. In Ohio, breeding females left by mid-October and males left a little later (Arcese et al. 2020; Brewer et al. 2018; Campbell et al. 2001; Nice 1937; Nice in Austin 1968; Nolan in Austin 1968).

In southern Ontario, migrants arrive by mid-March with the main influx in the first 3 weeks in April. In the southern Shield, most arrive in late March. Southward movement begins in September with greatest numbers moving through in October with the main flight of other sparrows. Most leave the province by mid-November but some may remain into early December (LaForest 1993; Lancaster et al. 2002; Mills 1981; Tozer 2012: Weir 2008).

At Delta Marsh, there was no significant relationship between Song Sparrow arrival date and temperature from 1939 to 2001 (Murphy-Klassen et al. 2005). In Rhode Island, Smith and Paton (2011) analyzed weather and autumn arrival dates over a 45-year period. The mean autumn temperature increased by 0.03°C per year 1960-2007. The mean arrival time of the Song Sparrow was 15 days later in 2007 than in 1960, a delay of about 3.2 days per year.

In Algonquin Park, spring migrants are first seen at feeders or along shorelines where the snow has melted. Those that stay late in autumn are often in dense vegetation bordering water (Tozer 2012). Migration habitat is similar to breeding habitat, with less reliance on the presence of water.

During migration, the Song Sparrow is rarely found far from cover. In British Columbia, migrants occur in a variety of habitats including among driftwood and flotsam on beaches; forest edges; sedges or cattails bordering lakes, ponds, and marshes; shrubby tangles at woodland edges; patches of fireweed; meadow marshes; shrubby farm clearings; weedy vacant lots; hydro corridors; roadsides; and hedgerows (Campbell et al. 2001). In New York, it used mature shrubland habitat more than early successional forests. An exception was that 1 forest patch supported almost as many sparrows as shrublands. It had a more open canopy with greater than 60% coverage by shrubs that were mostly fruit-bearing honeysuckles. Detections increased as coverage by gray dogwood increased and decreased with the abundance of shrubs 0-2.5 m above ground and with Bella honeysuckle fruit abundance. Gray dogwood appeared to be important habitat in autumn (Mudrzynski and Norment 2013).

In Algonquin Park, spring migrants fed at edges of ice where debris and seeds may accumulate (Tozer 2012). Dance et al. (2012) observed the Song Sparrow eating giant ragweed seeds in Oxford County during autumn and winter and foraging for arthropods on this plant. In New York, 5% of autumn migrants had consumed honeysuckle fruit, but none had eaten dogwood or buckthorn berries. Gray dogwood patches were preferred habitat but its fruit was avoided as food (Mudrzynski and Norment 2013). In Georgia, a spring migrant aggressively defended a board supplied with millet and canary seeds from Northern Cardinals, Eastern Towhees, White-throated Sparrows, Swamp Sparrows, and Field Sparrows. It won all encounters except 2 with the towhee, and often maintained exclusive control of the food (Young 1990). An autumn migrant in North Dakota spent 10 minutes on top of a shed, repeatedly darting up into a cloud of midges, turning and snapping frenziedly in every direction. Although 1 pursuit was further into the air, most were only 30 cm or less (Royall 1991).

The Song Sparrow seldom strikes towers and other human-made structures during migration (Arcese et al. 2020).

James (1991) considered the Song Sparrow a common migrant in Ontario. It may be locally abundant in some areas with daily numbers of 200-500 (Curry 2006; LaForest 1993; Weir 2008).

Hussell et al. (1992) reported a nonsignificant decline of 0.9% per year in Song Sparrow captures at Long Point Bird Observatory 1961-88. Trends by period were: 1961-70, +0.3%; 1970-79, −8.2%; and 1979-88, +5.7%.

WINTER

During winter, the Song Sparrow is absent from areas with a minimum January temperature lower than −12°C. In the east, most concentrations are in regions that receive more than 102 cm of precipitation annually. Abundance peaks within this area are associated with open water (Root 1988). It is an avoider of snow. The longer the snow season length, the less likely it is to be present (Keyser et al. 2023).

Smith (2003) analyzed results of southern Ontario Winter Bird-Population Studies to determine general habitat preferences of the Song Sparrow. Densities per km^2 included 5.8 in natural urban areas (ravines, valleys, woodlots, and parks), 3.3 in urban areas with ponds, 1.0 in mixed rural areas, 0.6 in forests, and 0.1 in small urban natural areas. It was not reported in farm fields or in commercial

and residential areas. In Ontario, it appears to be most common where there are bird feeders or open water. It may be most common in cattail marshes but also occurs in swamps, dense shrubs along open streams and rivers, and in weedy fields (Curry 2006; LaForest 1993; Mills 1981; Nolan in Austin 1968; Sheppard et al. 1936; Tozer 2012).

The Song Sparrow has winter habitat requirements that are similar to its breeding habitat, but in many areas it has a preference for cattail marshes with open water, habitat that is not usually used during the breeding season. Other habitats that it frequently uses include old fields, fencerows, drainage ditches, shrubby areas along streams and margins of water bodies, and numerous other locations where shrubs or tall grasses and herbaceous species provide food and cover (Kalinowski and Johnson 2010; Knapton and Krebs 1974; Smith et al. 2005; Young 1990). In Ohio, Doherty and Grubb (2000) studied the usage of small woodlots (less than 6 ha) by the Song Sparrow. Its probability of occurrence declined as woodlots became more isolated. Its probability of occurrence decreased from early to mid-winter and increased from mid- to late winter. In Ohio, it was abundant in brushy thickets, fallow fields with rank weedy growth, weedy fields of uncut corn, brushy edges and openings of woodlands, shrubby fencerows, shrubby and weedy swamps, weedy edges of a canal, and cattail marshes. It was less numerous or absent in snow-swept fields and pastures, farmhouse areas containing little shrubbery, and orchards and woodlots without ground cover (Nice in Austin 1968). In Vancouver, it inhabits patches of native and exotic shrubs bordering lawns, parking lots, and buildings, habitat that is not used during the breeding season (Arcese et al. 2020). In British Columbia, highest densities occur on vegetable farms. It seldom uses grass and grain fields, cropland, or dense forests of any type (Campbell et al. 2001). In Illinois, preferred winter habitats included ungrazed grasslands, shrub habitats, marshes, and drainage ditches (Graber and Graber 1963). Another Illinois study found it in low densities in bottomland hardwoods but it was absent in upland forests and urban residential areas (Graber and Graber 1979). In Kansas, it inhabited fields, meadows, and marshy areas with dense ground cover. Preferred escape cover included brush piles and fencerows of dogwoods, saplings, and vines. Highest densities occurred in marshy areas around edges of a pond where there were tangles of smartweeds, rice cutgrass, cattails, and other marsh vegetation. In old fields, it preferred weedy areas with foxtails (Fitch 1958). In North Carolina, prime habitat consisted of fields with crabgrass, asters, and shrubs, and to a lesser extent, broomsedge mixed with pines and tall herbaceous plants. It made almost no use of bare fields, horseweed, broomsedge, and pine and deciduous forests (Pulliam and Enders 1971).

Several studies demonstrated the importance of dense cover to wintering Song Sparrows. In Mississippi, Smith et al. (2005) established 6.1-m-wide borders dominated by crabgrass, Johnson grass, and a variety of herbaceous species around fields. Densities were significantly greater in fields with borders; it was 3.7 times more abundant in bordered fields. Once fields were harvested, borders provided suitable foraging and escape habitat. Evans et al. (2015) reported similar results in Arkansas, Kentucky, and Mississippi. Densities of Song Sparrows were 2 times greater in fields with buffers than fields without buffers. In Maryland, Blank et al. (2011) mowed portions of grassy and herbaceous buffers between row-crop fields and forested wetlands in autumn. Vegetation height in mowed areas was reduced to 10-15 cm. In winter, the Song Sparrow was the most abundant species in buffers, representing 45% of all detections. It was more abundant in buffers wider than 60 m than in those 30-60 m wide. Densities per km^2 were 21 in mowed buffers and 701 in unmowed buffers,

demonstrating the negative impacts of autumn mowing. In Virginia, Greenberg (1989) established feeders 1.5 and 2 m from cover and within cover. At 1.5 m from cover, there was a nonsignificant decrease of 6% in visitation to the feeders. Usage declined by 10.6% when the feeder was 7 m from cover. Ninety-two percent of all sparrow species observed feeding less than 1 m from cover were Song Sparrows, but it was observed away from cover out of proportion to its overall abundance. In Virginia, Beck and Watts (1997) cut vegetation to a height of 30 cm in half of plots, added brush to some, and added seed trays to some plots. The Song Sparrow exhibited a significant preference for cover and occurred significantly more often in uncut areas. It was also more abundant where supplemental food was provided. For food-addition plots, a shift into cut areas occurred when brush was added. Vegetation had a significant effect on its distribution. In cut areas, bird distribution was skewed to the centre of plots; birds were evenly distributed in uncut plots. More birds were associated with plots containing brush, which probably provided protection from predators. Birds responded positively both to cover that reduced predation risk and to food availability. In Georgia, Watts (1990) studied the Song Sparrow in dense homogeneous stands of horseweed. He mowed 2 plots to a height of 15 cm, mowed 2 30-m wide strips on 2 plots so they alternated with uncut strips, and left 2 plots uncut. All plots were within a bigger matrix of horseweed. Brush refuge stations were established at 1 end of each grid so that half the grid had no refuge cover and the other had 2 refuge stations. Eighty-five percent of Song Sparrows were observed on unmowed plots and 88.1% occurred on the brush-addition side of plots. Kills of Song Sparrows by Northern Harriers occurred significantly more frequently in open areas than expected; 88.4% of all observations were in uncut areas but 82.6% of kills were in mowed areas. The Song Sparrow accounted for only 13.8% of all sparrow observations but represented 71.8% of all harrier kills.

Greenberg (1988) demonstrated that the Song and Swamp sparrows partitioned their breeding habitat based on the presence of standing water. The habitat differences of these 2 species do not carry over into winter and they commonly co-occur in marshes with open water.

McNicholl (1979) reported communal roosting of the Song Sparrow in Prince Edward Island. Fifteen emerged in rapid succession from a hole 4 cm in diameter in a snowbank. The opening led to a tunnel 10 cm long into a cavity 18-20 cm long, 11-14 cm wide, and 8 cm deep; there was no other opening. Although it was early April, the weather was cold and windy. During severe winters in British Columbia, Song Sparrows roost together among bales of hay or in woodpiles in human-made shelters (Campbell et al. 2001). In Alaska, 1 roosted in a niche in a rock face (Arcese et al. 2020).

Migratory birds occupy home ranges in winter but do not defend them. Some birds may perch conspicuously and behave much like territorial residents but rarely interact aggressively. Most spend the majority of their time under or near shrub cover and behave in the same manner as nonterritorial floaters do during the breeding season. In British Columbia, individuals occupied very small home ranges (0.1 ha) from late September until they departed in late March. They mostly remained within their home ranges but occasionally fed together in small flocks. The sex ratio in this population was 10 males per female suggesting that males wintered further north than females (Schiffer and Smith 2000). In Kansas, the average winter home range of migratory birds was 2.75 ha and one had a home range of 3.60 ha (Fitch 1958). Resident birds remain on or near their territories in winter. Maintenance of winter territories is essential to retain ownership in spring. Territories may or may not be defended

and birds use a larger home range than the territory. Ohio males had an average winter home range of 3.4 ha, 6-10 times larger than the breeding territory. In cold weather, birds may travel 270-500 m to visit feeders. Resident winter birds remain solitary but may gather together in loose flocks during severe weather (Arcese et al. 2020; Nice in Austin 1968; Nolan in Austin 1968). In resident populations, a dominance hierarchy is established. In all hierarchies, the adult male and his female were the dominant birds at feeding stations located within their territory and juveniles were arranged in a linear fashion below them. Males were dominant to females which may result in higher average annual survivorship of males. Territorial males dominated at feeders and achieved 2 times as many displacements as they suffered, followed by territorial females, yearling males, and yearling females (Arcese et al. 2020; Knapton and Krebs 1976).

In a Kansas migratory population, 1 of 29 birds (3.4%) was recaptured in the same home range in a subsequent winter (Fitch 1958). In a California resident population, Sandercock and Jaramillo (2002) banded 1,107 juveniles and 825 adults in winter. The recapture rate was 54.3% for juveniles and 43.7% for adults. The winter survival rates were 31.0% for juveniles and 34.0% for adults after their first capture, and 55.8% in later years.

In winter, the Song Sparrow forages predominantly on the ground, in or near dense underbrush or thickets, in willows and other vegetation along watercourses, in cattail marshes, in grassy and weedy areas, and around root tangles and piles of driftwood. It entered barns to eat seeds. On a British Columbia island, 90% of adults left their territories temporarily and flew as far as 500 m to feed on seeds and tiny flies in a roost occupied seasonally by 12,000 European Starlings (Arcese et al. 2020). In North Carolina, it mostly ate seeds 1.5 mm in length, with lesser amounts of seeds 1.5-2.5 mm long and negligible amounts of items 6.5-8.5 mm long. Almost all food items larger than 3.5 mm were soft fruits; smaller items were hard seeds. Its seed-size utilization overlapped 100% with the White-throated Sparrow and Northern Cardinal and 0% with the Field Sparrow and Dark-eyed Junco. Feeding activities included 72% feeding from a standing plant while on the ground, 17% on bare ground, and 11% while perched on a plant. Abundance of the Song Sparrow was significantly correlated with food abundance. It spent 22% of its time in forest and 18% of the diet consisted of fruit that occurred only in forested habitat. It was limited by its winter food supply (Pulliam and Enders 1971). The Song Sparrow is a widespread user of winter bird feeders but abundance at Ontario feeders is usually only 1 or 2 birds. The Project FeederWatch season extends to almost the end of March so many birds recorded may be spring migrants rather than wintering birds. Larger numbers occur at rural and suburban feeders than at urban feeders. It selects small easily opened seeds over harder ones even if they have higher energy content. Favourite feeder foods are mixed seeds and millet. Infrequent choices include sunflowers, safflower, cracked and whole corn, milo, wheat, niger, hulled peanuts or hearts, peanut butter mixes, bird puddings, baked goods, water and sugar water, canary seed, and popped corn (Dunn and Tessaglia-Hymes 1999). Horn et al. (2014) determined that it preferred white proso millet over other seeds and preferred hopper feeders based on 9,090 feeding events.

James (1991) considered the Song Sparrow a rare winter resident north to Manitoulin Island and Ottawa and occasional and rare in the north near Thunder Bay. It occasionally winters in Muskoka District and Algonquin Park (Mills 1981; Tozer 2012). The number of birds that winter at Presqu'ile is

variable depending upon the weather (LaForest 1993), and this is likely true throughout the province.

Freedman and Riley (1980) analyzed Christmas Bird Count (CBC) results for southern Ontario during 1929-77. Numbers were stable until 1957, then increased, averaging 2 times more abundant after 1957. The increase was probably due to an increase in availability of seed crops, weedy fields, or cover. Curry (2006) considered the Song Sparrow fairly common in winter in the Hamilton area, but noted that numbers have been declining since the 1960s. He attributed this to a decrease in the number of weedy fields. CBC data indicate that the Song Sparrow decreased in Ontario at an annual rate of 1.82% 1970-2021 and increased at an annual rate of 0.69% 2009-21 (National Audubon Society 2022).

Lincoln's Sparrow

Melospiza lincolnii

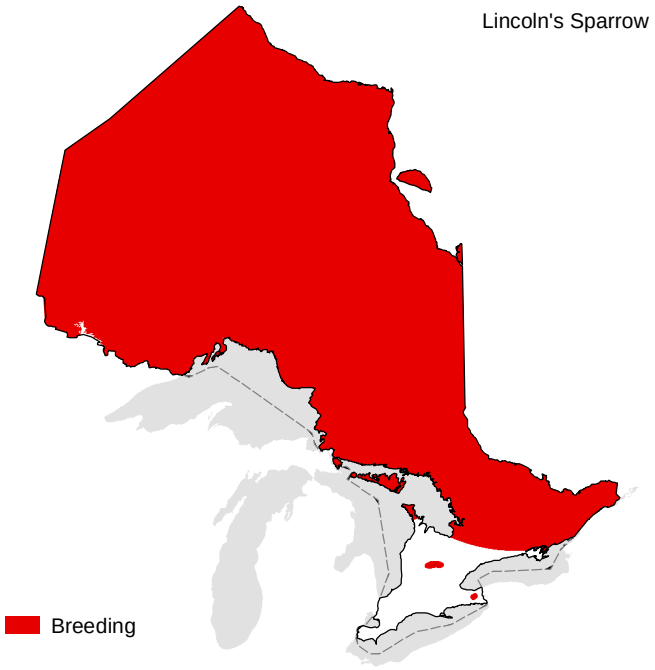
BREEDING SEASON

Habitat Requirements

Ontario Lincoln's Sparrow nests were in bogs and fens with growths of grasses, sedges, swamp laurel, Labrador tea, willow, black spruce, and tamarack (52.4% of nests); in alder and willow swales (19.0%); in shrubby roadside clearings (9.5%); in a small grove of black spruce (4.8%); in a rural garden near a woodlot (4.8%); on a river bank with fern clumps (4.8%); and in a wet pasture (4.8%). Eight-one percent of nests were in wet areas. Treed areas that were used were usually open and 2 bog areas were old burns (Peck and James 1987).

In the Hudson Bay Lowland, the Lincoln's Sparrow was one of the most common species in growths of willows and tamarack in the Moosonee town clearing (Manning 1952).

From Pickle Lake northward, the Lincoln's Sparrow was most numerous in coniferous scrub, followed by deciduous scrub, coniferous forest with understorey, mixed scrub, and coniferous forest



without an understorey. It was absent in deciduous or mixed forests, heath, and tundra (McLaren and McLaren 1981). Near Pickle Lake, it nested in small numbers in larger bogs (James 1980). At Dorion, an essential component of its habitat was the presence of low shrub growth, typically 1.2-2.4 m tall, with openings where tufts of grasses or sedges occurred. Territories were often swampy or wet, but this was not always the case. It occurred in recent clear-cuts full of brush piles and stumps, fallen logs, and new shrubby growth interspersed with grassy openings and rain pools. Marsh marigolds were a conspicuous feature of many territories. Other common plants included Labrador tea, sweet coltsfoot, wood anemone, and young cherry saplings. Small spruces, alders, willows, dogwoods, white birches, and trembling aspens occurred in most territories. Many territories were adjacent to stands of larger trees of trembling aspen, white birch, and spruce. Birds sometimes went into these woods when they were disturbed. Many territories included large isolated trees of these species that it occasionally used as perches. Nesting habitat consisted of the edge area between the forest and buildings with their surrounding lawns and roads. This area was brushed every few years to impede natural succession and cuttings and slash covered the ground. Most vegetation was about 30 cm tall and consisted of anemones, grasses, sedges, roses, strawberries, and the woody species previously mentioned. The actual species of plants were probably unimportant but their size and interspersion were important. Shrubs less than 2.4 m tall provided concealment and song perches; openings with grasses, heaths, or annuals less than 60 cm tall provided foraging sites; and a substrate of brush cuttings, grass clumps, or sphagnum provided a suitable nesting substrate. In Thunder Bay District, it occurred on high rocky hillsides with low shrub growth of dogwoods, alders, willows, and birches with occasional taller aspens and birches, and with openings where clumps of grasses and sedges grew around temporary pools. Habitat structure was very similar to that at Dorion except that the site was dry. In Abitibi Region, it frequently occurs in dry upland openings in the forest and in Nipigon District it nests in raspberry patches. Many nests have been documented in open sphagnum bogs in spruce forests. Originally and in areas currently undisturbed by humans, it depends on fires and margins of water bodies, watercourses, and wetlands to provide suitable habitat. It now nests in human-made openings such as clear-cuts and rights-of-way for roads and hydro transmission lines (Speirs and Speirs in Austin 1968). North of Lake Nipigon, the Lincoln's Sparrow was common in a clear-cut that was quite wet with alders 2.4 m tall (Kendeigh 1947). Near Hearst, it nested in an unharvested black spruce lowland forest, in clear-cuts in lowland coniferous forests 3-19 years old, and in clear-cuts in upland mixed forests 3-5 years old. Lincoln's and Savannah sparrows were the dominant species in the 3-year-old lowland coniferous clear-cut. This community was open, wet, and meadow-like

(Welsh and Fillman 1980). Near Manitouwadge, the Lincoln's Sparrow occurred in stands 1-21 years old but was absent in stands 24-36 and 60-223 years old (Venier et al. 2009). In jack pine forests near White River, it was significantly associated with stands that had been clear-cut 3-5 years previously. It was a significant indicator of this age class. This age class of forest was dominated by species that foraged and nested on the ground. Its abundance was significantly correlated with coarse woody debris volume and negatively correlated with vertical structure 2.5-5 m tall. It was associated with dense shrubs but avoided areas where woody vegetation height exceeded 2.5 m (Venier and Pearce 2003). In the Clay Belt, it was most likely to occur in black spruce stands followed by those dominated by jack pine, tamarack or white cedar, and white spruce–birch. It occurred predominantly on wet sites but occasionally in dry areas treed with jack pines. Most sites where it occurred were nutrient-poor, but a few were moderately rich in nutrients (Welsh and Lougheed 1996). Also in the Clay Belt, it nested at the edge of a spruce-tamarack-alder bog and in a spruce sphagnum bog (Smith 1957). In the eastern Boreal Forest Region, it occurred mainly in young or at least low spruces, and was one of the more common species in bogs and fens (Erskine 1977).

In jack pine stands near Gogama in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, it was rare and occurred only where the pines were small and well-spaced and where sedges, grasses, and scattered deciduous shrubs were present. It was absent where pines were more than 15 years old (James and Peck 1995a). In Algonquin Park, MacLulich (1938) observed it only around beaver meadows and in shrubby areas. Tozer (2012) reported that it nested in the park in bogs, beaver meadows, and dry upland clearings with low shrubby growth interspersed with open areas with grasses and sedges.

South of the Shield, the Lincoln's Sparrow nests almost exclusively in large bogs and fens (James 1991). Wainfleet Bog is the only breeding location within the Carolinian Forest Region (Black and Roy 2010).

Throughout its range, the Lincoln's Sparrow prefers short shrubs interspersed with open areas, predominantly in damp to wet locations. It nests in montane meadows, willow and alder thickets, aspen groves in the west, open spruce stands, bogs and fens, clear-cuts, burns, young coniferous plantations, drainage ditches along roads, moist overgrown fields, hydro corridors, shrubby beaver meadows, and riparian shrubs. In Quebec, it nests in drier shrubby portions of sphagnum bogs, especially older ones suitable for the production of peat rather than the wet sphagnum moss of more-recent bogs. It often frequents edges of bogs among Labrador tea, laurel, and rhododendrons with scattered conifers and a ground cover of cloudberry. In Matane, it nested among low alders fringing streams and, in Gaspé, it nested near the top of a mountain among scrubby conifers (Speirs and Speirs in Austin 1968). In Quebec, it prefers more remote habitat such as peatlands, wet meadows, clearings created by fire or logging, and thickets of alders, willows, or stunted conifers along rivers, streams, and lakes. In the James and Hudson bay regions, it occurs at margins of most open habitats, particularly those that are wet. It is often found inland among willows surrounding open grassy meadows. In northern Quebec, highest densities were in tamarack peatlands and shoreline scrub. In the Boreal Forest Region, it inhabits alder thickets in open areas where there is open water nearby (Langevin in Gauthier and Aubry 1996; Manning and MacPherson 1952). Near Quebec City, the Lincoln's Sparrow was absent in recent burns, common in clear-cuts with shrubs

less than 2 m tall, and absent where shrubs were taller than 5 m and in mature stands. Imbeau et al. (1999) considered it an early successional species associated with clearings due to recent clear-cuts. Although it is common in Quebec clear-cuts, it is absent in strip-cuts. It probably requires openings wider than 20 m in forest cover (Falardeau et al. 1999). In northcentral Quebec, it was typical of shrub stands and appeared after the falling of dead trees approximately 15 years after fire, and disappeared progressively as stands matured (Crête et al. 1995). In New Brunswick, it nested in spruce plantations 3-15 years old but was absent in older plantations (Freedman and Johnson 1999). In Newfoundland, Whitaker et al. (2008) netted Lincoln's Sparrows in natural landscapes where openings consisted mostly of peatlands and in harvested landscapes where openings were most clear-cuts as well as some peatlands. Sixty-seven percent of captures were in harvested landscapes suggesting that clear-cuts improved habitat. At another Newfoundland site, its overall occurrence tended to be higher in natural than harvested landscapes, especially at higher levels of forest cover. Its occurrence was positively correlated with scrub, bogs, and regeneration and it was negatively affected by the amount of forest cover within a 150-m radius. It was unaffected by the amount of forest cover within 1,250 m but declined nonsignificantly as forest cover increased. Probability of occurrence was 40% at 10-40% tree cover, 30% at 60% tree cover, 18% at 80% tree cover, and 0% at 97-100% tree cover. Taylor and Krawchuk (2006) considered the Lincoln's Sparrow an open and edge species. In Newfoundland balsam fir forests, it was documented only at edges between forests and clear-cuts or roads and not in riparian vegetation and forest interior. Whitaker and Montevecchi (1997, 1999) concluded that it was associated with early successional openings and edges and also occurred in riparian alder thickets. It was common in open bogs and low shrubs in the northeast. It was common in shrubs with scattered conifers and uncommon in young or low black spruce (Dawson 1979).

In the western mountains, particularly south of Canada, the Lincoln's Sparrow is most common in montane meadows. In Minnesota, it occurred in low shrubs along a hydro corridor and in open spruce stands (Niemi and Hanowski 1984a). In the Prairie Provinces, it occurred predominantly in wet marshy or boggy habitats and some riverine mixed-wood forests. It occurred in sites that were mostly nutrient-poor and wet. Forest stands it occupied were young. It was not detected in stands older than 20 years (Kirk et al. 1996). In Alberta, it was significantly more abundant in clear-cuts than in uncut forests. It was present in low numbers in forests prior to cutting and moved into clear-cuts in the first year after logging. In clear-cuts, it decreased in abundance with increasing basal area (Tittler et al. 2001). In aspen forests, it was rare in young and old-growth forests and absent in mature stands (Schieck et al. 1995). On Haida Gwaii, it breeds in open wet habitats with clumps of soft rush. In the mountains, it breeds in willow swamps. It prefers to nest in wet habitats with low dense shrub growth, particularly willows 1-2.5 m tall, with openings with mosses, sedges, or grasses. It nests in swamps, muskegs, bogs, thickets near beaver ponds, brushy fields, marshy areas with alder or willow thickets, sedge and rush meadows, streamside willows, black spruce–tamarack bogs, floodplain forests, regenerating burns and cuts, trembling aspen groves, subalpine parklands, and shrubby areas near the timberline. It also nests in roadside willows, red-osier dogwood, and fireweed with trees as tall as 8 m; wetlands with dwarf birch, rough horsetail, Labrador tea, sphagnum moss, and some open water; and in wet shrub thickets with a dense herbaceous understorey. In trembling aspen forest, it is most abundant in 4-6-year-old clear-cuts. Thirty-nine percent of nests were associated with wetland habitats, 25% with forested areas, and 19% with human-influenced areas.

Of the wetland habitats used, 14% were marshes, 11% were lakes, and 11% were willow swamps and balsam fir bottomland forests. Twenty-two percent of the total 25% of nests in forested areas were in trembling aspen or other deciduous woods. Human-influenced habitat included farmland, pastures, suburban areas, logged areas, and roadsides. Sixty-eight percent of nests were at forest edges and regenerating clear-cuts. It also nested in muskeg, beaver ponds, roadsides, farmyards, and airports (Campbell et al. 2001). In the Yukon, the Lincoln's Sparrow prefers moist shrubby habitats in or near forested areas with willow, dwarf birch, or a mixture of these species. It also breeds in wetlands including taiga and bogs where it nests in tall dense shrubs. It nests in marshy and shrubby areas adjacent to lakes and in streamside shrubs and clear-cuts (Sinclair et al. 2003). In Alaska, it was most abundant in floodplains and terraces, followed by lowlands, subalpine areas, hills and bluffs, and alpine areas (Handel et al. 2009). In the same state, it responded positively but not significantly to spruce mortality resulting from the spruce beetle. The beetles attacked only large white spruce, resulting in gaps in the canopy (Matsuoka et al. 2001). In Yellowstone National Park, there was no significant difference in its abundance in areas where willows averaged 66 cm and 152 cm tall. There was a tendency for a decline with increasing willow height but this relationship was not significant (Campbell et al. 2001; Olechnowski and Debinski 2008; Speirs and Speirs in Austin 1968). In Wyoming, it occurred at all elevations, but was most abundant in subalpine areas. Habitat there consisted of willow thickets interspersed with wet or boggy meadows surrounded by spruce-fir forests. It foraged and nested on the ground and selected habitats that were structurally simple. It preferred areas with a sparsely foliaged overstorey and few trees. It was positively associated with increasing shrub density and foliage density of the low understorey. Its habitat size was significantly less than random indicating that it was a habitat specialist (Finch 1989b, 1991a). Another Wyoming study found that its abundance was positively correlated with elevation. It was negatively correlated with non-willow shrub coverage 0.5-1 m tall (Anderson 2007). In montane habitat in the western United States, it was most common in moderately wet to flooded meadows with low levels of grazing damage. It was absent from the single site that lacked standing water and had signs of heavy grazing. It significantly selected for wet areas, with only 3% of birds occurring in areas of dry ground; 93.1% were seen in either boggy (54.2%) or flooded (38.9%) areas. Presence of nearby surface water was the most important attribute; presence of willow, pine, and corn lily were important. Eighty-four percent of males occurred near clumps of willow, significantly more than random, and 59% were in areas with at least scattered patches of corn lilies, although this relationship was not significant. Concentrations were significantly greatest near edges of meadows (67% of observations) where it often perched or sang in pines. Most were observed in meadows but singing males or pairs were occasionally seen in small nearby openings in surrounding forest provided that suitable habitat was present. Important breeding habitat attributes included boggy or flooded ground; thick ground cover by herbaceous plants, often with raised tussocks of live or dead grasses or sedges; patches of corn lily; willow thickets or other low shrubs; and some conifers. Raised clumps of herbaceous vegetation were probably critical for breeding under such wet conditions (Cicero 1997).

Some studies compared the habitat preferences of the Lincoln's Sparrow with other sparrows. Salt (1957) examined the distribution of the Lincoln's, Fox, and Song sparrows in willow marshes in Wyoming. The Lincoln's Sparrow occurred in drier areas where willows were in low scattered clumps 0.6-1.2 m tall with patches of grasses and sedges in between. The Song Sparrow inhabited dense

willows 1.8-3 m tall along watercourses and the Fox Sparrow occurred in drier glades surrounded by willows 3-3.7 m tall. The Lincoln's Sparrow is generally a species of grassy meadows, but it also occurs in willow scrub. It occasionally inhabits herbaceous undergrowth of aspen groves, but these groves are commonly near water and may represent peripheral foraging areas. In California and Oregon, there was a strong negative relationship between Lincoln's and Song sparrows. Although some meadows had approximately equal numbers of both species, most sites were dominated by one or the other species. Where the 2 species co-occurred, the Lincoln's Sparrow occurred in the wettest areas and the Song Sparrow occurred only in the drier, more heavily grazed areas (Cicero 1997). Ammon (2020) concluded that the Lincoln's Sparrow selected wetter sites for breeding than co-occurring White-crowned Sparrows and Dark-eyed Juncos.

Ammon (2020) stated that the Lincoln's Sparrow often occurred near forest edges, but most frequently in the open side of the edge. Forest edges are used by males for singing and sentinel perches. The territory and nest are not significantly associated with edge.

Most Ontario nests (82.4%) were on the ground, usually in pure moss or in moss, grass, or sedge hummocks. Other ground nests were in clumps of ferns and in goldenrod stems and raspberry canes. The remaining nests were 0.2-0.3 m above ground or water in shrubs. Sixty-four percent of ground nests were at the base of a small tree or shrub. Nests were often concealed by standing dead grasses and sedges (Peck and James 1987). A nest at Dorion was 4.9 m from an access road and 2.4 m from forest edge. Another was in a grass clump between a road and roadside ditch, 10 m from forest edge (Speirs and Speirs in Austin 1968).

Ammon (2020) considered the Lincoln's Sparrow a microhabitat specialist that nests on the ground, often in a low willow or dwarf birch with nearby sedge cover that is fairly dense. Nest sites are more elevated with denser ground and lower shrub coverage than random sites in the territory. Nests are typically well concealed at the base of shrubs but may be in forbs such as buttercups. Colorado nests had a distinct nest-entrance tunnel through ground vegetation oriented east to northeast, significantly different from random orientation. In shrub cover, nests are most often 30-50 cm inside the shrub's edge. Occasionally nests may be a few metres inside a forest. Usually more than 90% of nests are on the ground. Nests may be elevated as high as 1 m, but are usually 30 cm or less from the ground. Ground nests are in a depression in moss but nests in shrubs or grasses are woven among the branches or grass stems. If a nest is artificially removed after breeding, sometimes the same depression is used the following year (Ammon 2020; Campbell et al. 2001; Cicero 1997; Langevin in Gauthier and Aubry 1996; Philipp and Bowdish 1917; Sinclair et al. 2003; Speirs and Speirs in Austin 1968).

The territory is used mostly for nesting with much foraging taking place outside the territory. Territory boundaries break down temporarily 5-8 days after the young fledge but territorial activity resumes at the time when a second brood would be initiated even if one is not attempted. In Ontario, territories appeared to be occupied until autumn migration. Territories at Dorion were 0.4 ha; 2 territories near Lake Nipigon averaged 0.32 ha. In high-density populations in Colorado, territories averaged 0.09 ha (Ammon 2020; Kendeigh 1947; Speirs and Speirs in Austin 1968).

The only information on natal philopatry and adult site fidelity is from Colorado. Three of 137 young (2.2%) returned to the natal area over a 5-year period. Thirty-seven percent of 123 adult males and 36% of 85 females returned to breed (Ammon 2020).

Limiting Factors

Eggs have been reported in Ontario nests from mid-May until the first week of August, with most present in the last 3 weeks of June (Peck and James 1987). In many areas, territories are established immediately upon arrival but at Dorion males waited until it warmed up. Nest building did not start until 10-14 days after territories were established. Nest construction takes 3 days. Egg laying usually begins 2-4 days after the nest is complete but several more days may elapse before eggs are laid. Eggs are laid at the rate of 1 per day. Incubation begins with the laying of the last egg. The incubation period of 1 egg near Dorion was 13.25 days. In Colorado, the incubation period averaged 11.5 days (range 10-13 days). Eggs usually hatch within a 36-hour period but occasionally 1 egg hatches a day later, suggesting that incubation may begin with the laying of the penultimate egg in some cases. The nestling period at Dorion was 9-10 days; nestling periods of 10-12 days have been reported elsewhere (Ammon 2020; Speirs and Speirs in Austin 1968).

In Ontario, egg dates, resumption of courtship behaviour in early July, and presence of young juveniles in September all suggest that double broods may occur, but this has not been confirmed. In Colorado, only 1 brood was typically reared in a season. In a season where breeding started 10 days earlier than normal, 3 of 65 pairs (4.6%) attempted a second clutch. Second clutches were initiated before the nestlings of the first brood fledged. Renesting usually occurs if a nest is lost or abandoned. Clutches of 3-5 eggs (mean 4.08 eggs) have been reported in Ontario, with 76.9% of clutches containing 4 eggs. Three to 5 eggs are typically laid and 4 eggs is the most frequent clutch size. There appears to be no seasonal variation in clutch size. In Colorado, the mean clutch size was 4.24 eggs, increasing to 4.48 eggs during a year of insect outbreak (Ammon 2020; Campbell et al. 2001; Peck and James 1998b; Speirs and Speirs in Austin 1968).

Both sexes are capable of breeding when they are 1 year old, but many yearling males do not breed. The Lincoln's Sparrow appears to be monogamous. There is circumstantial evidence that extra-pair copulations may be part of its breeding strategy in high-density populations. Populations in Colorado and Newfoundland were strongly male biased and intense mate guarding occurred during nest building and egg laying (Ammon 2020; Whitaker et al. 2008).

The Lincoln's Sparrow forages predominately on the ground. Foraging occurs in dense cover where it scratches with both feet to uncover prey or chases prey on the ground. It mostly gleans on the ground and low vegetation but also on tree foliage and branch tips. It flycatches infrequently, but during moth outbreaks this may be a common foraging technique. It visits feeders at any time of the year and in the breeding season defends food resources at feeders even if they are outside its territory (Ammon 2020; Speirs and Speirs in Austin 1968).

Nestlings at Dorion were fed predominantly green caterpillars that were likely geometer moths, grayish caterpillars that were possibly owlet moths, small whitish moths, yellowish larvae that were possibly beetles, small caterpillars, and small larvae that may have been budworms. Females were observed feeding fledglings 20 days after they had left the nest. Caterpillars are a staple of the

nestling diet, but young are also fed other soft-bodied insects such as mayflies (Ammon 2020; Speirs and Speirs in Austin 1968).

Judd (1901) analyzed the contents of 31 adult Lincoln's Sparrow stomachs, mostly migrants collected in Massachusetts and New York. They contained 42% animal matter and 58% vegetation. Insects comprised 40% of the diet and the remaining 2% of animal food consisted of spiders and millipedes. The insects included hymenopterans, beetles, ants, flies, grasshoppers, and some bugs. Plant material in the diet included 27% grass seeds, 16% miscellaneous seeds that were predominantly weeds, 13% ragweed and smartweed seeds, and 2% grain. During outbreaks, it may forage mostly on moths during the breeding season. It has been documented eating clover-root weevils, alfalfa weevils, crane flies, and aquatic beetles (Ammon 2020). In Wyoming, Raley and Anderson (1990) compared the breeding-season diets of the Wilson's Warbler and Lincoln's Sparrow with each other and available prey. Fifty-four families of arthropods, excluding spiders, were identified in the Lincoln's Sparrow's diet in 2 years. It preferred beetles over all other groups. Larvae (immature beetles, hymenopterans, and caterpillars) ranked high in preference; stoneflies and mayflies ranked low. Preferred prey in decreasing order of preference included beetles, larvae, flies, soft-winged bugs, spiders, mayflies, hymenopterans, stoneflies, true bugs, caddisflies and adult lepidopterans. In this list, beetles through mayflies were used more than their availability and the remainder were used less than their availability. Soldier beetles represented a large proportion of the beetles that were consumed. These beetles have soft elytra, are fairly large (7 mm), are slow fliers, and tend to crawl rather than fly from disturbance. It selected more cryptic invertebrates than the Wilson's Warbler and those that were more uniformly distributed. It spent more time in any given shrub than the Wilson's Warbler and was more likely to detect cryptic prey. Fifty-three percent of the flies consumed were crane flies. These are slow fliers and tend to be in the inner and lower portions of shrubs where the Lincoln's Sparrow commonly foraged. Crane flies were also present in sedge-grass meadows. The Lincoln's Sparrow and Wilson's Warbler both selected prey disproportionately and preferred different prey items.

The Lincoln's Sparrow is an uncommon host of the Brown-headed Cowbird, probably because of the species' different habitat preferences. One of 28 Ontario nests (3.6%) was parasitized. In Colorado, 0-3% of nests were parasitized annually depending upon location and year. In British Columbia, 4 of 66 nests (6.1%) were parasitized. Lincoln's Sparrows were observed feeding cowbird fledglings there (Ammon 2020; Campbell et al. 2001; Peck and James 1998b; Speirs and Speirs in Austin 1968).

It is uncertain whether habitat loss and degradation are occurring for the Lincoln's Sparrow. Fire suppression has probably decreased the amount of available habitat, but clear-cutting and other human activities that create shrubby habitat are beneficial. Some populations south of the Canadian Shield may be at risk due to degradation of bogs and fens. At Wainfleet Bog, it formerly bred in the interior of the wetland, but the entire open area of the bog has been invaded by silver birch, making the habitat unsuitable. It now nests only at the edges of the bog (Black and Roy 2010). The Wylde Lake Bog at Luther Marsh supports a small population of Lincoln's Sparrow. This bog is becoming increasingly treed, although with native species typical of bogs and fens (Sandilands 1984). Invasion of both these bogs by trees is probably due to human alterations of their hydrology.

The Lincoln's Sparrow responds positively to forest management, but only when a high proportion of the canopy is removed. In Alberta, it colonized coniferous forests once 80-100% of tree cover was removed. In deciduous forest, colonization occurred when 25-100% of the canopy was removed, but the increase was not significant until 90% of trees were removed. In Newfoundland, breeding-season and annual survival rates were marginally higher in landscapes where most openings consisted of clear-cuts than in natural landscapes (Ammon 2020; Harrison et al. 2005; Whitaker et al. 2008). In Maine, Santillo et al. (1989) studied the effects of spraying glyphosate on clear-cuts on the Lincoln's Sparrow. It was significantly less abundant in treated than untreated clear-cuts. The application resulted in vegetation that was structurally and floristically less complex for 1-3 years after treatment. Invertebrates were less abundant in treated areas and confined mostly to untreated skipped areas. The reduction of invertebrates, berry-producing shrubs, and seed-producing grasses and forbs reduced food for it. The Lincoln's Sparrow particularly benefits from short-rotation logging (Imbeau et al. 1999). In Ontario, it was equally abundant in early successional and mid-successional areas created by fire and clear-cutting. It was significantly more abundant in early successional stands than mature stands. It was also more abundant in mid-successional than mature stands but not significantly (Zimmerling et al. 2017).

Browsing by ungulates can degrade habitat for the Lincoln's Sparrow. This is particularly true of livestock grazing, which can alter vegetation structure and even hydrological regimes. In Colorado, it avoided areas that were heavily grazed by cattle. Decreases in its abundance have been associated with livestock grazing in British Columbia and other locations (Ammon 2020; Campbell et al. 2001; Cicero 1997). In Wyoming, it was not sensitive to elk grazing and tended to be more common in heavier grazed areas. Most species that were adversely affected nested in willows but there were few effects on ground-nesting species (Anderson 2007). In Anticosti Island clear-cuts in balsam fir–dominated forests, Cardinal et al. (2012) recommended that deer densities should be 7.5 or fewer per km^2 to avoid adverse effects of browsing. Browsing is unlikely to be a significant limiting factor for the Lincoln's Sparrow in Ontario. Its main range is outside the area where heavy grazing by cattle occurs. Densities of other browsers of woody vegetation, such as moose, deer, and caribou are low within the core of its Ontario breeding range.

Bayne et al. (2016) studied the effects of oil and gas infrastructure on the Lincoln's Sparrow. It was significantly more abundant at pipelines and well pads than in forest-interior habitat adjacent to these features. There was no difference in its abundance at seismic lines and in adjacent forest interior. The larger forest openings created by pipelines and well pads were attractive to it but the narrower (8-10 m) seismic lines probably were not wide enough to be attractive. It did not shift frequencies of its song between noisy compressor stations and quiet well pads, but it sang more in noisy areas (Sánchez et al. 2023).

The Lincoln's Sparrow appears to be particularly sensitive to human disturbance and readily abandons its nest. Significantly higher desertion rates occur in sites used for picnicking, fishing, and hiking than in areas not used for recreation (Ammon 2020; Campbell et al. 2001).

Application of waste sludge from paper mills resulted in an almost doubling of the Lincoln's Sparrow's density in treatment areas. This was probably due to the increase in vegetation because the number of ground invertebrates did not change (Ammon 2020).

Price (2004) predicted that the Lincoln's Sparrow might no longer breed in southern Ontario if the average summer temperature increased by 2°C. In southern Quebec, DesGranges and Morneau (2010) considered it highly sensitive to climate change and projected that its range was likely to shift northward. It was a boreal forest species correlated with cooler and wetter summers. In central Quebec and Labrador, it was not significantly correlated with any climatic variables (DesGranges and LeBlanc 2012).

Status

McIlwraith (1894) considered the Lincoln's Sparrow almost unknown in eastern Canada but acknowledged that it could have been overlooked due to its retiring nature. The first record for Ontario consisted of 2 birds collected at Hamilton Beach on 23 May 1885 followed by 2 more 2 days later. After that, he knew of only single records at Ottawa and London and was not aware that it bred in the province. Baillie and Harrington (1937) stated that it was distributed locally from York Region to beyond the transcontinental railway at Smoky Falls, and probably northward to Hudson Bay. It occurred commonly in many localities in the more northern portions of the province. In addition, 6 pairs were found in Wainfleet Bog in Niagara Region in 1936. The first atlas revealed that the Lincoln's Sparrow bred throughout the Boreal Forest Region and Hudson Bay Lowland, although it was not documented in many blocks within these regions. This was attributed to the species being overlooked rather than being absent. Many breeding records were obtained in the southern portion of the Canadian Shield from Lake Nipissing south to the Perth area, a southward extension of the previously known breeding range. There were very few records south of the Shield, and these were associated mostly with large bogs and fens. Highest densities occurred in the north from the Wawa area north to James and Hudson bays (Speirs in Cadman et al. 1987). James (1991) considered the Lincoln's Sparrow common in the north, south to Thunder Bay and Kirkland Lake; and an occasional rare and local summer resident in the south, mostly on the Shield, but south to Luther Marsh and Wainfleet Bog.

The second atlas found no significant changes in the range of the Lincoln's Sparrow. It was found in almost all northern Ontario blocks confirming that it had simply been overlooked in some areas during the first atlas. Its probability of observation increased significantly province-wide and in all regions except the Carolinian Forest Region, where it continued to occur at Wainfleet Bog only. Although its increase may be due in part to increased song recognition by fieldworkers, it appears to have increased. The increase in the Great Lakes–St. Lawrence Forest Region both in and off the Shield may be due to its increased use of early successional upland habitats and shrub thicket swamps. It was most abundant in a broad band south of the Hudson Bay coast. Moderate densities occurred throughout the Hudson Bay Lowland and in a broad band of the Boreal Forest Region across the province north of Lake Superior. In the Hudson Bay Lowland, treed bogs and fens are abundant and provide excellent habitat. The band through the Boreal Forest Region where it reaches highest abundance coincides with the region where forest management has created young regenerating forests with dense shrub and sapling cover. In younger clear-cuts, it is often the most abundant bird species (Zimmerling in Cadman et al. 2007).

Breeding Bird Survey results from 1970 to 2021 indicate an annual increase of 1% in Canada and an annual decrease of 0.39% in Ontario. Trends 2011-21 were annual decreases of 1.44% in Canada

and 4.16% in Ontario. All trends were of medium reliability except for the short-term Ontario trend which was of low reliability (A.C. Smith et al. 2003).

POSTFLEDGING PERIOD

Young are largely flightless the day they leave the nest. They can fly 6-8 m 3-5 days after leaving the nest and more than 10 m 6 days after fledging. The first 4 days after fledging are mostly spent under dense cover. Brood division may occur, but no studies with banded birds have been conducted. Young often return to the nest for several nights after fledging. Older juveniles sleep on the ground in tunnels under ground vegetation. Five to 8 days after fledging, family groups begin to forage throughout the breeding habitat. No large aggregations of postbreeding birds occur and, once the juveniles are independent, most birds remain solitary or in pairs. Occasionally, the Lincoln's Sparrow forms loose foraging flocks with conspecifics and other sparrows. Juveniles remain in the vicinity of the nest until autumn migration (Ammon 2020; Langevin in Gauthier and Aubry 1996; Speirs and Speirs in Austin 1968).

MIGRATION

The Lincoln's Sparrow is a nocturnal migrant as evidenced by kills at towers and captures while netting for owls. It is unknown if any diurnal migration occurs. The entire population is migratory with no resident birds. During migration, it occasionally mixes with Song, Swamp, White-throated, and White-crowned sparrows. A juvenile banded northeast of Moosonee was captured in Michigan the following spring (Ammon 2020; Brewer et al. 2018; Speirs and Speirs in Austin 1968; Weir 2008).

In southern Ontario, most migrants pass through in the first 2 weeks of May, with the peak in the middle of the month. Birds may arrive in late April and most have passed through by the end of May (LaForest 1993; Mills 1981; Tozer 2012; Weir 2008). At Dorion, the Lincoln's Sparrow first appeared at a feeder on 16 May but none were seen on the breeding grounds until 19 May when the sky cleared and the temperature rose (Speirs and Speirs in Austin 1968). Kendeigh (1947) saw the first one north of Lake Nipigon on 17 May.

At a reclaimed landfill in New Jersey, the mean autumn stopover period of the Lincoln's Sparrow was 4.7 days (maximum 16 days; Seewagen and Newhouse 2018). Wilson and McRae (1993) considered singles seen on 4 dates in late August at Brant to be migrants. Migrants appeared in Moosonee in September with the highest count on 3 September. The Lincoln's Sparrow was last seen at Dorion on 19 September (Speirs and Speirs in Austin 1968). The main autumn migration in the southern Shield is from early September to early October, with most leaving by late October (Mills 1981; Tozer 2012). In southern Ontario, migration is noticeable by late August and continues throughout September with most leaving by mid-October, but with records to mid-November or rarely into December (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Speirs and Speirs in Austin 1968; Weir 2008).

During autumn migration along the James Bay coast, the Lincoln's Sparrow was abundant in willows at edges of sedge marshes on sandy islands. Those further north up the coast were in open spruce or deciduous thickets (Manning 1952). During spring migration at Dorion, it preferred watercourses lined with shrubs, but also occurred in dense shrubbery almost anywhere; it may occur in urban parks (Speirs and Speirs in Austin 1968). In Muskoka and Parry Sound districts, autumn migrants frequent overgrown fields and other scrubby areas (Mills 1981). During autumn migration

in Toronto, it prefers marshy areas and weedy fields where it is often found in the company of White-throated and White-crowned sparrows (Speirs and Speirs in Austin 1968). Autumn migrants at Algonquin Park skulk in dense vegetation such as raspberries (Tozer 2012). During migration, it inhabits shrub-dominated areas providing dense cover, especially in riparian areas. In the east, it often occurs in urban and suburban areas in shrubby forest edges, weedy fields, hedgerows, marshes, and raspberry thickets (Ammon 2020). Quebec migrants frequent thickets, fallow land, hedges, understorey of open woods, clearings, forest margins, and roadsides (Langevin in Gauthier and Aubry 1996). In the Saskatoon area, migrants are seen in underbrush in city gardens and rural areas (Leighton et al. 2002). In British Columbia, migration habitat includes logging slash, hydro corridors, hedgerows, shrubby field edges, old fields and shrubby pastures, young forests and older forest edges, orchards, grass and sedge meadows, river floodplains, native tussockgrass prairies, and shrub thickets adjacent to sewage lagoons, lakes, marshes, sloughs, swamps, beaver ponds, estuaries, and beaches (Campbell et al. 2001). In Minnesota, migrants frequent hedgerows, weed patches, borders of woods, tamarack swamps, and similar dense vegetation. Several autumn migrants fed on mudflats just outside grass cover where a lake had dried. At another lake, it frequented thick tangled weeds and grass in low areas and accompanied Harris's and White-throated sparrows in tall shrubby and weedy areas and in plum thickets. It was also common in cornfields and old grassy gardens (Speirs and Speirs in Austin 1968). In Kansas, migrants preferred low dense thickets in swampy areas. Spring migrants appeared to settle for days or even weeks within small areas. Patches of green foxtail near the edge of a woodlot were much used in late April. Late autumn migrants also used brush piles (Fitch 1958). On 2 islands in the Gulf of Maine, there was no significant difference in their usage by spring migrants. During autumn migration, significantly more Lincoln's Sparrows used the island with shorter trees and higher shrub density (Suomala et al. 2010). During spring migration in Pennsylvania, the number of Lincoln's Sparrows captured per 1,000 net-hours was 0 in forested habitat and 1.8 in shrub habitat (Smith and Hatch 2008). Presence of dense shrubby or herbaceous vegetation is the prime habitat requirement of the Lincoln's Sparrow during migration, and it is seldom seen outside dense cover. These microhabitat requirements may be found in a wide variety of macrohabitats, but it prefers areas without extensive tree canopy.

The Lincoln's Sparrow may visit feeders during migration, particularly in spring and infrequently in autumn. It uses only ground feeders close to dense cover; elevated platforms are not used. It has been observed eating rolled oats and millet at feeders (Ammon 2020; Leighton et al. 2002; Tozer 2012).

The Lincoln's Sparrow often strikes television towers and other tall structures during migration. Seven were killed out of 936 birds during 4 late September nights at the Barrie television tower and 18 were killed at the Lennox generating station chimneys from 1972 to 1981. It is one of the species most vulnerable to striking high-rise buildings in Toronto (Ammon 2020; Colling et al. 2022; Speirs and Speirs in Austin 1968; Weir 2008).

James (1991) considered the Lincoln's Sparrow an uncommon migrant in Ontario. It may actually be common but seldom seen. Records at Prince Edward Point indicated that it was far more common (daily maxima 35-60) than observations suggested. In southern Ontario, maximum daily

counts seldom exceed 20 birds (Curry 2006; LaForest 1993; Weir 2008). Wilson and McRae (1993) observed 50 at Moosonee on 3 September.

Captures of the Lincoln's Sparrow at Long Point Bird Observatory declined at a nonsignificant rate of 0.6% per year 1961-88. Trends by period were: 1961-70, −2.6%; 1970-79, + 0.3%; and 1979-88, − 0.2% (Hussell et al. 1992).

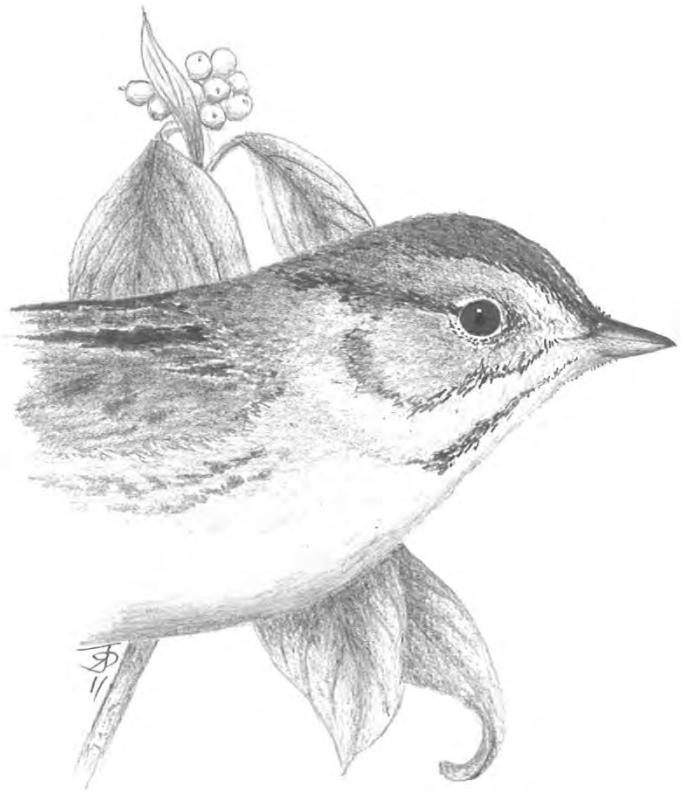
WINTER

Root (1988) reported that the Lincoln's Sparrow wintered north of latitude 35°N only in warm winters. The entire winter range, including the irregularly occupied northern areas, occurs where the average minimum January temperature is higher than −7°C. More regularly frequented wintering areas occur where the minimum January temperature is −1°C. Speirs and Speirs (in Austin 1968) stated that it rarely stayed as far north as New York to winter and its normal winter distribution extends only as far north as Georgia, Kansas, and Missouri (Ammon 2020).

James (1991) considered the Lincoln's Sparrow an occasional wintering species north to Peterborough. Almost all Ontario winter records are from late December and early January with no apparent February sightings (Curry 2006; LaForest 1993; Lancaster et al. 2004; Speirs 1985; Weir 2008). There are records from 31 March in Kingston, which was considered an early spring migrant (Weir 2008) and from 6 April in Hamilton (Curry 2006), which was considered a winter record. It is uncertain whether the Lincoln's Sparrow has ever successfully overwintered in the province. Most records of wintering birds appear to be of autumn migrants that have remained much longer than usual.

Swamp Sparrow

Melospiza georgiana



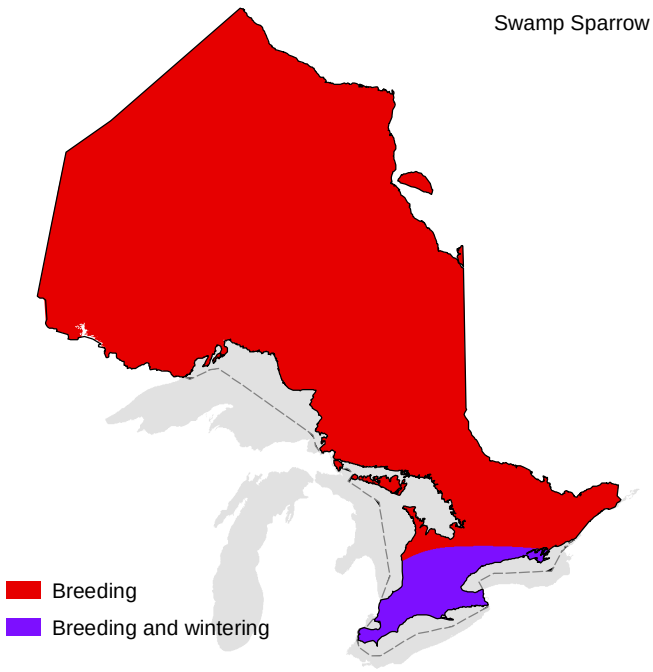
BREEDING SEASON

Habitat Requirements

In Ontario, the Swamp Sparrow breeds in wetlands and is an obligate wetland species throughout its range. Of nests reported in the province, 62.3% were in marshes of sedges, grasses, cattails, and other nonwoody wetland plants, and in marshy edges of lakes and rivers; 19.5% were in bogs and fens with growths of shrubs and small conifers; 13.8% were in shrubby areas in swamps, sedge meadows, and shorelines, and in willow thickets; 2.5% were in wet pastures; and 1.9% were in beaver ponds (Peck and James 1987).

In the Boreal Forest Region near Pickle Lake, James (1980) observed the Swamp Sparrow regularly in small numbers along margins of rivers and lakes. In the Clay Belt, it was common in swamps and marshes, particularly cattail marshes (Smith 1957). In forests in the Clay Belt, it was most

abundant in tamarack or cedar stands, followed by balsam poplar and black spruce stands. It was associated only with wet stands that ranged from nutrient-poor to nutrient-rich (Welsh and Lougheed 1996). Near Hearst, Welsh and Fillman (1980) found it in clear-cuts in lowland coniferous forests 3-17 years old, but it was most abundant in a 5-year-old clear-cut. Erskine (1977) concluded that the Swamp Sparrow and Common Yellowthroat were the most distinctive species of wetter areas in the Boreal Forest Region that were dominated by sedges and low shrubs such as sweet gale and willow. The Swamp Sparrow occurs mostly in bogs and fens.



In Quetico Park in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, the Swamp Sparrow occurred at low density in stands 1-23 years old, was rare in stands 112-176 years old, and was absent in stands 67-73 and 367-370 years old (Apfelbaum and Haney 1985). In Parry Sound and Muskoka districts, it inhabited open sections of bogs, marshes, and sedge meadows (Mills 1981). In Algonquin Park, it was a common inhabitant of low shores and marshes but not so much of wooded swamps (MacLulich 1938). Also in the park, it was the most abundant species in wet bogs and second in abundance in dry bogs. It inhabited areas with shrubs and a few scattered trees where it occurred from the ground to a height of approximately 3 m. The shrub layer was 1 m tall. Records of higher birds were probably of males on their singing perches. It also occurred in ecotones between poplar–white birch forest and bog. Martin (1960) considered it characteristic of bogs. Tozer (2012) reported that it preferred wetlands with alders and cattails in Algonquin Park, but that it also nested in sedge meadows, beaver ponds, bogs, and marshy shorelines.

Near Kingston in the off-Shield portion of the Great Lakes–St. Lawrence Forest Region, the Swamp Sparrow nests in large cattail marshes and at margins of wooded swamps (Weir 2008). It nested in a meadow overgrown with sedges near Fesserton and in a 14-year-old regenerating burn in Durham Region (Banville and Gauthier in Gauthier and Aubry 1996). It significantly preferred rural wetlands over urban wetlands in southern Ontario (Herbert and Mowbray 2020).

In the Carolinian Forest Region, the Swamp Sparrow was very common by the shores of Hamilton Bay where it occurred at the interface between land and water (McIlwraith 1894). Currently in the Hamilton area, it breeds locally in marshes, buttonbush sloughs, and low wet swales (Curry 2006). At Long Point, it favoured dense grassy marshes, particularly those with scattered shrubs or other tall plants. It was much less common in extensive cattail marshes. Small populations occurred in some of the marshy areas lying between the main ridges of the point (McCracken et al. 1981).

In Great Lakes coastal wetlands, the Swamp Sparrow was positively correlated with wetland cover, negatively correlated with the amount of urban land cover in the watershed, and was unaffected by water levels and the amount of agricultural land in the watershed (Tozer et al. 2024).

Throughout its range, the Swamp Sparrow nests in wetlands that may include marshes with expanses of open water, meadow marshes, shrub thicket swamps, bogs and fens, and young regenerating wet clear-cuts and burns. Treed swamps are not used except in open areas at their margins or in larger openings within the forest. In almost all cases, there is standing water in the territory. It is found predominantly in freshwater wetlands during the breeding season, but 1 subspecies confined to the New England coast, the Coastal Plain Swamp Sparrow, breeds in brackish estuarine and riverine marshes. Even this subspecies avoids saline habitats (Greenberg and Droege 1990; Herbert and Mowbray 2020).In Quebec, the Swamp Sparrow is abundant in large marshes along the St. Lawrence River, especially in brackish and freshwater habitat upstream of Trois Rivières. It occurs in pure cattail stands as well as in tangled mixed growths of sedges, reeds, cattails, and shrubs such as willows and alder. In southern agricultural and urban areas, it nests in marshes, pond and stream edges, ditches, and flooded lowlands. It occurs in almost all wetland habitats without a tree canopy regardless of size, provided that there is sufficient plant cover. In the north of the province, it occurs in shoreline scrub, wet meadows, and tamarack peatlands (Banville and Gauthier in Gauthier and Aubry 1996). In British Columbia, wetlands it used for breeding ranged from secluded woodland pools to brush-lined dugouts in open agricultural areas. It often inhabits flooded willow thicket swamps and beaver ponds. Typical nesting habitat includes dense beds of sedges, reed grass, or cattails, or where emergent vegetation meets a fringe of willow, Labrador tea, or other shrubs along margins of wetlands (Campbell et al. 2001).

Marshes and shrub thicket swamps are the most important habitats for the Swamp Sparrow. Although it frequently nests in emergent vegetation lacking shrubs, some shrubs or scattered trees provide singing posts and their presence usually results in higher densities. It nests in pure shrub thickets but is more frequent where there is a mixture of shrubs and emergent nonwoody vegetation. Favoured nesting locations include the interface between wetland emergent and upland shrubby vegetation. In large cattail marshes, it may be uncommon in extensive emergents but abundant at the edge where shrubby growth is available. The Coastal Plain subspecies is typically restricted to a narrow band of shrubby habitat at the interface of upland and marsh habitat. Dykes, roads, and causeways through extensive marshes often create habitat for shrubs and enhance conditions for the Swamp Sparrow. It breeds in a variety of marsh types. In Iowa, it breeds in temporary marshes dominated by reed canary grass and cattails, and in semipermanent to permanent wetlands dominated by cattails, bulrushes, sedges, and woody vegetation. Most occur in the transition zone between wetland and upland habitats. It was significantly more likely to occur in natural than restored wetlands. Restored wetlands lacked low prairie or wet meadow zones, which were present in all natural wetlands. The lack of natural transition zone vegetation was probably detrimental. In many areas, it breeds in freshwater marshes with cattails, sedges, bulrushes, bur-reeds, reed grass, or wild rye grass with an outer ring of willow and alder. In these wetlands, it usually occurs in the inner herbaceous or graminoid ring; the Song Sparrow and Common Yellowthroat inhabit the shrub zone. The Swamp Sparrow regularly breeds in emergent vegetation adjacent to glacial lakes, beaver ponds, and watercourses. In Great Lakes coastal marshes in

Michigan, it nested in wet meadows of grasses, bulrushes, cattails, willows, alder, submergent and floating aquatic plants, open water, and some trees and snags. In Wisconsin, it is common in alder thickets. In Ohio, it nests in swamp loosestrife–cattail marshes, and in communities dominated by rushes and bulrushes, mountain holly and alder, buttonbush and alder, soft rush, and leatherleaf. In the Yukon, it is considered a habitat specialist, nesting in shrubby wetlands with areas of dense emergent vegetation that is usually sedges. The shrub component is usually dominated by willow (Beadell et al. 2003; Delphey and Dinsmore 1993; Greenberg and Droege 1990; Greenberg et al. 2010; Harms and Dinsmore 2015; Herbert and Mowbray 2020; Hoffman 1989b; Riffell et al. 2001; Sinclair et al. 2003; Wetherbee in Austin 1968).

The Swamp Sparrow commonly nests in bogs and fens dominated by shrubs, often with scattered conifers such as tamarack, cedar, or black spruce. Wet bogs support higher densities than drier bogs. Typical shrub species found in territories include Labrador tea, leatherleaf, sweet gale, willow, and black huckleberry. In a Rhode Island bog-fen-swamp complex, few territories extended into the sedge fen, mainly because of the shortage of elevated song posts. Large expanses of unoccupied habitat were dominated by coniferous or deciduous forest communities or shrubs shorter than 0.7 m. In territories dominated by coniferous forest, nests were usually in shrubs or sedges on the edge of, or outside, the forest. It was not observed in the interior of forests or in unbroken forest stands. A 0.36-ha area of short shrubs dominated by leatherleaf and black huckleberry was not occupied, although taller shrubs of the same species were used. Medium-height shrubs were scarce and the short shrub community lacked sedges and open water, which rendered the habitat unsuitable (Dawson 1979; Greenberg and Droege 1990; Herbert and Mowbray 2020; Reinert and Golet 1979).

The Swamp Sparrow occurs much less frequently in brush prairies, recent clear-cuts, and burns (Mossman et al. 1991), and forested areas. Clear-cuts and burns that it inhabits are typically in lowland areas where there is growth of alders or willows with some standing water. In the Prairie Provinces, it occurred in wet forests 15-20 years old that were nutrient-poor (Kirk et al. 1996). In northeastern northern hardwoods, it occurred in 0% of plots in mature undisturbed habitats and 3% of disturbed and successional plots (Noon et al. 1979). In northeastern poplar–white birch stands, it occurred in low density in 2-year-old clear-cuts but not in sapling, pole-stage, or mature forests (Back 1979).

The presence of standing water in or adjacent to territories is a critical habitat component of the Swamp Sparrow. In Pennsylvania, whether a particular spot was defended by a Swamp or Song sparrow could be predicted with 90% accuracy based solely on whether standing water or saturated soils were present. Habitat of the Swamp Sparrow contained 97% water or saturated soils compared with 15.9% in Song Sparrow territories. A beaver pond was initially defended by 5 pairs of Swamp Sparrows. After it was drained it was defended by 5 pairs of Song Sparrows plus 1 pair of Swamp Sparrows in an area that remained flooded. Song Sparrow territories were established 4-6 weeks earlier than those of the Swamp Sparrow. None of the Song Sparrows set up territories in areas that later supported Swamp Sparrows (Greenberg 1988). In a Rhode Island bog, 11 of 18 Swamp Sparrow territories contained standing water. Birds commonly fed at the edge of water. Because not all territories contained water, open water did not appear to be a prerequisite for breeding. At least

early in the breeding season, standing water was characteristic of most communities. Presence of standing water beneath or near 50% of nests suggested that wetness was important in nest-site selection. Reinert and Dinsmore (1979) concluded that shallow standing water was 1 of 3 main habitat requirements for the Swamp Sparrow. Herbert and Mowbray (2020) concluded that water appeared to be the universal factor required for nesting. In British Columbia, Campbell et al. (2001) concluded that shallow standing water and dense cover were required for nesting. Where either of these was absent, so was the Swamp Sparrow. Reinert and Dinsmore (1979) also considered dense cover to be essential.

Suitable song perches are another important habitat feature. The Swamp Sparrow prefers to sing from a perch above the average height of the vegetation. In New Jersey and Delaware, it often used common reed stalks as song posts. In a Rhode Island bog, it used coniferous and deciduous trees with roughly equal frequency. Of 607 observations of singing males, 55% were in trees 2-6 m tall and 32% were in trees taller than 6 m. In 63% of observations, birds sang 1-4 m above ground. The mean height of singing birds in territories dominated by coniferous trees was 4.3 m and the mean height of song posts was 5.9 m. In territories with predominantly shrub cover, the mean height of singing birds was 3.1 m and the mean height of song perches was 4.6 m. Alders, willows, and cattails are often used as singing perches. In Iowa, males used dead and live cattails for singing perches. Females remained under shorter vegetation such as sedges and short cattails (Beadell et al. 2003; Harms and Dinsmore 2015; Reinert and Golet 1979; Wetherbee in Austin 1968).

Most studies concluded that features at the landscape level are unimportant to the Swamp Sparrow in habitat selection. The vegetative characteristics of individual wetlands appear to be most important. In Connecticut, isolation of wetlands appeared to have no effect (Craig 2008). In Michigan, Crozier and Niemi (2003) determined that landscape structure had no effect on it and Fairbairn and Dinsmore (2001b) reached the same conclusion in Iowa. Brown and Dinsmore (1986) concluded that it was more likely to occur in smaller marshes in Iowa when these marshes were in wetland complexes. In Minnesota, it was negatively affected by the proportion of agricultural cover at the 12.6-ha scale. Its frequency of occupancy was 85% at 0% agriculture and declined steadily to 40% at 100% agricultural cover. It was also affected by the amount of wetland at the same scale. Its frequency of occupancy was 50% at 10% wetland coverage, 80% at 40-70% coverage, and 60% at 100% wetland. Individual wetlands or small wetland complexes were adequate for providing habitat (Saunders et al. 2019).

Several studies examined microhabitat preferences of the Swamp Sparrow. In coastal marshes in Delaware, Maryland, and New Jersey, it was most abundant in shrub-cordgrass habitat at margins of wetlands (Greenberg and Droege 1990). Counts were significantly higher in plots with a greater proportion of shrub cover. Its abundance was negatively correlated with the amount of open water. It was positively correlated with common reed, but not significantly. It was negatively correlated with marsh hay and saltmarsh cordgrasses, but not significantly. Because of its preference for areas with shrub cover, suitable habitat extended only 200-400 m outwards from the edge of the marsh-upland transition (Beadell et al. 2003). In tidal marshes in Connecticut, it was associated with cattail marsh and common reed. It appeared to respond to plant structure rather than species because it was found in many different types and sizes of marshes as long as there was tall sturdy vegetation

present to support nests (Benoit and Askins 2002). In Iowa, average habitat characteristics over 2 years did not differ: percent water cover, 21.1% and 26.8%; percent bulrush cover, 31.6% and 31.0%; percent cattail cover, 50.7% and 58.0%; percent cover by sedges, 25.9% and 21.9%; percent cover by reed canary grass, 24.8% and 28.3%; percent cover by woody vegetation, 12.8% and 18.5%; and water depth, 30.1 cm and 34.6 cm. Its abundance was positively correlated with coverage by cattails and negatively correlated with increasing abundance of woody vegetation. Woody vegetation in this area consisted of black willow, sandbar willow, and cottonwood that commonly grew to a height of 6 m and occasionally as tall as 18 m. It avoided tall woody vegetation and was associated more with shrubs that grow to a maximum height of 2 m. Its abundance was positively influenced by water depth and it was commonly found in wetlands with water depths greater than 24 cm. Most were observed in the transition zone between wetland and upland habitats. Harms and Dinsmore (2015) concluded that it was associated with shorter vegetation and increased cover by cattails. Another Iowa study determined that its density was positively correlated with the area covered by weak-stemmed wet meadow vegetation (Fairbairn and Dinsmore 2001b). In Illinois grasslands, its abundance was positively associated with mean number of total contacts, the within-transect heterogeneity index, grass height, and percent live contacts. It was negatively correlated with the mean number of live grass contacts, mean vegetation height, and mean number of live forb contacts. Herkert (1994a) concluded that it preferred areas dominated by live vegetation. In Iowa marshes, its abundance was positively correlated with the percent of wet meadow within the wetland. It was negatively correlated with the amount of mudflats (Fairbairn and Dinsmore 2001b). In Great Lakes coastal marshes in Michigan, it was strongly associated with dense, tall stands of emergent sedges and grasses typical of the most productive wet meadows. It was positively correlated with tall dense grasses rather than bulrushes, with the area of wet meadows, with increasing frequency of deciduous trees and snags, with greater shrub diversity, and with greater frequency of willow (Riffell et al. 2001). In Pennsylvania, habitat of the Swamp Sparrow differed significantly from that of the Song Sparrow for 5 parameters. Values for these parameters for the Swamp and Song sparrows respectively were: percent forb cover, 34.4% and 59.4%; percent rush cover, 25.0% and 7.1%; percent raspberry cover, 0.1% and 2.7%; percent coverage by water, 92.2% and 13.2%; and percent cover by water and saturated soils, 97.0% and 15.9%. Other Swamp Sparrow habitat characteristics that did not differ from those of the Song Sparrow included 30.4% grass cover, 85.1% total ground cover, 0.81 m ground cover height, 0.03 viburnum density, 0.27 meadowsweet density, 0.30 dogwood density, and 7.4 cm water depth (Greenburg 1988). In a Rhode Island bog-fen-swamp complex, the frequency of occurrence of vegetation communities in territories was 91% medium-height shrubs (0.7-1.4 m tall), 100% medium-height shrubs when those in the understorey of coniferous forest are included, 70% shrubs taller than 1.4 m, 83% tall shrubs including those under coniferous forest canopy, 65% sedges, 61% conifers 2-6 m tall, 57% short shrubs (0.4-0.7 m tall), 30% conifers taller than 6 m, and 17% shrubs shorter than 0.4 m. The different height classes of shrubs were all comprised of sweet gale, leatherleaf, and black huckleberry. The frequency of occurrence of vegetation communities in 4-m^2 plots around nests was: 56% medium-height shrubs, 69% medium-height shrubs including those in the understorey, 31% sedges, 14% conifers 2-6 m tall, 14% short shrubs, 8% tall shrubs, and 11% tall shrubs including those in the understorey. Shrubs occurred in all plots with a mean density of 205.6 stems per m^2 and a mean height of 69.8 cm. Sedges (woolly-fruited sedge, beaked sedge, and bog-rush) occurred in 94.4% of plots with a mean density of 345.6

stems per m^2 and a mean height of 58.7 cm. The frequency, mean height in cm, and mean number of stems per m^2 respectively for various species included: 92, 78.0, and 97.2 for sweet gale; 75, 71.3, and 106.8 for leatherleaf; 69, 57.5, and 394.8 for slender sedge; 58, 54.0, and 44.0 for beaked sedge; 47, 72.9, and 25.6 for sweet pepperbush; 42, 38.1, and 36.4 for large cranberry; 35, 30.0, and 18.4 for Fraser's marsh St. John's-wort; 28, 73.8, and 94.0 for bog-rush; 28, 36.1, and 12.0 for green arrow arum; 22, 113.3, and 27.6 for Atlantic white cedar; 14, 66.4, and 21.6 for grey alder; and 17, 33.8, and 4.0 for red maple. The occurrence of medium-height sweet gale in very wet spots probably explained its frequent use as nest cover. This shrub comprised only 7% of the total cover but constituted 39% of cover in nest plots. The occurrence of tall shrubs in 82.6% of territories reflected their importance. The Swamp Sparrow used a wide variety of plant communities and species, but the basic structure of all territories was similar. The species of vegetation is not as important as the height and density of plants in the selection of nest sites (Reinert and Golet 1979).

Most authors concluded that the Swamp Sparrow is a wetland edge species, but 1 study concluded that it avoided edge. In New Jersey and Delaware, Beadell et al. (2003) observed it only within 200-400 m of the marsh edge and it was absent in the wetland interior. Other studies concluded that it was associated predominantly with the transition zone between wetland and upland (Delphey and Dinsmore 1993; Greenberg and Droege 1990; Harms and Dinsmore 2015a). In Iowa, it was positively correlated with the wetland perimeter-to-area ratio. Fairbairn and Dinsmore (2001b) concluded that wetlands with a high ratio had a greater potential to have wet meadow and low prairie vegetation, and that the Swamp Sparrow was a wetland edge species. Riffell et al. (2001) determined that it was negatively correlated with the perimeter-to-area ratio in Great Lakes coastal marshes. They concluded that it avoids edge.

Although 2 studies reported differing conclusions, the Swamp Sparrow is not an area-sensitive species. In Connecticut, Craig (2008) studied wetlands 1.5-131 ha in size and found no relationship between its density and marsh size. It was absent from some of the 3 smallest wetlands even though suitable habitat was present. Also in Connecticut, Benoit and Askins (2002) found no significant relationship between the Swamp Sparrow and wetland size. The smallest wetland where it was found was not larger than expected by chance. In Iowa, it tended to avoid wetlands larger than 20 ha and was detected most frequently in 10-20-ha wetlands. It was seen least frequently in wetlands smaller than 5 ha, but some of these may have been smaller than its territory size. Harms and Dinsmore (2015) sampled wetlands as small as 0.1 ha. Small to intermediate-sized wetlands had a more pronounced transition zone with diverse habitat characteristics that were attractive to the Swamp Sparrow. In Illinois grasslands, the probability of encountering the Swamp Sparrow was influenced by vegetative features only and not by patch size (Herkert 1994a). In Iowa, it was negatively correlated with patch size. Smaller wetlands tended to have a greater proportion of vegetative cover than larger wetlands (Fairbairn and Dinsmore 2001a). In Michigan, Crozier and Niemi (2003) reported that its abundance increased with patch size, but this was true of every species they examined. This is not a test of area sensitivity and one would expect larger patches to support more pairs of a given species simply because there is more available habitat. In Iowa, Brown and Dinsmore (1986) considered it area-dependent because its frequency of occurrence increased with wetland size: 42% in wetlands smaller than 1 ha, 50% in wetlands 1-4.9 ha, 83% in wetlands 5-10.9 ha, and 100% in wetlands 11 ha and larger. It occurred in almost half the wetlands smaller than

1 ha. This suggests that the Swamp Sparrow is not area sensitive. In addition, some of the wetlands sampled were smaller than its territory size.

The female roosts on the nest at night during the incubation and nestling periods. The male roosts in vegetation within the territory at night (Herbert and Mowbray 2020).

Most (75.0%) Ontario nests were slightly elevated over ground or water, with some on the ground. The distribution of elevated nests was 68.3% in sedge or grass clumps, 17.1% in cattails, 13.0% in shrubs, and 1 each (0.8%) in vines in a coniferous shrub and on top of an overgrown stump. Ground nests were under grasses, clumps of other plants, ferns, shrubs, and small trees. Four (9.8%) ground nests were on mossy hummocks and 1 nest had a short tunnel leading to it under the grass. Nests in shrubs were in 6 species of deciduous shrubs (18 nests) and a single nest was in a white cedar. Nests were 0.08-0.9 m above the substrate with most 0.2-0.3 m up (Peck and James 1987, 1998b).

Throughout its range, the Swamp Sparrow nests on the ground or a short distance above water or the ground. In a Rhode Island bog, nests were 0-75 cm above ground (average 30 cm). Fifty percent of nests were over or within 1 m of water. Sweet gale, leatherleaf, or both species together supported 91.7% of nests, sedges supported 63.9% of nests, and 2 nests were in cedars. Nests were well concealed among sedges or in the foliage of shrubs or cedars. They were 24-95 cm below the top of the vegetation canopy and lodged between plant stems rather than anchored to them (Reinert and Golet 1979). In a Pennsylvania marsh, nests were almost never on the ground but between cattail stalks or on bent-down clumps of stalks and leaves. They were almost completely hidden from above by cattail blades. Nests were often directly over water 15-60 cm deep and were usually about 30 cm above the surface of the water (Wetherbee in Austin 1968). Most nests are very well concealed and some are partially or loosely roofed with an entrance at the side. In Delaware, most successful nests were in American three-square bulrush and cordgrass. Old nests are not known to be reused (Herbert and Mowbray 2020).

In some areas, the Swamp Sparrow defends an all-purpose territory where all or most foraging and nesting occurs. At other sites, birds routinely leave the territory to forage. Birds without water in their territory may leave to feed in marshes with standing water. In Massachusetts, both sexes regularly foraged in an adjacent woodlot and in Quebec birds often left their territories to feed in fields and on lawns. Aggression among males is most common shortly after males arrive and during the establishment of territories. Aggression subsides once territories are established. In Rhode Island, a breakdown of territorial defence occurred during the first week of August when nesting activity ceased. When second broods are attempted, territorial singing continues and territories are maintained even if the clutch is unsuccessful. Females usually nest at the periphery of territories and occasionally select a nest site outside their mate's territory. In these cases, the male adjusts his territory boundaries to include the nest. Territory size is variable and probably related to the amount of standing water in it, with those with more water being smaller. Males may shift territorial boundaries in response to changes in surface water, expanding into newly flooded areas. Older males establish territories earlier than yearlings and have larger territories in prime habitat. Territory size appears to be unrelated to vegetation composition. In Algonquin Park, 82 territories averaged 0.15 ha (range 0.02-0.50 ha) and similarly sized territories were reported at Fesserton. In Quebec,

average territory size was 0.15 ha. In Delaware, Maryland, and New Jersey, territories were 0.4-0.5 ha. In Rhode Island, 24 territories averaged 0.17 ha (range 0.03-0.61 ha). Mean territory size in Minnesota was 0.16 ha and 0.13 ha in 2 years (Banville and Gauthier in Gauthier and Aubry 1996; Greenberg 1988; Greenberg and Droege 1990; Herbert and Mowbray 2020; Martin 1960; Reinert and Golet 1979; Willson 1966a).

Swamp Sparrow territories usually do not overlap those of other species, or do so minimally. There is a strong segregation between Swamp Sparrows and Marsh Wrens due to differences in vegetation preferences reinforced by interspecific aggression. The Swamp Sparrow consistently chases Common Yellowthroats from its territory (Herbert and Mowbray 2020). In Pennsylvania, there was minimal overlap in Swamp and Song sparrow territories. Song Sparrow territories were overlapped by an average of 4% by Swamp Sparrow territories and Swamp Sparrow territories were overlapped by an average of 5% by Song Sparrow territories. The study was restricted to Swamp and Song sparrow territories that abutted each other, so the overlap was considerably less than reported. Interspecific aggression was rare and these cases were outnumbered by observations of them feeding or singing close together without aggression. All acts of aggression occurred in the narrow zone of overlap of the territories of the 2 species (Greenberg 1988).

Natal philopatry appears to be low based on limited information. In Rhode Island, 1 of 56 banded fledglings (1.8%) returned (Herbert and Mowbray 2020).

In Rhode Island, 33 of 64 adults (51.6%) returned, including 51.2% of males and 52.4% of females. Fifty-nine percent of males occupied the same territory as in the previous year: 70% in 1 year and 49% in another year. Returning females settled in the same habitat type but usually not in the same territory. Seventy percent of 16 returning females selected nest sites less than 65 m from the previous year's nest. Often the nest was near the edge of her current male's territory; only 18.2% of nests were in the territory of the previous year's nest. Returning females that nested successfully the previous year built significantly closer to their previous nest (average of 42.9 m) compared with 162.0 m for those that had been unsuccessful (Herbert and Mowbray 2020).

Limiting Factors

Eggs are present in Ontario nests from the last week of April until the end of July, mostly from the third week of May until the end of June (Peck and James 1987). In Algonquin Park, eggs are present from early to late June, nestlings are present from mid-June to early July, and fledglings are present from late July to late August (Tozer 2012).

Males begin to establish territories shortly after their arrival and pairs form 1-2 weeks after the arrival of females. Nests are typically built in 3-4 days (range 2-7 days). The first egg is usually laid as soon as the nest is complete, but occasionally 2-3 days elapse before the first egg is laid. One egg is laid per day. Asynchronous hatching suggests that incubation may begin with the laying of the penultimate egg. The incubation period at 1 Ontario nest was not more than 14 days. Incubation in Rhode Island averaged 12.4 days (range 12-14 days); incubation periods as long as 15 days have been reported. The eggs hatch over a period of 36-48 hours. If undisturbed, nestlings remain in the nest 9-13 days, and often leave at age 9-11 days. Nestlings as young as 6.5-7 days may jump from the nest if they are disturbed (Herbert and Mowbray 2020; Peck and James 1987; Reinert and Golet 1979; Wetherbee in Austin 1968).

The Swamp Sparrow often raises 2 broods, particularly in the southern portion of its range. Second broods have been confirmed in southern Ontario, Quebec, and the Maritime Provinces. The interval between fledging of the first brood and initiation of the second nest averages 11.0 days (range 4-23 days). Renesting is common if a nest is lost. Females may lay as many as 4 clutches in an attempt to raise a single brood, occasionally without success in areas where the predation rate is high. New nests are initiated 0.5-5 days after nest loss. Clutches of 4-5 eggs have been reported in Ontario (average 4.21 eggs); most clutches contained 4 eggs. Clutches of 3-6 eggs have been reported throughout its range with 4 eggs most frequent. In New York, the mean clutch size was 4.6 eggs (range 4-6 eggs); clutches of 5 and 6 eggs represented 40% of the sample. The mean clutch size in Pennsylvania was 4.1 eggs. In Rhode Island, the mean clutch size was 4.12 eggs (range 2-5 eggs). May and June clutches were significantly larger (4.4 eggs) than July clutches (3.1 eggs). Second clutches of females were smaller than their first clutch. There is no significant difference in the clutch sizes of yearlings and older females. The mean clutch size of the Coastal Plain subspecies was 3.45 eggs (range 2-4 eggs). Its smaller clutch size may be an adaptation to the stochastic risk of total nest failure by flooding. The reduced clutch size may allow more nesting attempts (Greenberg and Droege 1990; Herbert and Mowbray 2020; Peck and James 1987; Reinert and Golet 1979; Wetherbee in Austin 1968).

Both sexes are capable of breeding when they are 1 year old. Some males are unsuccessful in attracting mates and it is probable that these are yearlings. In a Rhode Island bog, 2 of 18 males (11.1%) were unmated and 1 of 12 males (8.3%) in Massachusetts was unmated (Herbert and Mowbray 2020; Reinert and Golet 1979; Willson 1966a). Pair bonds are maintained throughout the season and occasionally for more than 1 year. The Swamp Sparrow is predominantly monogamous, but some males are polygynous. In Massachusetts, 2 of 12 males (16.7%) were bigamous. In both cases, the 2 females each had subterritories in which they nested and foraged. Males preferred perches between the females' subterritories and visited both areas frequently. In 1 case, one of the females left the territory permanently to feed fledglings. The male's territory then shrunk so that it was not much larger than the remaining female's subterritory. In a Rhode Island bog, 3 of 18 males (16.7%) were bigamous. Another study in that state determined that 3 of 43 males (7.0%) were bigamous. The Swamp Sparrow appears to be one of the marsh-dwelling species that is regularly polygynous. Extra-pair copulations may be common with extra-pair young occurring in 41.6% of broods in 1 population (Greenlaw 1989; Herbert and Mowbray 2020; Reinert and Golet 1979; Willson 1966a).

The Swamp Sparrow forages in moist ground below the shrub and forb canopy, in shrubs and lower portions of trees, on coarse stems of cattails and other marsh plants, along edges of shallow water, and occasionally in open water. It gleans invertebrates and possibly seeds from moist soil while walking, and scratches in leaves for insects and seeds. It frequently climbs up and down stems of shrubs, cattails, and other sturdy vegetation in a mouse-like manner. In water, it may wade breast deep and pick insects and seeds from its surface. One lowered its entire head into the water and appeared to turn over submerged leaves in search of food. It has a longer tibiotarsus and femur than the Song Sparrow and other sparrows. This allows it to hang on to vegetation while leaning to reach the surface of the water, and to wade in water. The Song Sparrow appears incapable of doing this, which may explain why Swamp Sparrow territories typically have water in them and Song Sparrow

territories usually do not. In a Rhode Island bog, the Swamp Sparrow often foraged under the cover of shrubs taller than 1.4 m, but used this habitat less frequently once nesting began. During midsummer when shrub communities were somewhat drier, adults commonly left their territories to gather food for their nestlings in a wet sedge community. These observations suggested that surface water was important in its feeding ecology. A captive bird showed an aversion to taking seeds from its seed cup and preferred to take them from the surface of its drinking cup. This suggested that it naturally gathers seeds in water or that it prefers wet to dry seeds (Carrier 1991; Greenberg 1988; Herbert and Mowbray 2020; Judd 1901; Reinert and Golet 1979; Wetherbee in Austin 1968).

Adults capture damselflies, dragonflies, and aphids from leaves of water-lilies to feed nestlings and fledglings. Nestlings are also fed snails (Herbert and Mowbray 2020).

Adults consume beetles and other aquatic invertebrates, indicating the importance of water to the breeding season diet. During spring and early summer, the Swamp Sparrow is highly insectivorous, with insects constituting about 88% of the diet. It most commonly eats beetles, ants and other hymenopterans, caterpillars, grasshoppers, and crickets. It tends to eat smaller beetles, has been observed picking at dead drying herring, and will eat bread crumbs. It also eats mites, spiders, bugs, and book lice. By late summer and autumn, it is predominantly granivorous with vegetable matter constituting 84-97% of the diet. At this time, seeds of sedges, smartweeds, panic grasses, and vervain are most abundant in the diet. Juveniles and adults also eat highbush blueberry fruits, extracting the flesh and discarding the skin (Harms and Dinsmore 2015; Herbert and Mowbray 2020; Reinert and Golet 1979; Wetherbee in Austin 1968; Willson 1966a). Judd (1901) analyzed 72 stomachs collected from all seasons, mostly from Massachusetts, Connecticut, New York, and Pennsylvania. They contained 47% animal material, nearly all insects, and 53% vegetation, nearly all seeds. Insects consumed included 17% bugs, ants, flies, and small dung beetles; 11% leaf beetles and weevils; 6% parasitic and predaceous insects; and 2% grasshoppers. It exhibited a preference for ants, with 14.3% of stomachs containing these insects. It consumed more smartweed seeds than most sparrows and ate numerous seeds of sedges and aquatic panic grasses that occur in marshes. Giant ragweed seeds were well represented in the diet.

The rate of parasitism by the Brown-headed Cowbird on the Swamp Sparrow varies geographically and depends on the size of the breeding patch (parasitism rates are lower in larger wetlands), and proximity to human settlement, with higher parasitism rates near settlements. In Ontario, 34 of 257 nests (13.2%) were parasitized. Parasitism rates in other areas include: 2 of 64 nests (3.1%) in Rhode Island; 34 of 322 nests (10.6%) in Quebec, 53 of 161 nests (33.0%) in the eastern United States; and 4 of 5 nests (80.0%) in Michigan. The effects of parasitism on the reproductive success of the Swamp Sparrow are unknown. It is capable of rearing cowbirds but it is uncertain whether it can fledge sparrows from parasitized nests (Campbell et al. 2001; Herbert and Mowbray 2020; Peck and James 1998b; Wetherbee in Austin 1968).

Extensive wetland losses occurred in southern Ontario from shortly after forest clearing until wetland policies were adopted in 1986. These policies protected larger and more significant wetlands but smaller wetlands are still subject to drainage or filling for agriculture and other land uses. These losses have undoubtedly reduced the amount of habitat.

The Swamp Sparrow nests a short distance above ground or water. It is highly vulnerable to even modest increases in water levels. Sudden increases in water levels during the breeding season may be one of its greatest limiting factors. Broods of an entire local population may be lost by increasing water levels (Banville and Gauthier in Gauthier and Aubry 1996; Herbert and Mowbray 2020; Wetherbee in Austin 1968). In Ontario, climate change is projected to result in more frequent and serious summer rainstorms. This may exacerbate the risk of flooding of Swamp Sparrow nests.

Practices that remove or thin tree canopy may be beneficial to the Swamp Sparrow, but only if the underlying substrate is wet. These habitats tend to be ephemeral and are suitable for only a few years until the canopy is restored through natural regeneration. Clear-cutting in lowland forests is usually beneficial. In Minnesota, it responded favourably to tree harvest in riparian buffers, and decreased with time after harvest. In the same state, a blowdown in spruce-fir forest created temporary habitat where none existed previously (Banville and Gauthier in Gauthier and Aubry 1996; Burris and Haney 2005; Hanowski et al. 2005). In the Canadian Shield of Ontario, it was significantly less abundant in early successional clear-cuts than in early successional burns but there was no significant difference in its abundance in mid-successional clear-cuts and burns. It was significantly more abundant in early successional than mature stands but equally abundant in mid-successional and mature stands (Zimmerling et al. 2017).

In Minnesota, Hanowski et al. (1997a) examined the potential effects of mosquito control of wetlands with Bti and methoprene. They observed no change in the abundance of the Swamp Sparrow as a result of either treatment.

In Alberta, the Swamp Sparrow was significantly less abundant at seismic lines than in adjacent forest interior when unlimited-distance point counts were used, but there was no significant difference on 50-m or 100-m fixed-radius counts. There were no differences in its abundance at pipelines and well pads than in forest interior adjacent to these features (Bayne et al. 2016).

In British Columbia, grazing of shoreline vegetation by cattle is the most significant cause of habitat degradation for the Swamp Sparrow (Campbell et al. 2001).

Price (2004) predicted that the range of the Swamp Sparrow might contract in southern Ontario if the average summer temperature increased by 2°C. In the Prairie Pothole Region, Harms and Dinsmore (2015) determined that abundance of the Swamp Sparrow was correlated with the amount of rain received that year. Higher water levels resulted in more sparrows. As a result of climate change, wetlands in the eastern portion of this region are projected to have increased water levels and longer hydroperiods; the opposite is predicted for the western portion.

Status

McIlwraith (1894) considered the Swamp Sparrow a common breeder throughout Ontario. Baillie and Harrington (1937) concluded that it was common in suitable habitat throughout the province, west to Thunder Bay District and probably to the Manitoba border. The first atlas confirmed that its distribution included the entire province. There were some gaps in its distribution in southwestern Ontario in intensively farmed regions such as Essex, Chatham-Kent, Lambton, and Huron counties. It was absent in Toronto and portions of Niagara Region (Rising in Cadman et al. 1987). James (1991) considered the Swamp Sparrow a common to abundant summer resident throughout the province.

The second atlas demonstrated that there had been no significant change in the distribution of the Swamp Sparrow since the first atlas. Its probability of observation increased significantly province-wide and in the Canadian Shield and Hudson Bay Lowland. Several scattered areas of high density corresponded with areas with considerable wetland habitat. They included the southern and eastern portions of the Hudson Bay Lowland, including Akimiski Island; in Rainy River and southwestern Kenora districts and along the Manitoba border near Red Lake where there are prairie-like wetlands; in southeastern Ontario and the southern edge of the Canadian Shield; in an east-west band south of Lake Nipissing through Algonquin Park; and along the Niagara Escarpment and in the Dundalk Highlands. It was least abundant in southwestern Ontario (Rising in Cadman et al. 2007).

Population trends of the Swamp Sparrow in Ontario are uncertain because it is not adequately sampled throughout its range. The Breeding Bird Survey (BBS) seldom samples extensive wetland areas and its results may be misleading. In addition, it only monitors the southern portion of its breeding range (Herbert and Mowbray 2020). BBS results indicate annual increases of 1.04% in Canada and 1.11% in Ontario for 1970-2021. For 2011-21, it experienced an annual decrease of 0.388% in Canada and an annual increase of 0.739% in Ontario. The Canadian results were of medium reliability; the Ontario results were highly reliable (A.C. Smith et al. 2023). The Marsh Monitoring Program (MMP) is conducted within wetlands and is better suited for documenting the status of the Swamp Sparrow. Results of the MMP, which was initiated in 1995, indicate a nonsignificant decline in Ontario. The rate of decline is increasing and was 0.2% per year in 2004, 0.4% per year in 2011, and 0.5% by 2012 (Anonymous 2012b; Timmermans et al. 2006; Tozer 2013). The MMP samples mostly the Great Lakes basin and not populations in northern Ontario away from the Great Lakes. In coastal Great Lakes wetlands, it decreased at an annual rate of 0.77% 2011-21 (Tozer et al. 2024). In the Hamilton area, Curry (2006) concluded that populations appeared to have remained stable since McIlwraith's (1894) time. At Long Point, the Swamp Sparrow was not common in 1907 or 1931. Numbers have since increased substantially, probably due to the creation of suitable marsh habitat at the base of the point following construction of the causeway in 1928 (McCracken et al. 1981). Populations have declined in Elgin County. In 1891 it was quite common, especially in larger marshes. By 1954, it was a regular but not common breeder and by 2000 it was an uncommon breeder. Numbers declined due to losses of smaller swales, swamps, and marshes (Lancaster et al. 2004).

POSTFLEDGING PERIOD

After leaving the nest, fledglings remain close to the nest on the ground or in low vegetation. In the first 1-4 days after fledging, they make only short flights between low branches and stalks of grasses and reeds. They spent most of their time on the ground in dense cover. They can fly between shrubs 4-6 days after fledging and may be fed by the female for 6-17 days after fledging. Late in the season, postbreeding birds assemble in loose foraging flocks with other sparrow species (Herbert and Mowbray 2020).

In a Rhode Island bog, fledglings often occurred in shrub communities taller than 1.4 m and dominated by sweet gale, leatherleaf, and black huckleberry (Reinert and Golet 1979). In Michigan, postbreeding birds preferred mature riparian forests to mature upland forests. Riparian forests had

a canopy of aspens with a mix of alders and honeysuckles. Upland forests were dominated by 100-year-old trembling aspen and large-toothed aspen. Captures per 100 net-hours were 1.3 in riparian forests and 0.2 in upland forests; 71% of juveniles were captured in riparian forests (Akresh et al. 2009).

MIGRATION

All populations of the Swamp Sparrow are migratory, with movements occurring at night. A bird banded at Rondeau travelled southeast to the Atlantic coast of Virginia. Band returns suggest that birds retrace the same route each year in both directions. During spring migration, it may stop at specific locations for 1-2 weeks. Autumn stopovers average 1 week but some birds may remain in a single location for 2 weeks before continuing migration. It may associate with other species during migration, especially in autumn. It may be observed in flocks comprised solely of Swamp Sparrows or in the company of Song, Lincoln's, and White-crowned sparrows (Brewer et al. 2018; Greenberg et al. 2010; Herbert and Mowbray 2020; Wetherbee in Austin 1968).

Males arrive in spring about a week earlier than females but in Rhode Island females did not arrive until 3 weeks after males had established territories (Herbert and Mowbray 2020; Reinert and Golet 1979). In southern Ontario, the Swamp Sparrow typically arrives in early to mid-April but may arrive as early as mid-March. Most migrants occur from mid-April to mid-May; most have passed through by the end of May (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). Birds arrive in the southern Shield in late April with migration extending into mid-May (Mills 1981; Tozer 2012).

Wilson and McRae (1993) observed 40 migrants at Ekwan on 4 September. In the southern Shield, autumn migration begins in early September and continues until late October and rarely into November (Mills 1981; Tozer 2012). In southern Ontario, migration extends from mid-September until mid-November (Black and Roy 2010; Curry 2006; Lancaster et al. 2004; Weir 2008).

During migration, the Swamp Sparrow is most frequently seen in dense vegetation near water. In addition to typical breeding habitat, it may occur in old fields, shrubby growth, hedgerows, pastures, raspberry thickets, and even residential shrubbery. During autumn migration, it may form large roosting flocks of 50-60 birds at night and loose foraging flocks of 6-10 during the day (Herbert and Mowbray 2020). During spring migration near Kingston, birds are often seen foraging in dry woodlands (Weir 2008) and autumn migrants at Presqu'ile concentrated in patches of beggarticks (LaForest 1993). Wetherbee (in Austin 1968) stated that spring migrants were found in many swamps where they did not breed. In autumn, some left marshes and occurred in all habitats except deep woods. In British Columbia, most migrants use habitats that are similar to breeding habitat. These include smaller damp areas such as tall grass near water, weedy spots along edges of wetlands, and damp brushy edges of fields. Any shrubby habitat near water may be used such as willow thickets, puddles on a trail through alders and trembling aspen, and a large revegetated burn (Campbell et al. 2001). Suomala et al. (2010) surveyed migrants on 2 islands in the Gulf of Maine. During both migration periods, it was significantly more abundant on the island with shorter trees and a higher density of shrubs than on the treed island.

Some Swamp Sparrows may be killed as a result of adverse weather during migration. More significant are losses due to striking television towers, buildings, and other tall structures (Herbert

and Mowbray 2020). Twenty were killed at the Lennox generating chimneys from 1973 to 1980 (Weir 2008). In the United States at all types of buildings, it was 16.7 times more likely to be killed than average and was the 11th most vulnerable species. It was not among the top 20 species killed at 1-3-storey residences. At low-rises, it was 50.6 times more likely to strike a building than average and 18.1 times more likely to strike a high-rise than average (Loss et al. 2014).

James (1991) considered the Swamp Sparrow a common migrant in Ontario.

Hussell et al. (1992) reported a nonsignificant decline of migrating Swamp Sparrows of 1.7% per year 1961-88 at Long Point Bird Observatory. Trends by period were: 1961-70, +0.9%; 1970-79, –4.2%; and 1979-88, +3.2%.

WINTER

The winter distribution of the Swamp Sparrow is confined to areas below altitude 300 m; highest concentrations occur near water. Peak winter abundance in North America is in bayous along the Louisiana coast with areas of high concentration extending up the Mississippi River (Root 1988). Birds wintering within the breeding range are usually more northern birds that have replaced the breeding population. Peak overwintering within the breeding range occurs during mild winters (Herbert and Mowbray 2020).

Curry (2006) reported that a few overwinter in sheltered marshes along Hamilton Harbour and Lake Ontario. In much of its northern winter range, the Swamp Sparrow prefers cattail marshes even when the water is frozen. Spring-fed marshes may be particularly attractive due to the presence of open water. Open marshes and streams are preferred provided that dense cover is available. It is rarely found in thickets or underbrush far from water. It also inhabits bottomland fields overgrown with broomsedge if the soil is damp and there is a stream nearby. Shrubs, bulrushes, and cattails bordering streams, ponds, rivers, lakes, and reservoirs provide good habitat. It also overwinters in wet fields with shrubby margins, seasonally flooded fields, roadside ditches, and brackish marshes at mouths of major rivers. In North Carolina, it winters in a variety of wetlands in blackberries, asters, horseweed, swamp milkweed, water dock, foxtails, sedges, rushes, willows, red maple, and Manitoba maple in varying combinations. In Texas, it overwintered in coastal prairies dominated by little bluestem, saltmarsh cordgrass, and a mixture of these 2 grasses (Baldwin et al. 2007; Campbell et al. 2001; Herbert and Mowbray 2020; Root 1988; Wetherbee in Austin 1968).

In Maryland, Blank et al. (2011) examined Swamp Sparrow usage of herbaceous buffers planted between row crops and forested wetlands. Some had been mowed the previous autumn and had significantly lower vertical density, maximum height, percent coverage by grass, and percent coverage by forbs than unmowed buffers. Densities per km^2 were 0 in mowed buffers and 55 in unmowed buffers. In Arkansas, Kentucky, and Mississippi, it was significantly more abundant in row-crop fields with a vegetated buffer of native grasses and forbs than in similar fields without buffers. It was significantly more abundant in fields with buffers wider than 23 m than in fields with narrower buffers (Evans et al. 2015).

In Texas coastal prairies, the Swamp Sparrow was positively associated with both little bluestem and saltmarsh cordgrass communities but was uncommon where the 2 species were mixed. It was not associated strongly with prairie species and overwintered in a variety of habitats. It was most

common in areas of dense shrubs. It was most abundant where there were numerous water-bounded areas with the highest concentration of shrubs and small trees. It was unaffected by different frequencies of burning (Baldwin et al. 2007).

Wintering birds often roost in large flocks in shrubs such as willow and buttonbush at edges of marshes (Herbert and Mowbray 2020). In British Columbia, a roosting bird wintered each night in vegetation overhanging a small creek (Campbell et al. 2001).

Swamp Sparrows may return to the same location to winter in subsequent years. In Mississippi, 7 of 27 birds (25.9%) were captured at the same site in the following winter (Herbert and Mowbray 2020).

The Swamp Sparrow has a strong aversion to foraging in open situations. Greenberg (1989) placed feeders within cover and 1.5 m and 7 m from cover. When the feeder was 1.5 m from cover, the visitation rate was significantly lower at 34% of the rate of the feeder in cover. When the feeder was 7 m from cover, it almost stopped visiting it entirely. Only 8% of Swamp Sparrows were observed foraging more than 1 m from cover.

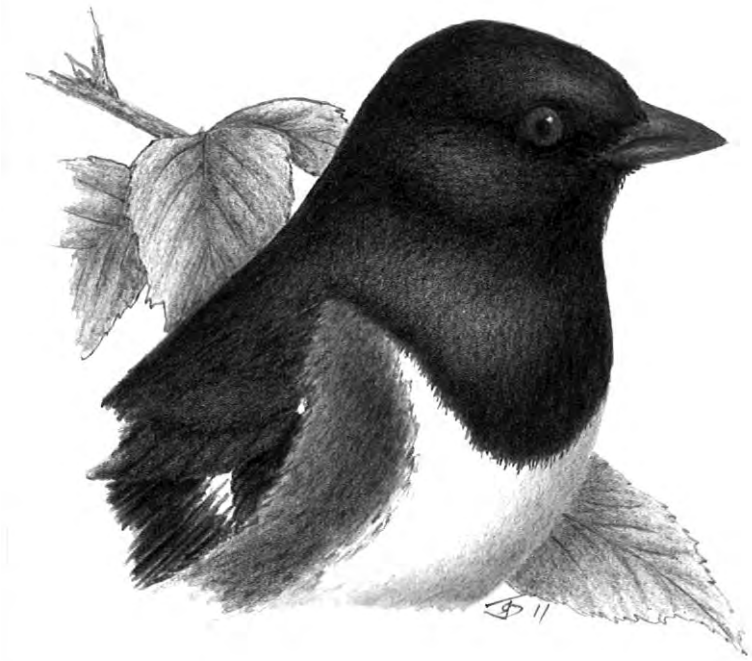
In winter, the Swamp Sparrow eats predominantly seeds and fruits but consume terrestrial and aquatic invertebrates when they are available. In North Carolina, its diet was comprised almost entirely of seeds of sedges, water dock, foxtails, panic grasses, and vervain (Herbert and Mowbray 2020).

James (1991) considered the Swamp Sparrow a rare winter resident in the south north to Barrie and Kingston. Lancaster et al. (2004) stated that it was common in winter in Elgin County, especially when the weather was warm. In Niagara Region, it is a winter straggler, with only 2 records (Black and Roy 2010). On 16 February, approximately 50 were seen near Cayuga (personal observation). The maximum winter count in the Hamilton area is 20 (Curry 2006). The Swamp Sparrow overwinters at Presqu'ile and the Kingston area only occasionally (LaForest 1993; Weir 2008).

Freedman and Riley (1980) analyzed Christmas Bird Count data for southern Ontario for 1929-77. In 1929, it averaged 0-0.01 birds per observer, started to increase around 1953, averaged about 0.11 per observer in 1974, peaked at 0.41 per observer in 1976, and decreased to 0.02 per observer in 1977. They concluded that the increase was possibly due to increased availability of seed crops, weedy fields, or cover.

Eastern Towhee

Pipilo erythrophthalmus

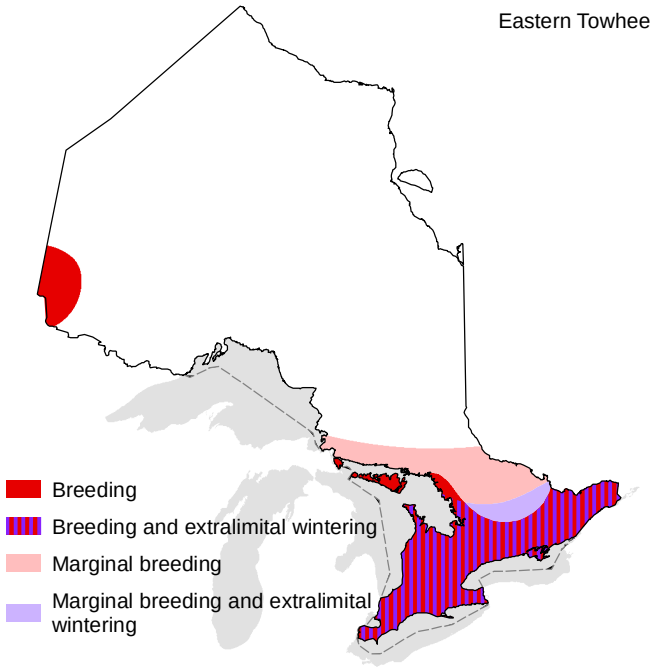


BREEDING SEASON

Habitat Requirements

Ontario Eastern Towhee nests were in coniferous, mixed, and deciduous woods (75.9% of nests); in overgrown fields (17.2%); in vines and shrubby tangles (3.4%); on overgrown bedrock outcrops (2.3%); and on slash on a pipeline right-of-way (1.1%). Wooded areas used for nesting were open; many nests were near woodland edges or clearings. Other nests were near roads or water, indicating a preference for open areas near the nest. Most nest sites were dry and where the ground cover was dense (Peck and James 1987).

Near Parry Sound, low densities of the Eastern Towhee occurred in jack pine stands. These stands had an open canopy and were mixed with a variety of deciduous tree species; bedrock outcrops were common (James 1979a). It nests throughout Parry Sound and Muskoka districts, but is most abundant along the eastern shoreline of Georgian Bay and in the southern part of this area.



It was very common in southwestern Muskoka District where the habitat consisted of bedrock outcrops with scattered common juniper and scrubby forests. Six Parry Sound nests were in similar juniper habitat on bedrock outcrops (Mills 1981). In Algonquin Park, it nests in burns, blowdowns, clear-cuts, open woods, regenerating jack pine stands, and in shrubbery, particularly on the drier side of the park (MacLulich 1938; Tozer 2012).

In Durham Region, it inhabited a black spruce bog surrounded by white spruce and tamarack with a red maple–poplar swamp. It also nested in a forest with an open canopy, areas of standing water, and a rank growth of ferns, raspberries, and other shrubs and saplings. Speirs and Orenstein (1975) considered it a mid-successional species.

Near Hamilton, highest densities occurred on limestone alvars in Flamborough Township. These include stands of scattered red cedar on bedrock but also open deciduous stands (Curry 2006). The bedrock inhibits forest growth but these sites eventually become closed-canopy stands in the absence of fire or forest management. In Niagara Region, it is particularly common in the shrubby habitat of Wainfleet Bog (Black and Roy 2010). At Point Pelee, it nested in low density in mature woodlands containing a high proportion of green ash. These stands are vulnerable to attack by the emerald ash borer and loss of these trees from the canopy may promote shrub growth and enhance conditions for the towhee (Dodds and Otis 2009). It occasionally nests in plantations in Ontario. Suitable plantations include young conifers where a canopy has not yet been established, plantations that have been thinned and have a shrub or sapling layer, and mature mixed plantations of pine and oak (personal observation).

The Eastern Towhee's requirement for open habitat and a dense layer of shrubs is almost universal. Highest densities occur in the pine and oak barrens of New York, New Jersey, Massachusetts, and Wisconsin and pine stands in the southeastern United States. It is often the most abundant species in barrens. Barrens are characterized by pine and oak stands with an open canopy or clumps of these species within an open matrix. Inhabited areas within barrens typically have a dense understorey, often of oak (Brush 1987; Brush and Stiles 1990; Mossman et al. 1991). In Quebec, it avoids wetlands, cultivated lands, and urban areas. Highest densities occur on rock outcrops with scattered red oak, often in association with white or red pine. It prefers dry habitats dominated by pines or oaks. Pine stands on the sand terraces of the Ottawa River provide ideal habitat. It also occurs in other dry brushy habitat such as abandoned fields and pastures (David in Gauthier and Aubry 1996). In Wisconsin, it is common in river terraces in stands dominated by jack pine, red cedar,

and oak (Mossman et al. 1991). In Indiana, it bred at edges of old fields with scattered brush and large patches of Virginia broomsedge, at edges of fields densely covered with raspberries, throughout fields that still supported grasses and blackberries but contained dense stands of small trees, and in fields with about 50% shrub and sapling coverage. Habitats commonly used in the eastern United States include clear-cuts, dry forests provided they have an open canopy and a dense woody understorey, recent burns, regenerating old fields, forest edges and openings, rehabilitated strip mines covered in shrubs, near trails and ditches or other disturbances in forests, roadside thickets, shrubby riparian areas along streams, shrubby sand dunes, oak savannahs, utility rights-of-way, coniferous plantations, and shrubby prairies. Wet habitats are much less likely to be inhabited, but it occasionally nests in bottomland hardwoods and deciduous swamps. Although pines and oaks appear to be greatly preferred, it occasionally inhabits stands dominated by sugar maple and aspens. The towhee has been described as an edge-associated generalist that occupies mesic and xeric habitats characterized by dense coverage near the ground by shrubs or saplings and a well-developed litter layer. The dense low cover may be continuous or discontinuous with patches of more open ground. In Kansas, it inhabited thickets of wild plum, crabapple, fragrant sumac, Osage orange, and locusts. Trees may or may not be present in the territory. If present, they are typically scattered or have an open canopy (Back 1979; Barbour 1951; Bielefeldt and Rosenfield 1994; Capen 1979; Dawson 1979; Dessecker and Yahner 1987; Dickinson in Austin 1968; Fitch 1958; Golet et al. 2001; Greenlaw 2020; Hoffman 1989a; Hurst and Bourland 1996; Karr 1968; Krementz and Powell 2000; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991; Nolan 1963; Noon et al. 1979; Rich et al. 1994; Samson 1979; Shugart and James 1973; Suthers 1988; Taylor and Taylor 1979; Yahner 1986, 1987; Yahner et al. 2002).

McClure et al. (2013a) examined the habitat preferences of the Eastern Towhee at the landscape and territory levels in Alabama. At the landscape scale, habitat was characterized by an avoidance of hardwoods, both on upland sites and on floodplains. Once general habitat had been selected, ground cover was an important criterion in selecting territories. Occupancy was negatively correlated with ground cover and vegetation taller than 7.6 m. It was less likely to use sites with a deep litter layer. It first selected sites that were not within hardwood forests then selected sites with certain characteristics of ground-level vegetation, depending upon whether it was summer or winter. In North Carolina, it was positively correlated with elevation at the 200-m scale, indicating that it is capable of occupying high-elevation landscapes with limited disturbance and only small forest gaps. It was positively correlated with habitat heterogeneity at the 200-m and 1,000-m scales, but not significantly. Heterogeneous landscapes consisted of a mosaic of forest patches, lawns, and pastures with scattered infrastructure. Homogeneous landscapes consisted of unbroken forest tracts. It was not correlated with the amount of exurban development (Gilbert and Ferguson 2019). It preferred areas with 23-58% forest cover in New York (Cunningham and Johnson 2019).

Numerous studies examined the microhabitat preferences of the Eastern Towhee. In Pennsylvania, it was characteristic of the ground stratum, occurring significantly more than expected 0-1 m from the ground and significantly less than expected in other strata (1.1-6.0 m, 6.1-12 m, and above 12 m). It was observed more than expected in large-toothed aspen, pitch pine, white and chestnut oak, and slash; in black cherry in proportion to its availability; and was not observed in red or scarlet oak, scrub oak, and red maple. It was positively correlated with lower

midstorey aspen and the ground stratum, negatively correlated with overstorey oak, and not associated at all with pitch pine canopy. Its density and the number of territories were negatively correlated with the density and basal area of overstorey trees, which included aspen, oak, hickory, and pine. It was positively correlated with the density of shrubs 0.5-1.5 m tall. High shrub density provided suitable foraging and nesting habitat (Yahner 1987). In Massachusetts, significant predictors for the towhee were the amount of litter 0-0.1 m from the ground, medium-height shrubs (0.5-1.0 m), and tall shrubs (2.0-5.0 m). It was negatively correlated with grass 0.1-0.5 m tall. Densities were highest in shrublands that had been burned or left unmanaged (Zuckerberg and Vickery 2006). In Arkansas, it was associated with the densest shrub vegetation (Shugart and James 1973). In Georgia, it was an indicator of shrub habitat (Brittain et al. 2010). In West Virginia, its density was positively correlated with raspberries, black cherry, black locust, grape, and hickory shorter than 3 m. It was negatively correlated with black gum, red maple, spicebush, witch-hazel, and tulip tree. Highest densities occurred on ridgetops where there was the most open canopy, lowest tree density, and lowest small-tree density. It was positively associated with plant species that were most abundant on drier ridgetops and midslope plots and negatively associated with plants that grew in the moister valleys. The negative correlation with small-diameter trees may be because a high density of trees results in less space to carry out activities such as foraging. Raspberries and grapes appeared to provide a more appropriate dense cover close to the ground (Bell and Whitmore 1997). In northeastern mixed-wood forests, Temple et al. (1979) considered it a mid-successional species associated with increasing abundance of sugar maple and yellow birch. In the mid-Atlantic states, its abundance was positively correlated with the amount of canopy coverage by conifers. It was negatively correlated with moisture and overall canopy cover (Robbins et al. 1989). In Maryland, it was positively correlated with tree density and negatively correlated with tree diversity (Lynch 1987). In 1 of 2 years in Illinois, it was positively correlated with hawthorn, black cherry, and basal area and negatively correlated with the number of tree species (Blake and Karr 1987). In pine and oak barrens in Wisconsin, it increased with increasing coverage by tall shrubs (Mossman et al. 1991).

In a Connecticut woodlot over a 59-year period, there was a progressive shift to larger trees, a sparser shrub layer, and a less diverse tree canopy dominated more by oaks and maples due to a severe decline in hemlock. The Eastern Towhee declined within the woodlot, but at a lower rate than it did statewide (Buchanan et al. 2016).

Most authors consider the Eastern Towhee a species that may occur both at forest edges and within the interior of forests (Askins et al. 1987; Austen et al. 2001; Freemark and Collins 1992). In New Jersey, Suthers (1988) considered it an obligate edge species. In Tennessee, it was significantly more abundant at the edge of a forest than in its interior. It was not detected further than 268 m from edge (Kroodsma 1984). In Pennsylvania, it exhibited the greatest horizontal breadth of any species, indicating a lack of specialization with reference to edge (Yahner 1987). In Ohio clear-cuts, Rodewald and Vitz (2005) mist-netted at distances of 20, 50, and 80 m from edge. There were no significant differences in capture rates among distances from edge for either adults or juveniles. Keller et al. (2003) found that it exhibited no edge preference in New York clear-cuts. In North Carolina shrub patches, Shake et al. (2012) found no evidence for an effect of patch shape or edge on the towhee. In New Jersey forests, there were no differences in its abundance on plots in forest edge and forest interior (Rich et al. 1994). In Mississippi, it was absent in fields with no borders and

borders 10 m or less in width, and uncommon in borders 30 m or more in width (Conover et al. 2009). In forested habitat, the towhee may be restricted to edge or occur throughout the forest. This is a function of habitat suitability. If the forest interior has a closed canopy and limited understorey, it is likely to be avoided but the interior of forests may be inhabited if there is a dense shrub layer. In shrubby patches, it occurs throughout with no evidence of avoidance of either edge or interior.

Corbat et al. (1988) and Freemark and Collins (1992) did not consider the Eastern Towhee an area-sensitive species. All researchers agreed except for two. Rodewald and Vitz (2005) mist-netted birds in small (4-8 ha) and large (13-16 ha) clear-cuts in Ohio. There was no significant difference in capture rates of either adults or juveniles in small or large patches. In southern Ontario, its abundance was positively correlated with the amount of forest cover 100 m or more from edge and negatively correlated with forest size, forest cover within 2 km, and the amount of regional forest. Only the latter relationship was significant (Austen et al. 2001). In Illinois, its abundance was unrelated to forest size (Blake and Karr 1987). In red maple swamps in Rhode Island, it was equally abundant in patches smaller than 1 ha, 1-5 ha, 6-10 ha, and 11-20 ha (Golet et al. 2001). In North Carolina, Shake et al. (2012) surveyed patches 0.3-24.9 ha in area and found no evidence of area sensitivity by the towhee. It was also unaffected by the amount of forest cover within 1 km. In Pennsylvania, it was more likely to be captured in large than small patches (Keller and Yahner 2007). In Missouri, Hayden et al. (1985) considered the towhee area sensitive. The smallest patch it occurred in was 2.2 ha and 100% occurrence was attained in forests 42.2-53.6 ha in size. The authors acknowledged that categorizing it as an area-sensitive species was statistically questionable.

The few nocturnal roosts that have been described were 3-5 m above ground in dense foliage. The towhee appears to roost solitarily (Greenlaw 2020).

Of 106 Ontario nests, 84 (79.2%) were on the ground and 22 (20.8%) were elevated in shrubs, trees, vines, saplings, and brush piles. Of 63 ground nests, 60.3% were under or at the base of a tree, shrub, or sapling; 11.1% were amidst plant stalks and leaf litter, 7.9% were in tufts of grass, 6.3% were under fallen branches, 6.3% were among dead limbs and tall grasses, 3.2% were in tangles of grapevines, and 1.6% each were under a log, in a patch of shrubs, and on mosses. Ground nests were often well hidden and 9 were in depressions in the ground. Four species of coniferous trees and shrubs supported 57.9% of elevated nests and 42.1% were in 4 species of deciduous shrubs, trees, and vines. Junipers and hawthorns were the most frequently selected species. Elevated nests were 0.5-2.4 m from the ground, with most 0.6-1.2 m up (Peck and James 1987, 1998b). In Parry Sound District, Mills (1981) reported 6 nests, 4 of which were 0.3-1.2 m from the ground in common junipers and 2 were on the ground.

Throughout its range, the Eastern Towhee either nests on the ground or a short distance above it in shrubs, vines, and saplings. Replacement nests and those at more southern latitudes are most likely to be elevated. In Kentucky, all first nests were either on the ground or on small stumps. Subsequent nests were 0.76-2.84 m from the ground (average 1.37 m). Only 2% of Michigan nests were 0.3-0.6 m from the ground in a shrub or tangle of vines. Ground nests are in a dry spot, usually at the base of a shrub or sapling, or in clumps of grasses and forbs. They may be hidden under brush piles. Nests may be either well concealed or fully exposed, but most are well shaded by overhead vegetation. Elevated nests are usually less than 1.5 m from the ground but 1 was 5.5 m up. In Indiana,

elevated nests were 0.75-3.1 m from the ground (average 1.6 m). It nests both in coniferous and deciduous trees and shrubs, including hophornbeam, white pine, red cedar, multiflora rose, hawthorns, blueberries, oaks, wax myrtle, elm, and shagbark hickory. Tangles of vines such as wild grape, Japanese honeysuckle, and greenbrier are favoured nesting sites. Nests may be elevated in clumps of grasses, on rotting stumps, or among roots of old treefalls. There is no evidence of nest reuse (Barbour 1951; Dickinson in Austin 1968; Greenlaw 2020; Hoyt 1948; Johnston 1993; Krementz and Powell 2000; Nolan 1963; Zimmerman 1989).

The Eastern Towhee defends its territory by singing, chasing, and fighting. In larger territories, males may have 2 activity centres focused on the nest and a foraging area. The females' activity centres are around the nest. In Kansas, some territories contained 2 or 3 shrub thickets separated by a field approximately 150 m wide. Birds regularly flew across the field but never used it. In Pennsylvania, territories were large and often contained different forests: 1- and 5-year-old clear-cuts and 60-year-old uncut stands. In New Jersey mesic oak stands, territories averaged 1.6 ha (range 0.64-2.44 ha); in xeric pine-oak stands, territories averaged 1.2 ha (range 0.71-1.65 ha). In Kansas, territories that were confined to a single shrub patch were 0.8-1.7 ha (average 1.16 ha). Territories that encompassed 2 or 3 discrete shrub patches were larger, with an average size of 2.23 ha (range 1.8-2.7 ha). In Massachusetts pine barrens, average territory size was 0.52 ha. Males may travel as far as 300 m outside their territories to encroach on other males' territories (Corbat et al. 1988; Fitch 1958; Greenlaw 2020; Wasserman 1983). Krementz and Powell (2000) studied daily movement patterns of towhees in mature pine stands and clear-cuts planted with pines in South Carolina. Except for the incubation period when females remained on or near the nest, both sexes moved over the entire stand where they had been captured. Outside the incubation period, only 2 females remained in the same stand and the other 15 moved among stands. Those marked in young stands moved to either intermediate-aged stands 20-35 years old or to mature stands. Birds marked in mature stands moved to intermediate-aged stands. No birds moved to young stands. These were daily movements and were not permanent. Daily movements averaged 99 m (range 39-173 m). The maximum distance moved over the sampling period averaged 464 m (range 110-1,256 m). Daily distances moved were unrelated to sex or stand type. Excursions from the daily activity centres were common, sometimes long, and crossed through different-aged pine stands, with intermediate-aged pine stands being the usual targets of these movements. In pine barrens in Massachusetts, towhee territories were evenly distributed in each year indicating that intraspecific competition was important in determining the dispersion of individuals (Morimoto and Wasserman 1991a). In the same study area, Wasserman (1983) made 10%, 20%, 30%, or 50% of existing food in territories inaccessible. When 0-30% of foraging areas in territories were made unavailable, there was no change in territory size, indicating that adequate food was still available. Only when 50% of foraging areas were made unavailable did males increase the size of their territories. Territories typically contain more than adequate food supplies.

Natal philopatry rates are approximately 2%. In Ohio, 3 of 170 juveniles (1.8%) were encountered as adults and 2 (1.2%) were discovered in the natal clear-cuts (Lehnen and Rodewald 2009b). Schlossberg (2009) reported a natal philopatry rate of 2% based on 1 study of 199 juveniles. In New Jersey, 2 of 108 yearlings (1.9%) returned to breed (Suthers 1988).

In Ohio, 12 of 77 adults (15.6%) returned and 11 (91.7% of returning birds) were encountered in the same clear-cut (Lehnen and Rodewald 2009b). Return rates were 43% in New Jersey and 48% in Pennsylvania. One New Jersey male returned to the same section of a 24-ha oak forest in 5 of 6 years (Greenlaw 2020). Schlossberg (2009) calculated an annual site fidelity rate of 28% based on 2 studies and 206 adults. The low rate of site fidelity may be an adaptation to the temporary nature of its habitat. Most early successional habitats are suitable for only short periods.

Limiting Factors

Eggs have been reported in Ontario nests from the beginning of May until mid-August, with most present from the last week of May until the last week of June (Peck and James 1987). The female starts building the nest approximately 1 week after pairing. Nest construction takes only a few hours, but may be spread over 5 days. As many as 3 days may elapse between nest completion and laying of the first egg but in most cases the first egg is laid the day after the nest is completed. Incubation may start with the laying of the penultimate or last egg. In Ontario, incubation periods of 11-13 days have been reported and 12-13 days have been reported elsewhere. The nestling period is 10-12 days, but young may leave the nest at age 7-8 days if they are disturbed. Although it has been concluded that the breeding season is over in all areas by mid- to late July, later nesting has been reported in Ontario and Virginia (Dickinson in Austin 1968; Gates and Gates 1975; Greenlaw 2020; Johnston 1993; Peck and James 1987).

Egg dates suggest that second broods may be raised in Ontario but this has not been confirmed (Peck and James 1987). David (in Gauthier and Aubry 1996) concluded that it was likely that only a single brood was raised in Quebec due to the shortness of the season. In the northeastern Atlantic states, second broods are undertaken in late June or early July. In the United States, 1 brood is considered likely in the northeast, 2 broods occur elsewhere, and third broods have been reported in Florida. Double broods have been positively confirmed only in New Jersey, Massachusetts, South Carolina, and Kentucky. The rate of second broods was 50% in climax oak forests in New Jersey, 16.7% in Kentucky, and 0% in New Jersey pine barrens. The second clutch is reared in a new nest, and the first egg of the second clutch is laid 7-21 days after the first brood fledges. Replacement clutches are commonly laid in a new nest if the first clutch is lost. The first egg is laid in replacement nests about 9 days after the loss of the first nest (Barbour 1951; Dickinson in Austin 1968; Greenlaw 1978, 2015; Krementz and Powell 2000). Ontario nests had clutches of 3-6 eggs (mode 4 eggs, mean 3.84 eggs; Peck and James 1998b). Throughout the towhee's range, clutches of 2-6 eggs have been reported, with most containing 3 or 4 eggs. Clutch sizes may increase northward, with mean clutch sizes of 2.4 eggs in Florida, 3.0 eggs in South Carolina, 3.4 eggs in New Jersey, and 3.6 eggs in Indiana. Early clutches may contain 0.5-1.0 egg more than later clutches. In New Jersey and New York, mean clutch sizes for early nests were significantly larger in oak-hickory forests (3.88 eggs) than in pine-oak barrens (2.67 eggs), and pitch pine barrens (3.25 eggs). The disparity in clutch sizes was because towhees in forests started nesting 2 weeks before those in barrens due to earlier leaf-out and greater abundance of arthropods in forests. In forests, 4- and 5-egg clutches were prevalent in May and early June; 2- and 3-egg clutches were frequent thereafter (Dickinson in Austin 1968; Greenlaw 1978, 2020; Krementz and Powell 2000).

Both sexes are capable of breeding in their first year. It is likely that all yearling females breed but some yearling males may be unsuccessful in attracting a mate. A New Jersey population consisted of 46 pairs on territories and 15 unpaired males that held territories for a few weeks before disappearing. The mating system is monogamous but 1 case of polygyny has been documented. The pair bond is retained for the entire breeding season, including for replacement nests and second broods. There is 1 case of a pair remaining together for at least 3 breeding seasons and they maintained the same territory in each year. The male guards the female closely once pairing occurs. Guarding is infrequent or absent after egg laying and the male begins to make long excursions at this time. This suggests that extra-pair copulations may be part of the towhee's breeding strategy (Dickinson in Austin 1968; Greenlaw 2020).

A high proportion of the Eastern Towhee's foraging occurs on the ground, where it uses a 2-footed scratching behaviour to displace loose litter on the ground and uncover hidden seeds and arthropod prey. Foraging usually occurs in dense low cover that provides a well-developed litter of deciduous leaves, conifer needles, or a mix of these. It may occasionally feed in the open briefly, but is seldom far from cover. Scratching for food occurs year round, but is especially important in winter when nearly all its food comes from the ground. In late spring and summer, both sexes often search for prey in arboreal foliage, particularly when new leaves are developing or defoliating caterpillars are abundant. In trees, most foraging is by gleaning, but it may also flutter down through the canopy after falling prey or sally from a perch to vegetation that is otherwise out of reach; flycatching is infrequent by males. Other foraging strategies from the ground include stretching or leaping at overhead vegetation and sallying from the ground, sometimes followed by hovering or clinging to the side of a trunk. There are no differences in the feeding behaviours of the sexes (Burtt and Hailman 1979; Greenlaw 2020). In Massachusetts pine barrens, the sexes foraged similarly, feeding 75-80% of the time on the ground. Ten percent or less of foraging occurred at heights of 0.5-1 m, 1-1.5 m, 1.5-3 m, and 3-6 m. No foraging occurred above 6 m. When the towhee foraged above ground, it preferred pitch pine, deciduous trees (predominantly oaks), and scrub oak, and avoided herbaceous species and ericaceous shrubs. It foraged significantly more along the distal half of branches. Females foraged distally significantly more often than males (Morimoto and Wasserman 1991b). In Pennsylvania clear-cuts, it often foraged around slash piles and in aspen stands that were only 1 year old (Corbat et al. 1988). In New Jersey pine barrens, it foraged less in oaks and more in pines as the breeding season progressed. It used oak in proportion to its foliage density in May, but disproportionately less in June and July when arthropod abundance declined in oaks. In a second study area, it used oaks more than expected in May and foraged on both oaks and pines in proportion to foliage density in June and July. It chose tree genera and habitat according to the relative biomass of arthropods in the foliage (Brush and Stiles 1990).

In Kentucky, the diet of 18 nestlings consisted of (by volume) 30.77% caterpillars, 15% adult beetles, 10% orthopterans, 7.22% lepidopteran cocoons, 6.68% beetle larvae, 3.61% spider eggs, 2.78% adult spiders, 0.83% fly pupae, 0.61% snails, 0.28% crustaceans, and 21.39% inorganic matter. Other food items in the diet of nestlings include moths, ant pupae, and fruits of wintergreen, blueberries, and huckleberries (Barbour 1951; Dickinson in Austin 1968; Greenlaw 2020).

Adults eat a mixture of animal and plant foods. It has been suggested that the towhee eats everything it uncovers while scratching in the litter, but it demonstrates clear preferences for certain food items and the proportions of animal and vegetable matter in the diet change seasonally. The diet, by volume, in the northeast in January and February consisted of 34.5% invertebrates and 65.5% plant material. The invertebrates included 27.2% adult insects, 4.1% immature insects, 0.4% spiders, and 2.5% millipedes. In March and April, the diet consisted of 59.1% invertebrates and 40.9% plant material, with the invertebrates including 48.7% adult insects, 7.2% immature insects, 1.2% spiders, and 0.4% harvestmen. In May and June, the diet consisted of 36.2% invertebrates and 63.8% plant material, with invertebrates including 29.6% adult insects, 5.4% immature insects, 0.3% spiders, 0.5% millipedes, and 0.3% snails. In July and August, the diet consisted of 21.4% invertebrates and 78.6% plant material, with invertebrates including 16.8% adult insects, 4.0% immature insects, 0.1% spiders, 0.3% millipedes, 0.3% centipedes, and 0.1% harvestmen. In September and October, the diet consisted of 2.4% invertebrates and 97.6% plant material, with the invertebrates including 0.6% adult insects, 0.8% spiders, 0.6% millipedes, and 0.4% centipedes. The most frequently consumed insects included beetles (14 families documented in the diet, including ground beetles and others found in litter such as weevils and leaf beetles), 5 families of grasshoppers and crickets, stink bugs, 3 families of bugs, hymenopterans (4 families including ants and wasps), and 5 families of moths and caterpillars. It eats beetles more frequently than any other insect group and particularly favours weevils. Moths, caterpillars, bugs, and ants are important in the diet and it also eats scale insects, cicadas, leafhoppers, carpenter ants, and sawflies. It also eats numerous spiders and snails and lesser numbers of harvestmen, millipedes, centipedes, isopods, ichneumonid wasps, cockroaches, and walkingsticks. It prefers ant pupae to adults. At 1 site in New Jersey where ants were abundant in the litter, they comprised 40% of the adult diet in early summer but were unrepresented in the diet in another area where ants were less prevalent. When adults are feeding nestlings, they eat invertebrates almost exclusively. Caterpillars are the favoured food at this time. Although hairy caterpillars, such as those of the gypsy moth, may be consumed, hairless caterpillars are greatly preferred. Plant material is particularly important in the diet in late summer and autumn, but some is eaten at all times of the year. The towhee occasionally eats soft foliage buds, young furled grass stems, and the soft flower buds of Virginia spring-beauty. It has been reported that it eats small acorns that have fallen to the ground, but this appears to have been documented only once. Most plant material that is eaten consists of seeds or fruits. Favoured seeds are those of ragweeds, smartweeds, foxtails, panic grasses, and docks. In autumn, it may eat seeds of wheat, oats, and flax. Frequently consumed fruits included those of strawberries, huckleberries, blueberries, bayberry, and blackberries. It also eats the fruit of red elderberry and mulberries. It rarely eats vertebrates such as snakes, lizards, and salamanders. On an annual basis, the diet consists of approximately 30% animal matter and 70% vegetation (Bell and Whitmore 1977; Dickinson in Austin 1968; Greenlaw 1978, 2020; Holt 1918; Stutchbury et al. 2005a).

The Eastern Towhee is a common host of the Brown-headed Cowbird. The towhee is an acceptor species that has not been documented rejecting eggs, covering eggs, or abandoning the nest in response to parasitism. The impacts of parasitism on the towhee are uncertain, but it is capable of fledging both species. It is likely that cowbirds remove some towhee eggs, thereby decreasing productivity. In Ontario, 30 of 164 nests (18.3%) were parasitized. Parasitism rates in other

areas include 4 of 109 nests (3.7%) in Georgia and South Carolina, 15 of 15 nests in Kansas resulting in 50 cowbird fledglings, 13 of 24 nests (54.2%) in Pennsylvania, 21 of 42 nests (50.0%) in Wisconsin, 2 of 6 nests (33.3%) in Michigan and Kentucky, 22 of 103 nests (21.4%) in Ohio, 3 of 41 nests (7.3%) in West Virginia, 3 of 57 nests (5.3%) in Missouri, 4 of 81 nests (4.9%) in Massachusetts, 2 of 58 nests (3.4%) in New York and New Jersey, 2 of 4 nests (50.0%) in Illinois, 2 of 12 nests (16.7%) in Indiana, and 2 of 9 nests (22.2%) in New York (Barbour 1951; Bell and Whitmore 1997; Greenlaw 2020; Hahn and Hatfield 1995; Kilgo and Moorman 2003; Nolan 1963; Peck and James 1998b; Rivers et al. 2010; Roach et al. 2018; Robinson 1992; Rothstein 1975).

Habitat loss and degradation are probably the greatest limiting factor to the Eastern Towhee. Direct habitat loss may occur due to urbanization, tree planting, and conversion of shrublands to agriculture. Urbanization may result in increased pressures due to cowbird parasitism and predation by cats, raccoons, and skunks. Habitat is also impaired or lost as forests mature and lose their woody understorey (Anonymous 2003; Hagan 1993; Greenlaw 2020; Krementz and Powell 2000).

Browsing by the white-tailed deer has the potential to decrease the density of shrubs and saplings, thereby degrading habitat for the towhee. In 1 Virginia study area, the ground cover in forests was almost completely eradicated because of overgrazing by deer. Towhees nested there in roadsides that still had shrubby borders (Johnston 1993). In Delaware, Tymkiw et al. (2013) compared towhee abundance in areas of low (10 or fewer per km^2), moderate (11-19 per km^2), and high (20 or more per km^2) deer densities and found no significant differences. In much of the eastern United States, deer densities have been increasing at a rate of 6% per year, consistent with the hypothesis that deer browsing caused the decline in towhees. In New Hampshire, both deer and towhee populations are declining, so deer are unlikely to be the sole reason for the decline of the towhee (Hagan 1993).

In Massachusetts, Zuckerberg and Vickery (2004) examined the effects of management for grassland birds on the towhee. Prescribed burning, repeated mowing, and brush cutting were conducted to maintain grassland habitat. In 2 of 3 breeding seasons, the towhee was more abundant in control or burned shrublands than in shrublands that had been mowed. It was most abundant in areas that had been burned, with no significant difference between controls and mowed areas. Abundance decreased with the frequency of mowing. After a single mowing event, abundance dropped by about 25%. After a second mowing, abundance was 47% of that in unmowed areas. Abundance was greatest in shrublands that had been burned or left unmanaged. It generally benefits from burning, but the frequency of burning must be considered. In Florida, densities were highest about 4 years after fire in scrub pinelands, followed by declines afterwards. In Indiana oak savannahs and woodlands, its density peaked at intermediate fire frequencies of about 4 every 15 years. Numbers declined once fire frequency increased above this level (Greenlaw 2020; Grundel and Pavlovic 2007a). In North Dakota, it responded favourably to fire, but occurred more frequently only after severe fires. It was most abundant in areas that burned 5-10 years prior to sampling (Rose and Simons 2016).

The Eastern Towhee benefits from forest management because opening the canopy promotes shrub growth. In New York, Keller et al. (2003) determined that it responded positively and immediately to clear-cutting, remaining abundant for 6 years after cutting. It was in a guild of early

successional species that gradually declined as leaf area and canopy increased. In Pennsylvania, Stribling et al. (1990) compared stand improvement cuts where snags were cut to those where snags were retained. Stand improvement involves removal of dead, dying, diseased, suppressed, or low-quality trees. Towhees were more abundant in stands where snags were retained. Snag retention resulted in greater availability of woody plants 0-1.5 m from the ground, and this enhanced habitat. In aspen and oak forests in Pennsylvania, 60-year-old forests were divided into 4-ha blocks and these were subdivided into 1-ha squares. Over time 0-3 of the squares in each block were cut. The towhee was 1 of 3 species that increased significantly and immediately after cutting. It was absent in 0% cuts, became the dominant species in 50% cuts, and was encountered more than expected in 75% cuts. It increased on the site but decreased regionally during the same timeframe (Yahner 1993, 2003). In the same general area, Corbat et al. (1988) found no difference in its abundance in cut and uncut areas. This was because mature aspen stands had a dense understorey of scrub oak so that cutting did not increase shrub density or habitat for the towhee. Five-year-old stands were used more than their availability, 1-year-old stands were used in proportion to their availability, and mature stands were used less than their availability. Aspen stands were used more than their availability and oak stands were used less than their availability. Habitat preferences were related to shrub density.

Windthrow, tree diseases, and defoliating insects may open the forest canopy, promote shrub growth, and improve towhee habitat. In West Virginia, gypsy moths retarded succession by decreasing the number of large overstorey trees and increasing the amount of understorey vegetation and the number of regenerating small trees. Density of the towhee increased 9 fold after the outbreak and its density was significantly higher on all 42 plots. These results support the hypothesis that forest succession is a major cause of the decline of the towhee (Bell and Whitmore 1977). The towhee is likely to benefit from the invasion of the emerald ash borer in Ontario, which is killing large numbers of ash trees.

Farwell et al. (2019) studied the effects of shale gas infrastructure (well pads, access roads, and pipelines) on the Eastern Towhee in contiguous forest in West Virginia. It exhibited no significant response to any of these features.

In South Carolina, nests suffered very high rates of predation. Towhee nests are especially vulnerable to predation because they are close to the ground. Where predators include high populations of snakes and mammals, predation may be a contributing cause of towhee declines (Krementz and Powell 2000).

In New York and New Jersey, food availability affected the timing of nesting and reproductive rates. Invertebrate biomass densities were significantly higher in an oak-hickory forest than in pine barrens. In the oak-hickory forest, the first 10% of nests were initiated by early to mid-May. The first 10% of nests in pine barrens were not initiated until the last half of May and mostly in the last week of May. Clutches in the oak-hickory forest were significantly larger than those in the pine barrens. Second broods were fairly common in the oak-hickory forest but rare or absent in the pine barrens. These differences were due to plant phenology and the subsequent relative abundance of food. In the oak-hickory forest, an herbaceous layer appeared in late April and early May but not on the sterile sandy soils of the barrens. Invertebrates occurred in concert with the development of leaves and

herbaceous vegetation. In the barrens, foraging birds seldom captured food above ground from late April to mid-May buts such manoeuvres were frequent at this time in the oak-hickory forest. Spring weather may also affect leaf-out, invertebrate availability, and towhee fecundity. Early springs advance the onset of breeding and result in increased production of fledglings. Late springs delay breeding and few young are likely to be produced (Greenlaw 1978, 2020).

In Chicago woodlots, Schneider and Miller (2014) examined the effects of invasive shrubs on the towhee. It was negatively associated with litter. Sites dominated by buckthorn were characterized by very little ground litter. There were almost no remaining native shrubs in the area, so buckthorn appeared to provide a nesting substrate. The scarcity of litter suggests that food resources may have been low for the towhee in this habitat.

Near lead mines in Missouri, elevated lead concentrations in soil near towhee nests decreased the probability of a female fledging a young from 51% to 15%. Most nest failures were due to predation, suggesting that lead affected birds' behaviour and activity at nests, or affected nest-site quality (Thompson et al. 2024).

Price (2004) concluded that the range of the Eastern Towhee might increase in southern Ontario if the average summer temperature increased by 2°C.

Status

The status of the Eastern Towhee prior to deforestation by European settlers is uncertain. Extensive tracts of mature forest would have provided little habitat but forest fires would have provided suitable conditions. It is likely that it benefitted from forest clearing. It appears as though its current range extends further northeast than it did historically. McIlwraith (1894) reported that it was unknown from the Ottawa area and David (in Gauthier and Aubry 1996) stated that it did not occur in Quebec at the turn of the 20th century. In Elgin County, it was common in 1891 and 1954 but was only a local breeder in 2000, suggesting that it had declined (Lancaster et al. 2004). Baillie and Harrington (1937) considered it a fairly common breeder throughout southern Ontario north to Muskoka District and east at least to Leeds County and Ottawa. They had records from Algoma District suggesting that it bred further north. Godfrey (1986) reported that it occurred north to Sudbury, North Bay, and Ottawa. The first atlas confirmed that the towhee was widespread south of the Canadian Shield, including on Manitoulin Island. In the Shield portion of the Great Lakes–St. Lawrence Forest Region, it was most widespread along the eastern Georgian Bay shoreline with scattered records further east and north to north of Lake Nipissing and in the Rainy River area. Extensive forested areas, such as Algonquin Park, and intensively farmed areas, such as portions of Essex and Lambton counties, were avoided. Some areas of apparently good habitat were unoccupied and it was less abundant than anticipated. There was some evidence that it was declining in the northern portion of its range and it appeared to be extirpated in Sudbury District (Inch and Inch in Cadman et al. 1987). James (1991) considered the towhee an uncommon summer resident north to Muskoka District and Ottawa, rare to Sudbury, and a vagrant to Fort Severn and James Bay.

The second atlas revealed that there had been no significant change in the distribution of the Eastern Towhee since the first atlas. Breeding was confirmed in western Rainy River District, representing the most northern occupied area in the province. There was no difference in its

probability of observation province-wide, but significant declines occurred in the Carolinian Forest Region and the Shield portion of the Great Lakes–St. Lawrence Forest Region. Most losses in the Shield were in more southern areas, possibly a result of forest maturation. There was considerable turnover in the squares that were occupied between atlases, possibly reflecting the transitional nature of its preferred habitat. There were several areas of high abundance. The largest area was from Prince Edward County east to the United Counties of Leeds and Grenville. Other areas of high abundance included the eastern shoreline of Georgian Bay, the Carden Plain, and the northern shoreline of Lake Erie from Rondeau to the Norfolk Sand Plain. Its areas of high abundance corresponded well with those of other shrub-dependent species such as the Field Sparrow (Timpf in Cadman et al. 2007).

Hagan (1993) analyzed population trends of the Eastern Towhee in the United States using the Breeding Bird Survey (BBS), autumn migration data from the Manomet Bird Observatory in Massachusetts, and Christmas Bird Counts (CBC). BBS data indicated that significant declines had occurred in 18 states and Ontario since 1966. The most severe declines occurred in the New England states where decline rates were higher than 5% per year. The rate of decline in Ontario was 3.2% per year. Of 52 species analyzed for their trends at Manomet, the towhee showed the most dramatic decline. In 1970, 2.7 were caught per 1,000 net-hours compared with 0.3-0.5 in 1988. CBC results showed significant declines of 2-5% per year, stronger declines than indicated by the BBS. This was expected because the CBC measures populations of both northeastern breeders and southeastern residents. Greenlaw (2020) summarized BBS data and concluded that the towhee had been declining since 1966. From 1966 to 1979, significant declines were observed in 21 states and provinces compared with only 10 states 1980-95. Despite the declines, it still remains widespread and common in some habitats. BBS results for 1970-2021 indicate annual decreases of 1.55% in Canada and 1.62% in Ontario. For 2011-21, it increased at annual rates of 1.11% in Canada and 1.3% in Ontario. The long-term trends were highly reliable; the short-term trends were of medium reliability (A.C. Smith et al. 2023).

Hanberry and Thompson (2019) compared BBS trends and forest composition over time in the eastern United States. They attributed the decline of the Eastern Towhee in part to the reduction in the amount of open forests and increase in the amount of closed-canopy forest. Savannahs and open woodlands were formerly more abundant but have undergone succession to closed-canopy forests.

POSTFLEDGING PERIOD

Brood division may occur once young leave the nest. If the female initiates a second brood, the male cares for the first brood. Adults continue to feed the young 3-4 weeks after they leave the nest, but the average duration of dependence is 30 days from hatching (Greenlaw 1978, 2020). In Rhode Island, fledglings 0-6 days out of the nest could not fly above 2-3 m and were mostly confined to the ground or to making short jumps. Seven to 13 days out of the nest, they could make lateral flights of 5-15 m but were unable to reach the canopy or high perches. By 14-20 days out of the nest, they were capable fliers that could reach high perches and the canopy. By 21 or more days, they were fully independent and received little or no parental care, but adults still occasionally moved with the young (Brenner and McWilliams 2019).

During the postfledging period, adults, young, and family groups may be common in young clear-cuts and on shrubby hydro transmission line corridors. In Pennsylvania, Stoleson (2013) captured 7 adults and 32 juveniles in 3-6-year-old clear-cuts that supported 10-15% residual basal area. In adjacent mature forest, 1 adult and 1 juvenile were captured. In Ohio, Vitz and Rodewald (2003) captured 19 adults and 100 juveniles in clear-cuts 4-7 years old. Marshall et al. (2003) captured 16 adults and 2 juveniles in 4-10-year-old clear-cuts in Virginia and West Virginia. In Missouri, Porneluzi et al. (2014) netted in clear-cuts 2-15 years after cutting and captured 13 towhees. Four were captured 2 years after cutting, 5 were captured 3 years after cutting, 2 4 years after cutting, 1 5 years after cutting, and 1 10 years after cutting. None were captured 5-8 and 11-15 years after cutting. There were too few captures to determine statistical significance, but 92.3% of captures were 2-5 years after cutting. On a shrubby hydro transmission line corridor, it was one of the most abundant species during the postfledging period; adults, juveniles, and family groups were common. None were seen in the forested habitat that the corridor passed through (Yahner et al. 2002).

Brenner and McWilliams (2019) studied postfledging movements and habitat use of the Eastern Towhee in Rhode Island in areas managed for the American Woodcock. Management provided early successional forests by clear-cutting, brush thinning, and mowing. Six study areas 4 km^2 in area were selected that consisted of recent (less than 15 years) forest clear-cuts 0.76-10 ha. These were classified as areas of high likelihood or low likelihood of woodcock use. High-likelihood areas had more early successional forest or upland shrubs, more hydric soils, and more mature deciduous or mixed forest. Low-likelihood areas had more mature coniferous forest and less early successional forest and upland shrub areas. Adult towhees were radiotracked from the first week that their young fledged for at least 3 weeks. Home range size of adults averaged 2.8 ha (range 0.78-8.06 ha), with no significant differences in high-likelihood (3.09 ha) and low-likelihood (2.37 ha) landscapes. Environmental variables did not explain home range size, which was determined by the fledgling development phase and landscape type. During the early, mid-, and late-fledging periods, there were no significant differences in the daily distance travelled by adults in high- and low-likelihood landscapes. Adults moved 37-47 m per day during these periods. Once fledglings reached independence, adults in high-likelihood landscapes travelled significantly further (49.5 m) than those in low-likelihood (36.7 m) landscapes per day. Most (54.5%) adult towhee locations occurred within young forest and scrub, with 26.2% of locations in mature upland forest and 14.6% in grasslands and fields. Adults in high-likelihood landscapes used less young forest and scrub than those in low-likelihood landscapes during the early fledgling stage (51.7% compared with 69.3%) and the mid-fledgling stage (43% compared with 60%). There was no significant difference in use of young forest and scrub by adults in high-likelihood and low-likelihood landscapes during the late fledgling (55% compared with 60%) and independence (55.4% compared with 60%) stages.

MIGRATION

The Eastern Towhee is a nocturnal migrant; it is unknown if it migrates in flocks or singly. At stopover sites, it often associates with the Dark-eyed Junco and White-throated Sparrow. Most birds in the northern portion of the breeding range migrate to the southeastern states to winter, although a few stay over winter even in the extreme northern portion of the range. More birds remain northward in mild than in severe winters. Southeastern and Gulf State populations are largely sedentary or

partially migratory (Greenlaw 2020). One banded in southeastern Ontario was recovered in Tennessee. One banded at Long Point was recovered almost due west in Michigan and another travelled almost due east to New York. These recoveries were 1-3 years after banding, so they may have travelled south for the winter before being recovered (Brewer et al. 2018). McIlwraith (1894) observed that the towhee always arrived at London and Chatham in spring before it did in Hamilton. He concluded that it probably entered the province in the southwest. In New Jersey and New England, autumn migration spans 4-5 weeks compared with 2-3 weeks for spring migration (Greenlaw 2020).

At Long Point Bird Observatory (LPBO), males arrived before females and adults arrived before yearlings. Mean capture dates of males were 21.2 April for adults, 25.2 April for yearlings, and 23.3 April for birds of undetermined age. For females, mean capture dates were 0.4 May for adults, 2.3 May for juveniles, and 2.0 May for birds of undetermined age (Stewart et al. 2002). In Massachusetts, males arrived an average of 4.8 days before females. Over a 32-year period, neither sex arrived significantly earlier with time; the timing differential between the sexes was not related to any climate variables (Bauböck et al. 2012). In Ontario, birds arrive in late March or early to mid-April and the peak of migration occurs in the first half of May (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

No information is available on the relative timing of autumn migration of sex or age classes. In Rhode Island over a 45-year period, migration was delayed by about 5 days per decade, the greatest increase of all species examined. During this period, the temperature increased by 1.44°C. Smith and Paton (2011) concluded that these results were likely specific to their region. In the southern Shield, autumn migrants occur from late August until October (Mills 1981; Tozer 2012). In the Kingston area, migration is from late August until mid-October (LaForest 1993; Weir 2008). In the southwest, migrants arrive from mid-September to early or late October and leave early to late November, with occasional stragglers until early December (Black and Roy 2010; Curry 2006; Lancaster et al. 2004).

The Eastern Towhee was more likely to be found in fragmented than forested landscapes during migration in Pennsylvania. There is more edge habitat in fragmented landscapes which may be attractive to the towhee (Keller and Yahner 2007). Migration habitat is similar to breeding habitat, but it often occurs in isolated habitat during migration that is too small or wet to support breeding. These may include wooded fencerows, cemeteries, blackberry or cherry thickets or other shrubby patches in residential suburban areas, and wetland thickets (Greenlaw 2020). In Pennsylvania during spring migration, detections per 100 m of transect totalled 0.01 in forest and 0.36 in shrubs; captures per 1,000 net-hours were 0.6 in forest and 4.2 in shrubs. It was significantly more abundant in shrubby areas than in forests (Smith and Hatch 2008). During spring migration in Wisconsin and Minnesota, the towhee was one of few species that was significantly more abundant in mature upland forests than mature floodplain forests. Upland forests were dominated by oak and elm. Floodplain forests were dominated by silver maple and green ash. Despite the fact that floodplain forests leafed out earlier and may have supported more arthropods, it selected the drier oak forests (Kirsch et al. 2013).

The Eastern Towhee is vulnerable to being killed at towers and other tall structures during migration, particularly in autumn (Greenlaw 2020). At the Lennox generating station chimneys near Kingston, 0 were killed in autumn 1973-82 but 3 were killed during spring migration (Weir 2008).

James (1991) considered the towhee an uncommon migrant in Ontario.

At LPBO, the towhee declined at a significant rate of 4.1% during migration 1961-88. Trends by period were: 1961-70, +0.4%; 1970-79, –14.8%; and 1978-88, –3.4%. More recent data from LPBO indicate long-term declines of 2.8% per year in spring and 2.4% in autumn (Anonymous 2003; Hussell et al. 1992).

WINTER

Wintering towhees avoid areas with an average minimum January temperature lower than –7°C. It occurs in high concentrations in areas of mixed and deciduous forests where there is an average minimum January temperature warmer than about –4°C. Root (1988) concluded that it was most likely to be found in hedgerows, thickets, shrubby woodlands, swamps, thickets along forest edges, and in the understorey and second growth of semiopen forests.

At the landscape level in Alabama, the towhee avoided areas dominated by hardwoods. In the breeding season, it was more likely to colonize sites with dense ground cover and less likely to colonize areas with deep leaf litter. Habitat selected in winter differed from breeding habitat. It was negatively associated with dense ground cover in winter. This may be related to the increased importance of plant material in the winter diet or the need for leaf litter for nesting and foraging in summer. McClure et al. (2013a) concluded that sites managed for breeding towhees were unlikely to support any in winter.

In Kansas, wintering towhees inhabited blackberry thickets at or near edges of woodlands. Within a day, they shifted among thickets and spent little time in other habitats. They were most often seen outside thickets when the ground was covered with snow and food was scarce (Fitch 1958). In Kentucky, it inhabited an area that was predominantly forested and another area that was predominantly herbaceous. It was associated mostly with forest edges, but also with streams. Six of 9 flocks were found most often along edges of large streams. The other 3 flocks frequented streams that were often dry. They were attracted by the abundant food and cover that was available along watercourses; presence of water was not essential (Barbour 1941). In winter, the Eastern Towhee continues to be strongly associated with shrubby habitat. In Kentucky, it selected shrubby habitat (45% of locations compared with 35% availability of habitat). Blackberry thickets were the most abundant habitat (39% coverage) but least used (19%). When snow was present, it moved into wooded habitat. In the north, it is frequently associated with bird feeders, including those in residential areas provided that shrubby habitat is nearby. In the Hamilton area, it winters in sheltered valleys. Wintering birds are occasionally seen in winter north and east of their breeding range. Some older reports may refer to the Spotted Towhee which occasionally wanders eastward in winter. Prior to 1995, the Spotted and Eastern towhees were considered conspecific and were called the Rufous-sided Towhee (Curry 2006; David in Gauthier and Aubry 1996; Dickinson in Austin 1968; Martin et al. 2021; Greenlaw 2020). In Arkansas, Kentucky, and Mississippi, it was equally abundant in row-crop fields with and without buffers of native grasses and forbs (Evans et al. 2015).

In most cases, the towhee winters solitarily, although it is often associated with the Field Sparrow, Song Sparrow, White-throated Sparrow, Dark-eyed Junco, and Northern Cardinal. In Kentucky, towhees occurred in flocks; 9 flocks averaged 17 birds (range 8-27). These consisted mainly of males, with females representing only 23.7% of flocks. This was probably because females migrated further south. One flock of 27 birds had a home range of 4.4 ha; another flock of 20 had a home range of 12.5 ha. In the latter area, food and cover plants were much sparser. The area used by a flock was determined by flock size, the amount of cover present, the amount and quality of food available, and weather conditions (Barbour 1941). In Kansas, the average home range size of individual males was 7.0 ha (Fitch 1958). At a Kentucky site, the mean home range was 7.31 ha and the mean core area was 1.52 ha. The mean overlap of the home range of any 2 individuals was 3.16 ha (36%) and the mean overlap of core areas was 0.42 ha (24%). Occasionally 3 home ranges overlapped (Martin et al. 2021).

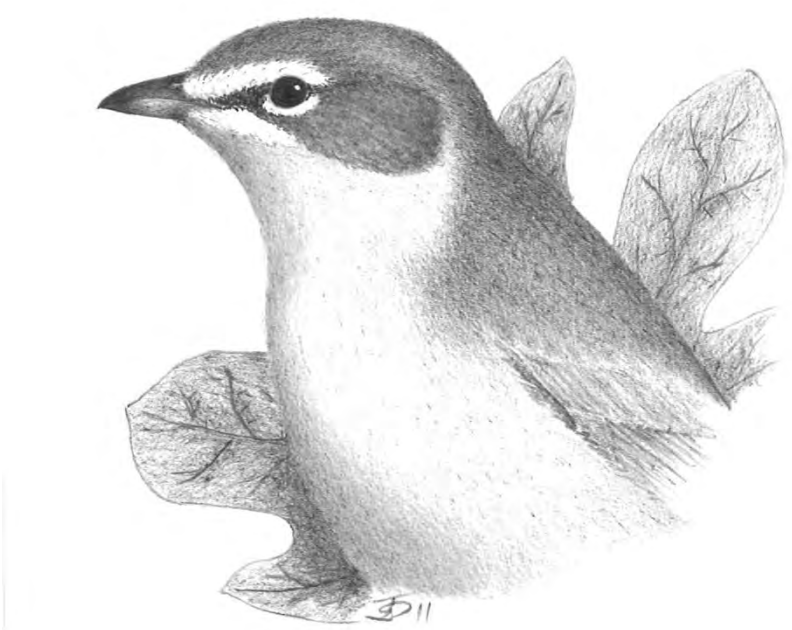
During winter, the towhee mostly scratches the ground to obtain food, even where food is abundant at bird feeders. In autumn and winter, the diet consists mostly of vegetable matter, including seeds of grasses and herbaceous species, grains, fruits, and fallen acorns. In winter, it eats berries of Canada moonseed and holly. At feeders, mixed seeds and millet are preferred food items. Less frequently, it consumes sunflower seeds of any type, cracked corn, suet, peanut butter, bird puddings, water, canary seed, milo, and wheat (Breiding 1946; Dunn and Tessaglia-Hymes 1999; Fitch 1958; Petrides 1942). In the north, the towhee may be dependent upon feeders for winter survival (Greenlaw 2020).

In Illinois, Graber and Graber (1979) documented the effects of severe winter weather on the towhee. Prior to and after the storm, it was absent in upland forest and urban residential habitats. In bottomland forests, it declined from an initial density of 43.0 per km^2 to 5.2 per km^2 after the storm, a decline of 87.9%. They found 4 dead towhees and concluded that it had suffered very high mortality. It is particularly vulnerable to snowstorms (and probably ice storms) because it is a ground feeder.

James (1991) considered the towhee rare in winter in the south north to Sault Ste. Marie and Sudbury, with scattered records in the north from Geraldton, Thunder Bay, and Marathon. It is possible that some of the northern records may have been Spotted Towhees. McIlwraith (1894) had no winter records for the province. In Hamilton, 1, 2, or more Eastern Towhees are reported each winter. March observations suggest that most of these successfully overwinter (Curry 2006). In the Kingston area, it was recorded in 20 of 60 winters (Weir 2008). Most winter observations are at feeders.

Yellow-breasted Chat

Icteria virens

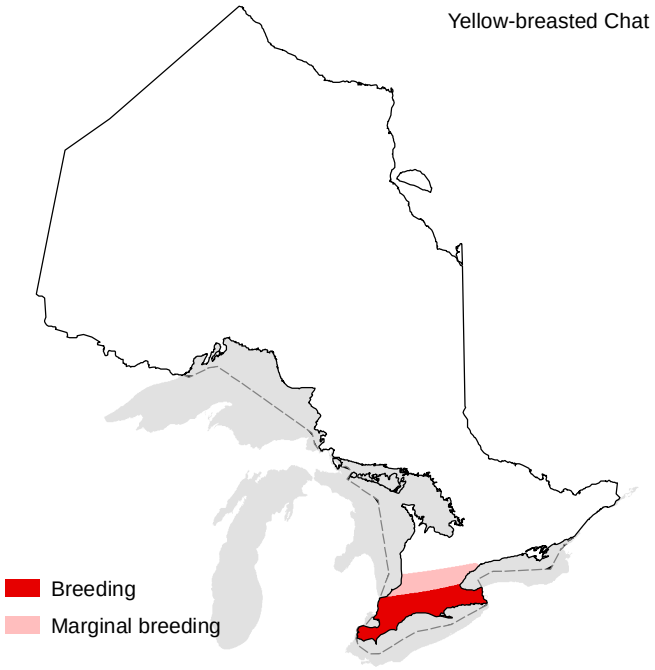


BREEDING SEASON

Habitat Requirements

In Ontario, the Yellow-breasted Chat nests regularly only in the Carolinian Forest Region with scattered and irregular breeding in the Great Lakes–St. Lawrence Forest Region south of the Canadian Shield. Nests have been reported in shrubby fields and pastures overgrown with dogwoods, hawthorns, raspberries, roses, grapes, and willows; and in open deciduous woods and clearings within woods with dense undergrowths of raspberries, grapes, and other shrubs (Peck and James 1987).

Ontario habitats include early successional areas that may include dense low deciduous or coniferous vegetation. Coniferous vegetation within territories is often red cedar but the Yellow-breasted Chat may frequent very young coniferous plantations that are still overgrown with shrubs. It may inhabit abandoned agricultural fields, railway and hydro transmission line rights-of-way,



fencerows, forest edges and openings, and thickets near streams, ponds, and swamps. It occurs in young shrublands where there are scattered deciduous trees and patches of herbaceous vegetation. The most consistent nesting locations in the province are at Point Pelee and on Pelee Island. Tangles of raspberries and grape vines are common features of territories. Habitat at Point Pelee consists of regenerating abandoned farmland. On Pelee Island, prime habitat is shrub alvar that is succeeding to treed alvar. At Rondeau, it was unknown as a breeding species until a severe windstorm opened up the forest canopy and created suitable habitat. In Niagara Region, it nests in shrubby thickets in and adjacent to Wainfleet Bog. A nest discovered in 1884 in Waterdown was in an abandoned mill race that had grown up in dense raspberry thickets. Almost all nesting territories contain patches of very dense shrubs. These consist either of raspberry stands or taller deciduous shrubs covered with grapes or other vines (Austen et al. 1994; Black and Roy 2010; Cadman et al. 2011; Kirk and Pearce 2011; Lancaster et al. 2004; McIlwraith 1894; Peck and James 1998a).

There are 2 subspecies of the Yellow-breasted Chat and both occur in Canada. The eastern subspecies occurs in Ontario and the eastern United States west to Texas. The western subspecies occurs in British Columbia, Alberta, Saskatchewan, and the western United States (Eckerle and Thompson 2020). Habitat structure used by the 2 subspecies is similar. Western birds nest almost exclusively in riparian shrub thickets that are permanent and do not regenerate into forests or other late-successional habitats. The eastern subspecies nests in early successional habitats dominated by shrubs. These regenerate into forests unless they are managed or the tree canopy is opened up as a result of fire, wind, insect damage, tree diseases, or harvesting. In Ontario, alvars provide the most permanent habitat but eventually even these become treed. The eastern subspecies nests in rehabilitated strip mines, burned and clear-cut forests, regenerating old pastures, young plantations that are still dominated by shrubs, sapling-stage forests, forest openings, shrubby hedgerows and roadsides, abandoned orchards, lightly grazed pastures, shrubby ravines, forest edges, shrubs adjacent to watercourses and water bodies, shrub thicket swamps, and hydro and railway rights-of-way. In the east, dense patches of raspberries or hawthorns may be preferred, but it may inhabit any area of very dense shrubs. In British Columbia, the chat nests almost exclusively in patches of wild rose. Hawthorn thickets are available there but not used. It also nests in thickets dominated by snowberry, willow, and other shrubs with an open overstorey of birch or cottonwood. Thickets that it uses are typically in low-elevation riparian areas such as streams, oxbows, and other wetlands. In Alberta, it is found mostly in the understorey of riparian poplar forests in major river valleys or in

dense tangled shrubbery along smaller watercourses that lack tree cover. It occasionally nests on shrubby slopes in upland areas, but upland areas usually are not suitable habitat. Mostly it uses thickets dominated by buffalo-berry, hawthorn, rose, willow, and birch. In Saskatchewan, it nests along major watercourses and in dune complexes where it selects the densest tall shrubby vegetation, including hawthorn, willow, Saskatoon, chokecherry, and buffalo-berry. In North Carolina, numbers observed during the breeding season in different habitats included 3.96 in dry thickets, 2.92 in wet thickets, 1.11 in pine-hardwood forest, 0.37 in floodplain forest, 0.20 in oak-hickory forest, and 0 in pine and beech forests. In Indiana, the chat preferred to nest in fields that supported grasses and blackberry thickets with dense stands of small trees 1-7 m tall. It was also present in old fields with poor soils due to erosion, thin ground cover, few shrubs, and with large patches of Virginia broomsedge; and in fields with dense coverage by blackberry, rose, herbaceous plants, and numerous small trees 0.3-5 m tall. In the early 20th century, it occasionally nested in villages but villages and rural residential lots no longer provide suitable habitat (Alterman et al. 2005; Bent 1953; Brooks 1940; Buffington et al. 1997; Campbell et al. 2001; Chapman 1907; Dennis 1958; Eckerle and Thompson 2020; Fitch 1958; Graber et al. 1983; Harrison 1984; Hurst and Bourland 1996; Karr 1968; Kirk and Pearce 2011; Miño et al. 2011; Nolan 1963; Parnell 1969; Ricketts and Ritchison 2000; Shugart and James 1973; Thompson and Nolan 1973).

The chat has been described as an obligate open-country species, nesting in areas with an open overstorey and a shrubby understorey, with its population density directly related to shrub density to a height of 4.5 m. Open areas of grasses and forbs are tolerated within the territory as long as dense shrub thickets are nearby. Once a tree canopy forms, habitat becomes marginal or unsuitable (Eckerle and Thompson 2020). In the east, most suitable habitat is short lived. Populations peak when dense shrub thickets with scattered trees are available and decline when trees become dominant. On Illinois rehabilitated strip mines, the population increased to a maximum in shrub habitat that was 1.5-4.6 m tall 14-20 years after mining and then declined. At peak populations, the oldest trees were 10 years old and no chats remained once trees were 37 years old. In New York clear-cuts, it occurred at high density 2-9 years after cutting and began to decline in the tenth year (Graber et al. 1983; Karr 1968; Keller et al. 2003; Kirk and Pearce 2011).

At the landscape level, the percent forest cover within the landscape did not appear to have any effect on shrub patch occupancy by the chat in North Carolina (Shake et al. 2012). The landscape of southern Ontario is ill suited to supporting the Yellow-breasted Chat. It consists predominantly of blocks of agricultural land, forest, or urban areas. There are few large patches of shrubs and these tend to either regenerate into forest or be converted to agricultural or urban land uses (Cadman et al. 2011).

Microhabitat preferences of the Yellow-breasted Chat are similar for the 2 subspecies. In British Columbia natural habitats, territories that had a higher percentage of shrub cover within 50 m were occupied in earlier years than those with less shrub coverage. In restoration sites, areas that had lower shrub coverage were not occupied later than those without higher shrub coverage. Vegetation at the nest site did not influence daily nest survival or parasitism rates (Forrester et al. 2020). In Texas, its abundance was positively correlated with the number of shrubs and shrub stems, foliage density at heights of 1 and 3 m, and percent coverage by pines 5-16 cm diameter at breast

height (DBH). It was negatively correlated with vegetation height, canopy closure, foliage density 12-15 m from the ground, percent coverage by pines 17-32 cm DBH, and number of stems 17-32 cm and larger than 32 cm DBH. It was associated with low shrubby vegetation, increasing density of shrub stems, foliage density within 1 m of the ground, number of shrub species, and sapling pines. The chat and White-eyed Vireo were associated with foliage density at 1 and 3 m and favoured later successional stages than the Prairie Warbler (Conner et al. 1983). In Kentucky, foliage cover below 2 m was significantly greater at nest sites than other areas of the territory; nest sites had more lateral cover below 1 m. Differences in these parameters had no effect on nest success (Ricketts and Ritchison 2000). In Arizona, the chat was associated with dense low shrubs (Brown and Trosset 1989). In Missouri, Burhans and Thompson (1999) measured vegetation parameters in an 11.3-m radius around nests and the patch dimensions in which nests were located. Nest patch diameter varied from 0.3 to 65 m (median 5.5 m). They grouped patches into large (5.5-m diameter and greater) and small (less than 5.5-m diameter). Large patches were selected significantly more for nesting (52% of nests in large patches) than small patches (19% of nests). The chat tended to place nests in larger patches with more small stems than those in unused sites, but patch size was the only variable distinguishing nest sites and random sites. Nest predation was lower but parasitism rates were higher in large than small patches. Large patches may have made it more difficult for predators to find nests, but they tended to have more large stems that provided perches for cowbirds. Predation and parasitism rates cancelled each other out so that there was no difference in success rates of nests in large and small patches. In Tennessee, it selected areas with dense overstorey vegetation and an open subcanopy layer. Understorey plants were typically smaller than normal. These habitat features were often in areas that had been burned. It was correlated with the foliage, branch, and biomass of trees 1.2-8.4 cm and 8.5-22.8 cm DBH, the number of trees 8.5-22.8 cm DBH, and the foliage, branch, bole, and stump biomass of trees larger than 22.8 cm DBH (Anderson and Shugart 1974). In the mid-Atlantic states, it was positively correlated with canopy cover and percent coverage by conifers. It was negatively correlated with slope, moisture, the number of trees, and trees larger than 38 cm DBH (Robbins et al. 1989). In British Columbia, Campbell et al. (2001) reported nests in thickets 9-195 m^2 comprised predominantly of roses. Rose height within used thickets averaged 1.25 m and large shrubs were usually about 3.5 m tall. Trees growing close to or in the thicket did not exceed 6 m. It was absent where pathways or cattle trails dissected the thicket or where there was a tall overstorey of trees. In British Columbia territories, the average cover consisted of 48% shrubs, 31% trees, 20% grasses and forbs, 1% bare ground, and 1% other cover. Wild rose was the dominant shrub with an average coverage of 30%. Alder was the main tree in the subcanopy and constituted 30% of cover in 20% of territories. Dominant trees included balsam poplar, birch, and willow. Vegetation parameters were measured in 50-m radius plots within territories and in random areas. Percent coverage by shrubs (43.9% in territories and 32.4% in random areas) and percent wild rose coverage (27.3% in territories and 18.4% in random areas) were significantly higher in territories. The percent coverage by trees (30.0% in territories and 35.3% in random areas), coverage by grasses or forbs (23.7% in territories and 28.7% in random areas), and coverage by balsam poplar (5.9% in territories and 10.3% in random areas) were significantly lower in territories. Vegetation was characterized in 5- and 11.3-m radius plots around 238 nests. Wild rose was the dominant species in both-sized plots and covered 41-57% of 5-m plots and 32-48% of 11.3-m plots. There were significant differences between the 2-sized plots. Coverage by wild rose and snowberry

was significantly higher in 5-m plots. Coverage by birch, balsam poplar, willow, other trees, grasses and forbs, bare ground, and other cover was significantly lower in 5-m plots than 11.3-m plots. Nest patches had higher percent coverage by wild rose, red-osier dogwood, and willow and a lower percent coverage of bare ground, grasses, and forbs than random areas within territories. The chat consistently selected patches of wild rose with a specific mix of shrubs and avoided sparsely vegetated areas. Trees were a distinct component of the territory, but tended to be distant from the nest site. Grasses and forbs were always part of the territory, but presence of dense shrubs was more important (McKibbin and Bishop 2010). In Texas, nests were in sites with greater concealment at nest level and with more vines and less grass below the nest (Novak et al. 2016).

Some studies concluded that the chat avoids edge and is thus a shrubland-interior species; other research found no evidence of edge avoidance. In Maryland and Delaware, it was equally abundant in riparian vegetation 50-800 m wide. This was forested habitat so the study did not deal with edge avoidance in shrub patches (Keller et al. 1993). In Ohio, Rodewald and Vitz (2005) set mist nets in a clear-cut 20, 50, and 80 m from the edge of a mature forest. There were no differences in habitat, fruit abundance, or arthropod abundance with distance from edge. Capture rates for juveniles per 100 net-hours were 1.5 at 20 m from edge, 2.1 at 50 m from edge, and 2.7 at 80 m from edge. Capture rates at these distances for adults were 1.0, 1.2, and 1.8. Habitat within 20 m of forest edge was used about half as much as areas 50-80 m from the same edge, suggesting edge avoidance. In Missouri, the area within 20 m of edge constituted 45% of the available habitat yet supported only 27% of nests. Habitat 21-40 m from edge represented 31% of the habitat and supported 37% of nests; the area more than 40 m from edge comprised 24% of the habitat and supported 36% of nests. Results within 20 m and more than 40 m from edge were significantly different from expected values. The chat preferred to nest in areas more than 40 m from edge and avoided areas within 20 m of edge. Habitat preference was not correlated with nest success and edges did not act as an ecological trap. Daily nest predation rate was lower within 20 m of an edge than more than 40 m distant from edge (Woodward et al. 2001). In North Carolina, Shake et al. (2012) assumed that it was an edge-avoiding species and predicted that it should decrease in irregularly shaped patches with a high shape index. They found no evidence for an effect of patch shape on occupancy. The most linear patch in their study area was approximately 30 m wide and it supported chats. They concluded that edge effects were not important but that patch size was. In Kentucky, it readily occupied linear strips less than 10 m wide that were larger than 0.5 ha and located along fencerows, roadsides, and edges of woodlots. Daily survival rates of nests in linear habitats were similar to those in larger, more rectangular habitats (Ricketts and Ritchison 2000). In British Columbia, the mean distance of 238 nests from patch edge was 26.9 m (McKibbin and Bishop 2010). The Yellow-breasted Chat is not an obligate shrubland-interior species, but there are areas where it is less abundant close to edge than in the interior of patches. Where edge avoidance occurs, it may be related to predation and parasitism pressures or to microhabitat.

Some studies determined that the chat is mildly area sensitive and others found no evidence of area sensitivity. In North Carolina, Shake et al. (2012) studied patches 0.3-24.9 ha (mean 6.1 ha). Occupancy rates of the smallest patches were low and patch size was a good predictor of chat occupancy. They estimated a minimum-area requirement (probability of occupancy of 50%) of 2.3 ha and an optimal area (90% probability of occupancy) of 4.4 ha. In Ohio, it was significantly more

abundant in large (13-16 ha) than small (4-8 ha) patches. Although patch size was a good predictor of abundance, productivity was similar in small and large patches (Lehnen and Rodewald 2009a; Rodewald and Vitz 2005). In Virginia, Dennis (1958) did not record it in small isolated patches of suitable habitat that were 1.2 ha or smaller. In Arkansas, it was common in 10-16-ha clear-cuts with residual seed trees. It nested in only 1 of 21 group-selection cuts and it was the largest cut at 0.79 ha. The other 20 cuts were less than 0.40 ha. Alterman et al. (2005) concluded that cuts this size were probably too small to support the chat. In British Columbia, Morgan et al. (2007) studied chats in 4 large (15-70 ha) riparian patches and 5 patches smaller than 2 ha. All sites were occupied, but incubation occurred later in the small isolated patches. This suggested that larger patches were preferred habitat that filled up earlier, forcing late arrivals to nest in small patches. In Kansas, one nested in a thicket that was only 0.36 ha and well separated from other suitable habitat (Fitch 1958). In Kentucky, it nested in patches smaller than 0.5 ha, but these were surrounded by old-field habitat (Ricketts and Ritchison 2000). The similarity of the surrounding habitat may have made these small patches more attractive. The minimum patch size that the chat will inhabit probably varies depending upon factors such as its local abundance, whether it is in the core or periphery of its range, and abundance of suitable habitat within the landscape. In Ontario, where the chat is rare and at the northern edge of the range and where suitable habitat is rare, it is likely that larger patch sizes will be necessary to attract it. The management plan for this species in Canada recommends maintaining minimum patches of 4 ha or more of suitable habitat until it is demonstrated that it successfully uses smaller areas (Cadman et al. 2011).

Ontario nests were in shrubs and vines, typically in dense growth, at heights of 0.3-1.8 m, with most 0.9-1.2 m from the ground. Shrub species supporting nests included 38.5% raspberries, 15.4% grape vines, 15.4% dogwoods, and 7.7% (1) in each of hawthorn, cedar, fragrant sumac, and common juniper (Peck and James 1987, 1998a).

Throughout its range, the Yellow-breasted Chat nests close to the ground in shrubs and vines and occasionally in tree saplings. Eastern nests have been documented in wild plum, sumac, raspberries, grape vines, roses, honeysuckles, dogwoods, black locust, red cedar, hawthorns, birches, huckleberry, hazel, crabapple, willows, white cedar, hackberry, ash, maples, gooseberry, elms, and holly. Raspberries are a common nest substrate in the east and supported 27.3% of Illinois nests. Almost half of Kentucky nests were in raspberries. Of 246 nests in British Columbia, 59.3% were in wild rose, 11.4% in snowberry, 3.3% in red-osier dogwood, 2% in poison ivy, 1.6% in smooth sumac, 1.2% in red raspberry, and 0.8% in dead shrubs; 1 nest each (0.4%) was found in Canada thistle, trembling aspen, Saskatoon, chokecherry, and birch. Forty-two nests (17.1%) were in a combination of 2 intertwined plant species and one was in a combination of wild rose, snowberry, and bracken fern. Other species that were intertwined as part of the nest support included balsam poplar saplings and rough horsetail. Nests were typically supported by stems smaller than 2.5 cm in diameter; 97-99% of stems in a radius of 25 cm below the nest were of this size. Average characteristics of nests were: nest-shrub height, 177.7 cm; shrub width, 82.8 cm; 92.0 cm of vegetation above the nest; 31.2 cm to the shrub edge; 63.4% nest concealment; 269.1 cm to the nearest patch edge; 5.4 stems smaller than 2.5 cm bracing the nest, 0.1 stem larger than 2.5 cm bracing the nest, and 98.9% of stems in a radius of 25 cm from the centre of the nest smaller than 2.5 cm. In New Mexico, the chat nested disproportionately more in Russian olive than its abundance. It is common in monotypic

stands of this nonnative shrub in Idaho. It was probably selected because its spreading growth pattern and thorns provide good protective cover. There was no difference in nest success rates in Russian olive and native shrub species. It appears to select species that provide the densest vegetation for nest concealment, and these species vary geographically. In most cases, the nest is shaded and well concealed. The chat tends to nest in the lower half of shrubs, typically at about 30% of shrub height. The overall range of nest heights is 0.15-2.4 m, but average nest height is usually under 1 m: 0.84 m in Illinois, 0.79 m in British Columbia, 0.79 m in Kentucky, 0.92 m in Texas, 1.0 m in Maryland, and 0.9 and 0.62 m in 2 Indiana study areas. Nests are not reused following predation or fledging but different females may build nests in the exact locations in different years. One pair began building a nest in a nest box. The box was blown down in a thunderstorm and subsequently replaced, but the chats did not return (Bent 1953; Campbell et al. 2001; Chapman 1907; Dennis 1958; Eckerle and Thompson 2020; Graber et al. 1983; McKibbin and Bishop 2010; Nolan 1963; Petrides 1938; Ricketts and Ritchison 2000; Stoleson and Finch 2001).

In Virginia, chat territories were clumped, with pairs congregating in a restricted area while identical surrounding habitat was unoccupied. The unoccupied habitat was rather limited in extent (Dennis 1958). Territorial aggregation has not been identified by other researchers, but is possible due to its mating system. Early arriving males may range over areas as large as 5 ha, but the defended area shrinks as more birds arrive. Despite defence of territories, intrusions by other birds of both sexes occur regularly; consequently, territory sizes are consistently smaller than home ranges. Territory boundaries may shift during the season. If 1 male shifts his area of high activity, neighbours may intrude into his former territory. When a neighbouring pair disappears, its territory may be absorbed by others. In Illinois, 18 territories were 0.4-1.4 ha (average 1.0 ha). In Virginia, territories were 0.51-1.01 ha; home ranges were much larger but their size could not be quantified. In Indiana, mean territory sizes over 4 years were 1.12, 1.22, 1.17, and 1.58 ha (overall average 1.24 ha). Mean territory size in 1 British Columbia study was 0.37 ha. One Virginia territory was estimated at 0.15 ha, but this may have been an underestimate. Territory size in another British Columbia study averaged 0.25 ha; 0.22 ha in isolated patches smaller than 2 ha and 0.29 ha in patches 15-70 ha. In a small tract of deciduous swamp and thicket around 3 Illinois ponds, territory size averaged 0.13 ha (range 0.06-0.29 ha). In Kansas, 1 territory coincided with the boundaries of an isolated thicket that was 0.36 ha; another territory in more extensive habitat was 0.8 ha. In British Columbia, birds had mean territory sizes of 0.62 ha and home ranges of 1.16 ha. Territory sizes were determined for additional birds that were not radiotracked and these averaged 0.54 ha. When territory sizes of both radiotracked and non-radiotracked birds were combined, they averaged 0.55 ha (range 0.29-0.95 ha). Territories seldom overlapped but home ranges frequently overlapped. In Ohio, birds occasionally moved as far as 1 km from their territory and sometimes left their patch to travel to nearby patches. One Virginia male was caught 530 m from its territory, but it may have been unmated (Brewer 1955; Davis 1987; Dennis 1958; Fitch 1958; Graber et al. 1983; Lehnen and Rodewald 2009a; McKibbin and Bishop 2010, 2012a; Morgan et al. 2007; Thompson and Nolan 1973).

Almost no information on natal philopatry is available for the eastern subspecies. In Indiana, 0 of 39 nestlings returned; 0 of 15 juveniles banded in the area that were not produced there returned (Thompson and Nolan 1973). In Ohio, 2 of 270 young (0.8%) returned and 1 (0.4%) returned to the natal patch (Lehnen and Rodewald 2009b). In British Columbia, 39 of 385 nestlings (10.1%) returned

to nest. None returned to the natal territory but 62% of males and 54% of females returned to the natal habitat patch. Seven of 10 returning male nestlings that returned to a study area other than their natal site were observed the year after banding and dispersed 2.5-15.6 km from their natal site (median 10.3 km, mean 10.2 km). Two of 6 returning female nestlings were observed the year after banding at a site other than the natal study area. They dispersed distances of 2.3 and 2.6 km. The large size of the study area (189 ha) may have contributed to the higher return rate (McKibbin and Bishop 2012b). It is unlikely that natal philopatry rates are as high for the eastern population because adult site fidelity is much lower in the east than the west.

Adult site fidelity rates vary considerably geographically. Stewart (1989c) summarized band recoveries of the Yellow-breasted Chat in North America. Of birds that were not recaptured in the same area shortly after banding, 46 of 55 (83.6%) were recovered in the same 10-minute latitude-longitude block occupied during an earlier nesting season. This indicated a strong tendency to return to the same general location in successive breeding seasons. Two birds (3.6%) were recovered outside their original latitude-longitude block but in the same state; 7 (12.7%) moved to another state. Birds went from Maryland to West Virginia, Massachusetts to New Jersey, Indiana to Ohio, and Ontario to Michigan. In Indiana, 5 of 63 males (6.3%) returned and probably bred. When an additional 49 ha of adjacent habitat was examined, only 1 additional returning male was discovered, bringing the total to 7.9% site fidelity for males. Of 57 females, none returned in subsequent years, but females are difficult to find so some may have been overlooked. There was considerable within-season movement of adults. Seventeen of 39 males (43.6%) disappeared during the breeding season; 8 were breeders and 9 were territorial nonbreeders. All 8 breeding males disappeared after their nests failed and their females disappeared from the study area. Twelve females disappeared during the breeding season and all did so shortly after nest failure. Some males that disappeared were reencountered in subsequent years indicating that they had moved from the study area rather than having died. None of the females that disappeared were seen again. Many birds that disappeared were replaced later in the season by birds that were new to the area. It was likely that most of the new replacement birds had nested earlier at another location because the females had brood patches. Eastern birds may breed at more than 1 location within a single nesting season (Thompson 1977; Thompson and Nolan 1973). In Ohio, Lehnen and Rodewald (2009b) radiotracked male chats in 3 clear-cuts separated from the nearest shrubland patches by 70-, 95-, and 100-m wide strips of mature forest. Of 464 adults, 92 (19.8%) were recovered in a subsequent year and 89 (19.2%) were recovered at the same site. The mean number of sites used by 37 males was 1.4, with 13 (35.1%) located in at least 2 patches. The mean distance moved by the 13 males was 502 m (median 531 m). The mean number of patches they visited was 2.2. Three males established territories in patches other than their original patches; 2 may not have established territories prior to being captured and the third moved after nest failure. Of the remaining 10 birds, 5 made numerous visits to a neighbouring patch, moving a mean distance of 179 m (range 88-330 m). The remaining 5 males made fewer extra-patch visits, but travelled further (mean 649 m, range 445-1,045 m). Patches visited by males were younger (mean 5.5 years) than those where they were originally captured (mean 7.3 years). Dispersing birds did not move to larger patches. Birds may have been assessing the quality of other habitat patches for future breeding, seeking extra-pair copulations, or foraging.

All information on site fidelity for the western subspecies is from British Columbia. Of 45 males, 20 (44.4%) were resighted in subsequent years: 15 the first year after banding, 4 2 years after banding, and 1 3 years after banding. Seventeen of the 45 males (37.8%) and 17 of 20 returning birds (85.0%) returned to the same study area. Of these 17 birds, 2 bred in the area in at least 5 years, 5 in 3 years, and 8 in 2 years. Twelve of the 17 returning males (70.6%) bred on the same territory they held previously. Two of the dispersing males bred an additional 2 years at their new site. Males that did not return to their original territories dispersed 6.4-42.9 km from the territory where they had been banded (mean 14.98 km). Four of 30 females (13.3%) returned, 3 the year after banding and 1 the following year. Returning females dispersed a maximum of 2.6 km from their original territories. Most birds remained in the same location for the entire season. Only 1 male relocated after the nest failed and his mate disappeared. He moved 12.3 km, defended a territory at the new site, and was successful in attracting a mate (McKibbin and Bishop 2012b).

Limiting Factors

Eggs have been reported in Ontario nests from 2 June to 1 July (Peck and James 1998a). No information is available on how long it takes to build the nest or if there is an interval between nest completion and laying of the first egg. Eggs are laid at the rate of 1 a day. Incubation begins the night before the last egg is laid. The incubation period at 1 Ontario nest was at least 11 days and 2 District of Columbia nests had incubation periods of 11 days. Five Indiana nests had an average incubation period of 11.6 days (range 10.7-12.3 days). The eggs hatch within 24 hours of each other. The nestling period at District of Columbia nests was 8 days. The nestling period in Indiana averaged 8.9 days (range 7-10 days). In British Columbia, the time between fledging of the first brood and laying the first egg of the second clutch averaged 7.4 days. In a single third clutch, the first egg was laid 6 days after the second brood fledged (Eckerle and Thompson 2020; McKibbin and Bishop 2014; Peck and James 1987; Petrides 1938; Schadd and Ritchison 1998).

Based upon Ontario egg dates (Peck and James 1998a), it appears as though only a single brood is raised. The number of broods that the chat raises is difficult to ascertain because individuals may raise broods in disparate locations within a single year. In Indiana, some birds arrived later in the season that had apparently bred elsewhere (Thompson and Nolan 1973). Some birds arrive in Mexico in late July to nest and females have a brood patch indicating that they previously attempted to raise a brood. Stable isotope analyses revealed that these birds originated in the eastern United States (Rohwer et al. 2009). In Kentucky, the chat was double brooded (Schadd and Ritchison 1998), but all birds in Georgia and South Carolina were single brooded (Kilgo and Moorman 2003). It is possible that this area is partially the source of birds that breed later in Mexico. In British Columbia, 50 of 384 females (13.0%) had 2 broods. Nests for the second brood averaged 25.8 m from the first nest. One female attempted to raise 3 broods. Her first nest fledged 2 chats and 1 cowbird, the second nest fledged 3 chats and 1 cowbird, and the third clutch consisted of 3 chat eggs but failed to fledge any young. The third nest was 34 m from the second nest and 14 m from the first nest. The female that initiated 3 broods was one of the first to lay eggs in the spring (McKibbin and Bishop 2014). The chat may renest after nest failure; renesting was confirmed in Elgin County (Lancaster et al. 2004). In Indiana, 11 of 20 males (55%) and 11 of 22 females (50%) that lost their nests initiated a replacement nest. Ten of the females that did not renest disappeared from the study area. The other remained but did not renest. It is possible that those that disappeared initiated a replacement nest

elsewhere (Thompson and Nolan 1973). Clutches of 3-5 eggs have been reported in Ontario, with 4 eggs most frequent (mean 4.15 eggs; Peck and James 1998a). Throughout its range, the chat lays 3-6 eggs, but typically 3-5 eggs with 3 and 4 eggs most common. In Indiana, 78.9% of 4-egg clutches were laid in the first half of the laying period. Only 27.8% of 3-egg clutches were laid then. Average clutch sizes reported elsewhere include 4.09 in Illinois, 3.5 in Indiana, 3.5 and 3.75 in British Columbia, 3.36 in Arizona, 3.8 in New York, 4.0 in Pennsylvania and New Jersey, 3.84 in Tennessee, and 3.5 in Maryland (Bent 1953; Brand and Noon 2011; Campbell et al. 2001; Chapman 1907; Eckerle and Thompson 2020; Graber et al. 1983; McKibbin and Bishop 2014; Miño et al. 2011; Morgan et al. 2007; Petrides 1938; Thompson and Nolan 1973).

It appears as though all yearling females breed. Some yearling males may not be successful in defending a territory or attracting a mate (Eckerle and Thompson 2020; McKibbin and Bishop 2014). In Indiana, there was a surplus of birds. Some were transients that failed to establish a territory and others were territorial but failed to attract a mate. Of 10 males arriving later in the breeding season, only 3 bred after replacing nonbreeding territorial males that disappeared. Although 1 nonbreeding territorial male remained all season, most eventually left the area. When mated males disappeared or died, they were quickly replaced by other males (Thompson 1977; Thompson and Nolan 1973). It is unlikely that Ontario nesting areas support surplus birds due to its rarity. Some territorial males may not attract a female simply because none are available. Thompson and Nolan (1973) recognized 3 types of male mating systems: monogamy, successive monogamy, and polygyny. Successive monogamy occurred when a male mated with 2 or more females in sequence, but without any overlap in the timing of association with the females. Overall, 66.7% of males were monogamous with a single mate during the breeding season, 16.7% were successively monogamous, 4.2% (1 of 24) were polygynous, and the mating strategy of 12.5% of males was undetermined. Females may be monogamous or polyandrous, nesting with different successive males, and they may be in relationships with males that are either monogamous or polygynous. In the single case of polygyny in Indiana, the male initially bred with a female whose nest failed. She disappeared and 2 females appeared. The nesting cycle of these females was synchronous with the first egg laid on the same date in both nests; 1 nest failed and the other was successful. Because birds frequently moved within breeding seasons, the mating systems of some birds may have been more complicated than what was documented (Thompson and Nolan 1973). At a Virginia site, 2 broods were produced but only 2 males and 1 female were present. A male cared for the first brood and the female for the second. It was unknown if the female was polyandrous or if 1 male was unmated and both broods belonged to the other male (Dennis 1958). In Kentucky, 9 of 10 males were monogamous and 1 was bigamous (Eckerle and Thompson 2020). In British Columbia, 1 male defended 2 territories about 700 m apart and females were present in both territories. This male had the largest home range of all males (McKibbin and Bishop 2012a). Nest failure can have a profound effect on the stability of pair bonds. Pairs with successful nests tend to remain together throughout the season. Of 11 Indiana males that renested after the first nest failed, 6 retained their mate and 5 acquired a new mate. Of those obtaining a new mate, 1 paired with a female that had been mated to another male earlier in the season and the other 4 paired with females that had no previous breeding experience in the study area; all had brood patches (Thompson and Nolan 1973). In British Columbia, no mate fidelity was observed between breeding seasons (McKibbin and Bishop 2012b).

Extra-pair copulations are an important component of the mating strategy of the Yellow-breasted Chat. Both sexes solicit extra-pair copulations by making extra-territorial forays. In Kentucky, 65% of females and 50% of males made at least 1 foray into neighbouring territories. When females moved off territory, 96% of telemetry locations were less than 2 m from the ground, 3% were 2-5 m from the ground, and only 1 was 5-15 m from the ground. Females remained near the ground where vegetation was the densest. Females stayed lower than males, with 4.7 points less than 2 m from the ground per hour compared with 2.15 for males. Males followed their mates and, in 2 cases, attempted to herd them back to their own territory. Birds also move and sing at night, activities that are associated with extra-pair copulations. In Kentucky, 33% of 9 broods contained at least 1 extra-pair young and 17% of nestlings were not related to their social father. In British Columbia nests, 49.1% of nestlings were full siblings, 21.8% were half siblings, and 29.1% were unrelated. Four of 13 nestlings (30.7%) were not sired by the social father. The clustering of territories in some areas could facilitate extra-pair copulations (Dussourd and Ritchison 2003; Eckerle and Thompson 2020; Mays and Ritchison 2004; McKibbin and Bishop 2012a; Miño et al. 2011). Intraspecific parasitism is also a component of the mating system. In British Columbia, 3 of 13 nestlings (23.1%) were unrelated to the social mother (Miño et al. 2011).

During the breeding season in North Carolina, the Yellow-breasted Chat foraged 25.7% of the time in the canopy, 45.7% in low trees, 28.6% in shrubs, and 0% on the ground. Singing males occurred at heights of 2 m to more than 15 m (average 8.8 m). Nonsinging birds occurred at 0-15.8 m (average 4 m; Parnell 1969). The chat foraged primarily by gleaning insects from the foliage of shrubs (Whitmore 1977).

Nests where both sexes provision the young are more successful, fledging an average of 3.14 young compared with 1.52 young for nests fed by a single adult. In Kentucky, 56.7% of prey items brought to young consisted of adult insects; 43.3% were larvae. Small prey (equal to or shorter than the length of the adults' bill) accounted for 15.8% of prey items, medium-sized prey (bill length to 2 times the bill length) constituted 56.8% of prey items, and large prey (greater than 2 times bill length) comprised 27.4% of food items. In Washington, DC, the food of nestlings consisted almost entirely of soft-bodied orthopterans and caterpillars, and 2 half-grown praying mantises were consumed. Brown, almost hairless caterpillars were the most abundant food item; young were also fed locusts and grasshoppers. Young at a western nest were fed beetles, grasshoppers, and butterflies, but hairless caterpillars were the dominant food item. In British Columbia, males were the main providers to first broods while females initiated second broods (Bent 1953; Eckerle and Thompson 2020; McKibbin and Bishop 2014; Petrides 1938; Schadd and Ritchison 1998).

Adults eat a mix of small invertebrates (almost exclusively insects, but a few spiders and crustaceans) and fruit. Birds collected early in the breeding season had eaten approximately equal proportions of insects and fruit. Commonly consumed insects include beetles and weevils, bugs, ants, bees, wasps, mayflies, grasshoppers, adult and larval moths, caterpillars (including those of the tent caterpillar), and cicadas. The chat eats fruit of strawberries, mulberries, blackberries, raspberries, elderberries, grapes, blueberries, Japanese honeysuckle, and Saskatoon. A British Columbia female ate rose petals (Bent 1953; Eckerle and Thompson 2020; Holt 1918; McKibbin and Bishop 2014).

The Yellow-breasted Chat is parasitized by the Brown-headed Cowbird at moderate rates. Early publications suggested that the chat invariably deserted its nest in response to parasitism, but it is now known that is not the case. In Michigan, only 3 of 10 nests (30%) were abandoned after they were parasitized. The chat is typically considered an acceptor of cowbird eggs, but it occasionally ejects them. In Missouri, nests were artificially parasitized with 2 cowbird eggs: one normally coloured and the other painted white. Half of white eggs were ejected and 1 of 9 normal cowbird eggs was ejected. Chats may have difficulty distinguishing cowbird eggs from their own and eject only those that differ in maculation. The impact of parasitism on the chat is uncertain, but appears to be much lower than for many host species. In Indiana, 7% of eggs were removed by cowbirds; 81% of eggs were lost due to predation. Nestling chats appear to be able to successfully compete against cowbird nestlings. Many parasitized nests successfully fledge both species. Parasitized nests are more likely to be depredated than unparasitized nests; cowbird nestlings may attract more predators. In Missouri, nest patches with stems larger than 10 cm were more likely to contain parasitized nests because the larger stems provided perches for cowbirds. There were no differences in daily survival rates in parasitized and unparasitized nests. Four of 19 Ontario nests (21.1%) were parasitized. Parasitism rates are variable: 12 of 50 nests (24.0%) in Illinois, 3 of 5 nests (60.0%) in Saskatchewan, 10 of 11 nests (90.9%) in Michigan, 0 of 49 nests in Kentucky, 0 of 15 nests in Texas, 21 of 113 nests (18.6%) in Georgia and South Carolina, 31% of 42 nests in Missouri, 2 of 52 nests (3.8%) in Arkansas and Oklahoma, 4 of 127 nests (3.1%) in Mississippi, 17-20% of nests in Indiana, 5% of nests in Maryland, 11% of nests in Arizona, 0 of 10 nests in Pennsylvania, and 13%, 17.4%, 23.5%, and 49% of nests in 4 British Columbia studies. In British Columbia, the parasitism rate was 21.4% before 1978 and 54.7% 2012-14 despite a decrease in cowbird abundance of 80% (Alterman et al. 2005; Brand and Noon 2011; Burhans and Freeman 1977; Burhans and Thompson 1999; Cadman et al. 2011; Campbell et al. 2001; Eckerle and Thompson 2020; Forrester et al. 2020, 2023; Graber et al. 1983; Hackemack et al. 2016; Harrison 1984; Kilgo and Moorman 2003; Kirk and Pearce 2011; Nickell 1955; Novak et al. 2016; Peck and James 1998a; Ricketts and Ritchison 2000; Thompson and Nolan 1973).

Scarcity of suitable habitat and loss and degradation of existing habitat are the greatest limiting factors for the Yellow-breasted Chat. It is uncertain if it occurred in Ontario before European settlers deforested the landscape. The amount of suitable habitat probably peaked in the mid-20th century. The amount of shrubland began to decrease around this time due to removal of hedgerows to create bigger agricultural fields, road widening and right-of-way management to remove shrubs, reforestation of abandoned agricultural land, reductions in the amount of pasture, natural regeneration, and fire suppression. Shrublands are scarce in the province now and are often regarded as wastelands that are frequently converted to agricultural or urban land uses. Point Pelee and Pelee Island formerly supported the highest numbers of chats, but both have become marginal habitat as a result of natural succession. It appears to be adapted to inhabiting areas that are short-lived due to natural succession in the east by having low site fidelity and readily moving to new areas of suitable habitat. Remaining suitable patches may be too small and isolated from each other to provide continuing habitat for the chat in Ontario. There appear to be no data on the amount of shrublands within the province during different periods, but it has been estimated that more than 50% of suitable habitat has been lost in the Lower Great Lakes Physiographic Region since 1966. The

entire eastern population depends predominantly on anthropogenic early successional habitat that is being lost due to natural succession and other factors. Habitat loss was identified as a problem shortly after the turn of the 20th century and conditions have continued to deteriorate. The western subspecies appears to be stable in British Columbia despite the loss of 87% of riparian shrublands. It is increasing in Saskatchewan due to increased shrub coverage due to a reduction in grazing (Austen et al. 1994; Cadman et al. 2011; Chapman 1907; Curry 2006; Eckerle and Thompson 2020; Graber et al. 1983; Kirk and Pearce 2011; McKibbin and Bishop 2010).

Another major limiting factor is that the eastern subspecies of the Yellow-breasted Chat is at the extreme northern extent of its range in Ontario. When species decline, their range typically contracts from peripheral areas first. This subspecies is declining so that even suitable habitat may not be occupied. This appears to be happening in the Windsor and LaSalle area, an area typically occupied by the chat, but where none were found in 2010. Numbers declined on Pelee Island despite the persistence of suitable habitat. Declining populations south of Ontario means that there is unlikely to be recruitment to the province from areas further south (Cadman et al. 2011; Kirk and Pearce 2011).

Factors that change shrub density have an effect on habitat suitability for the Yellow-breasted Chat. Livestock grazing in the west adversely affects habitat and it declines in grazed areas. It has responded positively to fencing of riparian habitat to exclude livestock and to the lack of grazing by bison in the Prairie Provinces (Campbell et al. 2001; Eckerle and Thompson 2020; Kirk and Pearce 2011; McKibbin and Bishop 2012b). It responds favourably to clear-cuts, utility corridors, and openings created in forests provided that these are large enough (Alterman et al. 2005; Conner et al. 1983; Eckerle and Thompson 2020; Keller et al. 2003).

Morgan et al. (2007) examined the effects of fragmentation in riparian habitat in British Columbia. They compared clutch size and the number of fledglings produced in isolated patches smaller than 2 ha to fecundity in patches 15-70 ha in area and found no differences. There was no evidence that fragmentation reduced reproductive success or increased parasitism. Habitat fragmentation probably is an issue for the eastern subspecies. Most populations consist of a series of spatially separated subpopulations linked by extensive movements of individuals among short-lived patches of early successional habitat (Eckerle and Thompson 2020). As individual patches disappear, shrink, or succeed into unsuitable habitat, linkages become weaker and this may affect the viability of the larger population.

The Yellow-breasted Chat appears to be sensitive to human disturbance. Earlier researchers concluded that nests were invariably deserted if disturbed by a human. It has since been determined that nests disturbed late in the nesting cycle are not usually abandoned and birds may be fairly tolerant of humans. In Indiana, 10 of 78 nests (12.8%) were found during the nest-building stage and all were abandoned (Petrides 1938; Thompson and Nolan 1973). In British Columbia, it occurred only in areas of low development and appeared to avoid even gravel roads and buildings. No suitable habitat adjacent to high-traffic roads was occupied. Centres of territories were 5-1,600 m from the nearest gravel road (mean 287.6 m) and 50-1,500 m from the nearest building (mean 443.8 m). Most territories were at least 148 m from roads and 126 m from buildings. In Oregon, nests were in areas

of almost no human activity and at least 400 m from the nearest building (Campbell et al. 2001; McKibbin and Bishop 2010).

In North Carolina pine-oak forests, the chat occurred much more frequently in burned than unburned areas, but only after fires of high severity. It occurred less frequently as the time since the burn increased and was most common in areas that had burned 5-10 years previously. Rose and Simons (2016) concluded that it should benefit from large patches of high-severity burns.

In habitat near roads, the chat may be vulnerable to being struck by vehicles. McKibbin and Bishop (2010) observed 2 cases of road kills in British Columbia.

Several studies examined microhabitat features and other factors in relation to nesting success. In Kentucky, successful nests had significantly higher forb cover (57.5% compared with 31.1%) and lower shrub cover (30.1% compared with 51.2%) than unsuccessful nests. Successful territories had greater foliage cover below 1 m and less canopy cover (16.0% compared with 31.6%) than unsuccessful territories. There was no difference in daily survival rate of early and late nests (Ricketts and Ritchison 2000). In Arkansas and Missouri, nests closer to the ground, further from forest edge, and in areas with fewer large trees and small snags were more likely to be successful (Alterman et al. 2005). In Texas, nest survival was positively influenced by decreased shrub density and increased nest concealment above the nest at heights of 1.5-2 m. Survival was also affected by edge, with lower survival 50-100 m from edge than 0-50 m from edge or in core areas (Novak et al. 2016).

Price (2009) predicted that the breeding range of the chat might expand in southern Ontario if the average summer temperature increased by 2°C. Although climate change may be favourable for the chat, it is highly unlikely that warmer temperatures will result in an increase in its abundance or range. Warmer temperatures are unlikely to overcome significant limiting factors such as rarity of habitat and increasing loss of habitat.

Status

The first Yellow-breasted Chat record for Ontario was at Point Pelee in 1879 and by 1884 it had been confirmed breeding. Early breeding records were from the Point Pelee area, the northern shore of Lake Erie, and the Hamilton area (Austen et al. 1994; McIlwraith 1894; Saunders 1885). Baillie and Harrington (1937) reported that the chat rarely occurred north to Middlesex County and Peel Region, the most easterly record based upon the presence of a pair in Erindale in 1934. At that time, breeding had only been confirmed in Essex and Elgin counties. It apparently nested in the west Hamilton area in 1937 and summered there for 4 more decades at several sites that were almost contiguous. Breeding also occurred in Oakville, at Six Nations, at Aldershot, and in the Dundas Valley (Curry 2006). By 1954, it was a rare and irregular summer resident in Elgin County, with breeding records from Port Burwell and St. Thomas (Lancaster et al. 2004). In the 1960s, it was thought to be increasing and breeding regularly in the Niagara Peninsula (Austen et al. 1994). The largest concentrations of breeding chats have always been at Point Pelee and Pelee Island, where as much as 40% of the population occurs (Cadman et al. 2011; Kirk and Pearce 2011). Breeding first occurred at Rondeau in 1980 after a windstorm created suitable habitat within the forest, but nesting persisted there for only a few years (Austen et al. 1994). During the first atlas, it occurred predominantly in the Carolinian Forest Region, particularly in the extreme southwest and the Niagara and Hamilton areas. There were scattered records further north to Shelburne and the Kingston area, but these may have been

nonbreeding males. The population was estimated at 50 pairs, with more than 10 pairs at each of Point Pelee and Pelee Island (Eagles in Cadman et al. 1987). James (1991) considered the chat a rare to locally uncommon breeder in the Carolinian Forest Region north to Peel Region, with summer sightings in the Kingston area. By the late 1980s, 6-15 pairs were estimated on Pelee Island but only 2 pairs and 2 singing males were documented there in 1991. In 1982, 10 pairs were estimated at Point Pelee compared with 5-10 in 1994. In 1994, the population estimate for the province was 18-38 pairs (Austen et al. 1994; Kirk and Pearce 2011).

The second atlas revealed that the range of the chat had shrunk since the first atlas, with only 2 records north of the Carolinian Forest Region. Breeding was confirmed at only 4 locations within the province. Its probability of observation declined significantly between atlases. It was documented in 45 squares during the first atlas and 27 during the second atlas. It was estimated that there was a minimum of 42 pairs present during the second atlas (Eagles in Cadman et al. 2007). The population appears to have continued to decline since the second atlas. At Point Pelee, 3 pairs nested in 2008 but only 1 pair was present in 2009 and 2010. In 2008, there were 5-6 pairs nesting on Pelee Island but only 1 pair in 2010. None were found in 2010 in Windsor or LaSalle where it formerly nested annually. In the Hamilton area, it was documented in 3 squares during the second atlas but most of these sites have since been abandoned. Since the 1960s, there have been only 8 summer records in Elgin County and evidence of only 3 successful nests. By 2011, it was estimated that the chat probably occurred at fewer than 10 locations annually in the province (Cadman et al. 2011; Curry 2006; Kirk and Pearce 2011; Lancaster et al. 2004).

Too few chats are detected on the Breeding Bird Survey (BBS) to determine trends in Canada. Nonetheless, all evidence indicates that the Yellow-breasted Chat is declining in Ontario. In addition to declines documented by the atlases, it declined at an annual rate of 21% per year 1995-2008 on Forest Bird Monitoring Program surveys at Point Pelee. At the Long Point Bird Observatory, it declined significantly 3.5% per year in spring and 2.3% in autumn 1960-2010. From 2000 to 2010, it declined there at a rate of 6.0% per year in spring and 11.5% per year in autumn (Austen et al. 1994; Kirk and Pearce 2011).

The Ontario Yellow-breasted Chat population was designated special concern in 1994 and 2000 and endangered in 2011. The objective of the 5-year management plan prepared in 2011 was to maintain the population at its current level. It was considered unlikely that any rescue would occur from southern populations. BBS data indicate long-term declines in states bordering Ontario and the various atlases confirm these trends. The exception is Ohio, but the population there is concentrated in the southern portion of the state. It was also recognized in the management plan that population changes at the continental level could have significant effects on the chat's Canadian and Ontario populations (Cadman et al. 2011; Kirk and Pearce 2011). The objectives identified for Ontario in 2019 were to halt the decline within 10 years and provide enough suitable habitat to support at least 8 pairs. The long-term objective beyond 10 years was to achieve a stable population within its range (Brett 2019).

POSTFLEDGING PERIOD

After leaving the nest, young remain nearby until they are able to forage for themselves. After becoming independent, juveniles usually leave the territory and often the entire area. In Indiana,

young that were raised elsewhere began to arrive as those that were raised on site left. Newcomers often stayed for the remainder of the summer until autumn migration. In Virginia, about half the population was gone by the end of July. There was no general exodus, but small areas were deserted as family groups departed. Some families left before other birds had finished nesting (Dennis 1958; Eckerle and Thompson 2020; Thompson and Nolan 1973).

Both adults and juveniles have been detected in clear-cuts in deciduous forests during the postfledging period. In clear-cuts 4-7 years old in Ohio, 127 adults and 173 juveniles were captured. The Yellow-breasted Chat was the second-most abundant early successional species and was more abundant than any forest-breeding species (Vitz and Rodewald 2006). In a Missouri clear-cut, it was the third-most abundant early successional species and was sixth in abundance overall. Mist netting was undertaken 2-15 years after clear-cutting and it declined significantly with time. Peak numbers occurred 3-4 years after harvest with 64-75 captured; in years 11-15, only 1-7 were captured (Porneluzi et al. 2014). Habitat used during the postfledging period appears to be similar to breeding habitat and consists of dense deciduous shrubs, saplings, and vines.

In British Columbia, juveniles travelled as far as 15 km from their natal territories (Miño et al. 2011). Much longer distances are travelled by eastern juveniles. Some birds leave the breeding areas in July and August and travel northeastward, appearing in New England and occasionally Quebec and the Maritime Provinces in late August into late September or October. Most appear to be juvenile birds. Some remain north of the normal breeding range into early winter. Prior to 1949, the chat was only a casual visitor to the northeast, but this is now a regular occurrence that involves many birds. The presence of these birds later in the breeding season often confounds assessments of its breeding range, particularly near the northern extent of its range (Dennis 1958, 1967; Eckerle and Thompson 2020; Kirk and Pearce 2011).

MIGRATION

The Yellow-breasted Chat is a nocturnal migrant that probably travels singly or in small groups (Eckerle and Thompson 2001). Early arrivals at breeding areas sing nocturnally and these songs appear to be important cues to migrants that suitable habitat is present. Alessi et al. (2010) broadcast the nocturnal song at night in unsuitable habitat that consisted of 6 rows of apple trees with mowed grass between them. The nearest shrubland supporting chats was 16 km away. Fifteen chats were captured, but only on mornings following broadcasts, and 8 (53.3%) were captured in nets closest to the speakers. Both sexes responded to the broadcast and only 1 bird was recaptured in a subsequent day. Nocturnal songs of diurnally active birds occur chiefly in species that breed in patchy or ephemeral habitat. Males may sing nocturnally for as long as 6 days after spring arrival, potentially providing social cues to returning females.

Males migrate earlier than females and tend to arrive about a week before females, but females are occasionally among the early arrivals. Over 4 years in Indiana, males arrived 3, 6, 4, and 3 days earlier than females. Spring arrival of the sexes overlaps and there is no significant difference in the duration of migration for the sexes (Bent 1953; Thompson 1977; Thompson and Nolan 1973). One spring bird remained at a Texas stopover site for 9 days (Eckerle and Thompson 2020). In southern Ontario, birds arrive in early to mid-May but may arrive at Point Pelee in late April. Most are on the

breeding grounds before the end of May, but some may still be migrating until the first week of June (Black and Roy 2010; Curry 2006; Speirs 1985; Weir 2008).

Autumn migration begins after a moult by both juveniles and adults in August and September (Thompson and Nolan 1973). True timing of autumn migration is often difficult to determine. Some birds leave the breeding grounds early and raise another brood further south. Others wander north of the normal breeding range from August to October and remain until early winter. Birds that remain in a single area all breeding season probably leave in late August or September. Individuals seen 11 October in Algonquin Park (Tozer 2012) and near Huntsville on 16 August (Mills 1981) were probably examples of birds wandering during the postfledging period. In the south, birds reappear in autumn at the end of August. Migrants may occur until mid-October or even until mid-November. There are rare records in December and January (Black and Roy 2010; Curry 2006; Weir 2008). In Texas, 3 autumn migrants remained at a stopover site for more than 3 days (Eckerle and Thompson 2020).

In North Carolina, the numbers of chats observed in different habitats per hour during migration included 4.48 in dry thickets, 2.00 in wet thickets, 0.30 in pine-hardwood forests, 0.15 in floodplain forests, 0.11 in pine forests, and 0 in beech and oak-hickory forests (Parnell 1969). During spring migration in Illinois, it occurred mostly in forest edge and shrub habitats (Graber et al. 1983). On 2 islands in the Gulf of Mexico, autumn migrants were significantly more abundant on an island dominated by shrubs than a treed island (Suomala et al. 2010). During migration, it favours dense thickets of shrubs and vines. Occasionally it occurs in suburban habitat (Bent 1953; Eckerle and Thompson 2020). During migration in British Columbia, it inhabits the densest available habitat, mostly balsam poplar riparian forests where there is an understorey of willow, alder, maple, elderberry, and other shrubs. It occupies forest edge thickets where tangles of shrubs and forbs provide a dense understorey. Thickets of roses, blackberries, or snowberry in uncultivated corners of fields, orchards, and vineyards provide good migration habitat. Density of cover is more important than the plant species (Campbell et al. 2001).

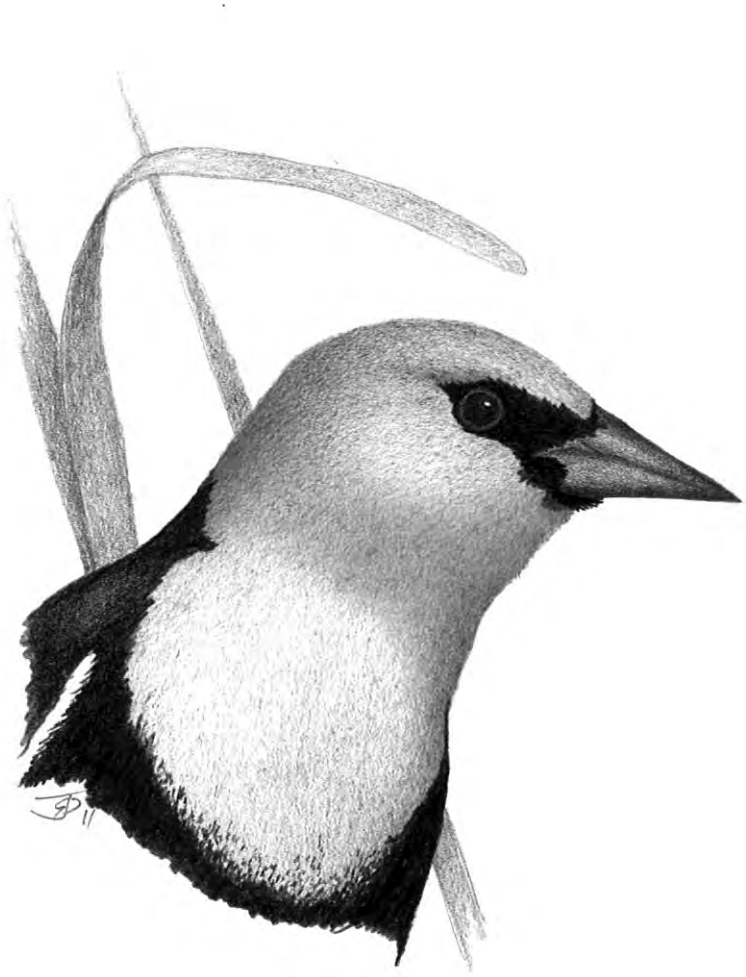
In North Carolina, foraging Yellow-breasted Chats during spring migration spent 22.9% of their time in the canopy, 36.8% in low trees, 40.5% in shrubs, and 0% on the ground (Parnell 1969). A bird in Virginia fed on small insects and Japanese honeysuckle berries in November (Kessler 1987).

The chat frequently collides with tall stationary objects during migration such as buildings, communication towers, and off-shore oil platforms. It becomes disoriented by bright ceilometers used at airports. Birds may fly around these until they are exhausted and fall to the ground (Eckerle and Thompson 2020).

James (1991) considered the Yellow-breasted Chat a rare migrant. There are both spring and autumn records far north of its breeding range, north of Lake Superior and in the southern James Bay area. Typically, only a single bird is seen at once but 12 were seen at Point Pelee on 12 May 1973 (Speirs 1985).

Yellow-headed Blackbird

Xanthocephalus xanthocephalus

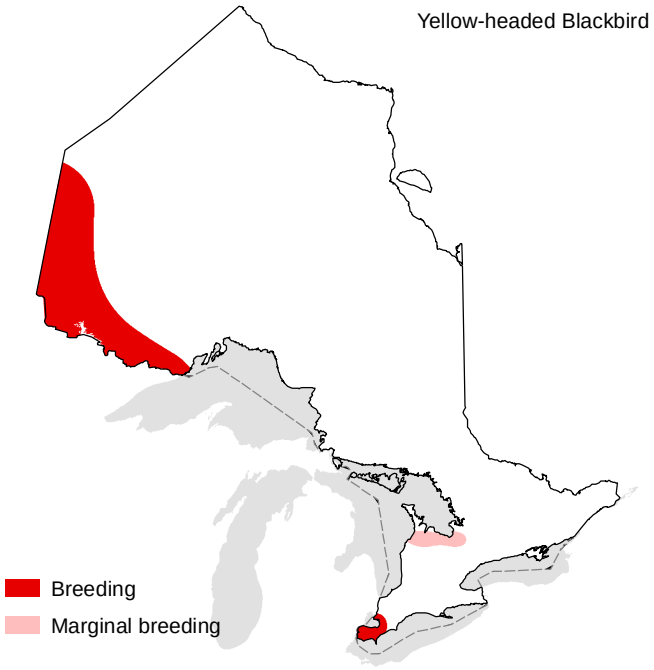


BREEDING SEASON

Habitat Requirements

Ontario Yellow-headed Blackbird nests were in both large and small marshes dominated by cattails, bulrushes, or common reed. Occupied marshes were in rivers or lakes (Peck and James 1987). At Mission Island in Thunder Bay, it nested in a marsh dominated by bur-reeds, bulrushes, and other emergent vegetation, with cattails lining the shore. The marsh contained a central area of open water and open pools were frequent (Harris 1989).

The Yellow-headed Blackbird is an obligate marsh-nesting species. It requires robust emergents to support its nest and is found most commonly in marshes dominated by cattails, bulrushes, and common reed, or a mix of these species. Less frequently, it nests in less robust emergents such as wild rice, bur-reeds, and sedges. It rarely nests in marshes with woody vegetation such as willows or



saltcedar. In Washington, a sparse population occurred in a wetland with many small trees. In British Columbia, all 750 nests were in wetlands with emergent vegetation; 97% of wetlands used for nesting had dense stands of cattails or bulrushes. The other wetlands that were used did not have these emergents but had willows growing over water or flooded willows. Most wetlands that are occupied are palustrine, either with no inflow or outflow, or limited outflow and no inflow. On lakes and rivers, it is restricted to shallow-water areas that support emergents. In addition to natural wetlands, potholes, and sloughs, it nests in constructed wetlands and sewage lagoons (Austen et al. 1994; Bent 1958; Campbell et al. 2001; Fautin 1940; Miller 1968; Picman and Isabelle 1995; Roberts 1909; Twedt and Crawford 2020; Weller and Spatcher 1965; Willson 1996b).

At the landscape level, the Yellow-headed Blackbird is associated with open areas. It is predominantly a western species associated with prairies and farmland. It also nests in the aspen parkland zone, margins of some of the larger lakes in the western mixed-wood zone of the boreal forest, mountain meadows, and in dry grasslands in arid regions. It avoids areas with trees around the margins of a wetland. A single tree that extends more than 30° above the horizon may occasionally be tolerated, but areas where tree stands extend this tall are avoided. Cliffs that extend this tall are also avoided. Treed areas are probably avoided because their shade reduces primary productivity in the marsh and therefore food availability, and they make the upland area less suitable for foraging. This blackbird is not particularly adept at capturing insects in trees. Its probability of occurrence in a given wetland is not affected by any other landscape attributes. It may nests in very small isolated wetlands where there are no other wetlands within 5 km (Beal 1900; M. Brown 1988; Campbell et al. 2001; Fairbairn and Dinsmore 2001b; Forcey et al. 2007; Miller 1968; Orians 1980; Twedt and Crawford 2020; Willson 1996b). In Minnesota, it was unaffected by the proportion of wetland cover at scales of 12.6, 50.3, and 4,000 ha. At the 12.6-ha and 4,000-ha scales, it was affected by the amount of agricultural cover and reached its greatest frequency of occupancy at 20-60% agricultural cover. It had a somewhat positive response to agricultural land, consistent with its use of pastures and crops for foraging. It was negatively influenced by the proportion of developed land at the 12.6-ha scale. Its frequency of occupancy was 70% at 0% developed land and dropped steadily to 10% at 100% developed land (Saunders et al. 2019).

Although marshes are relatively simple habitats, the Yellow-headed Blackbird has several habitat requirements that make it much more specialized than the Red-winged Blackbird, which is often present in the same marshes. Being a colonial nester, the Yellow-headed Blackbird tends to be

present in a marsh in numbers or completely absent, except perhaps at the periphery of its range. Critical habitat features include emergent vegetation sturdy enough to support nests, water at the base of the emergents supporting nests, a central area of open water in the marsh or openings among the emergents, and an abundant food source (Campbell et al. 2001; Miller 1968; Orians 1980; Twedt and Crawford 2020; Weller and Spatcher 1965). Absence of any of these factors makes the wetland unsuitable for nesting.

The most commonly used emergents for nesting include cattails, bulrushes, and common reed. These are tall, robust species that are capable of supporting a nest. The type of bulrush that is present is also important. In Saskatchewan and Iowa, the Yellow-headed Blackbird nested in hard-stemmed bulrush and river bulrush, but not in the less study soft-stemmed bulrush and American three-square. Other emergents that were present that were not used for nesting included rice cut-grass, arrowheads, spikerushes, sedges, bur-reeds, slough grass, sprangletop, and American manna grass (Miller 1968; Weller and Spatcher 1965). Height of emergents may be important. In a Utah marsh, a small area where the bulrushes had been burned and extended only 15-20 cm above the water was not occupied until all other available areas had been incorporated into territories (Fautin 1940). Nests higher above water are less vulnerable to flooding.

The Yellow-headed Blackbird will not nest in emergents that do not have water underneath them. Water provides aquatic insects that form the bulk of the diet and protection from land-based predators. Nests have been reported in emergents over mean water depths of 25-57 cm (range 15-120 cm). In Saskatchewan, the minimum water depth under a nest was 21.6 cm. It has been suggested that water depths as low as 15 cm are suitable (Bent 1958; Fautin 1940; Miller 1968; Picman and Isabelle 1995; Roberts 1909; Schroeder 1982b; Weller and Spatcher 1965; Willson 1966b).

Water levels are critical because they dictate the types of emergents that can grow and their density. Each species has a maximum water level that it can tolerate, and once water depths increase much over 1 m, all emergents begin to disappear. When the substrate is uneven and water depths are high, marshes tend to have openings among the emergents and an open-water centre. Under low water-level conditions, the entire marsh may consist of dense emergents. Ideal conditions for the Yellow-headed Blackbird consist of a central open-water area and robust emergents interspersed with patches of open water. The interface between deep open water and emergents is preferred habitat and territories are established there first in the season. Open water and openings among emergents allow sunlight to penetrate into the water column to the substrate. This increases local productivity of aquatic submergent plants and enhances the food supply for blackbirds. In many marshes, it is restricted to the central portion where the water is deeper. Areas nearer shore may be settled, but only where the water is deep and vegetation is sparse. Birds nesting near the centre of a marsh are more likely to fledge young than those nesting closer to edge and they also tend to fledge more young. A Wisconsin lake was completely covered with dense emergents and supported no Yellow-headed Blackbirds. Beavers built a dam and raised the water level, killing most of the cattails. Blackbirds colonized the marsh for 2 years until the cattails again closed in the lake. At a 160-ha marsh in Iowa, emergents covered 0-100% of the wetland over several years. It was absent when there was no open water and the number of pairs peaked at 70% open water. Another Iowa study determined that its presence was positively correlated with the amount of emergent

vegetation in the wetland and negatively correlated with open water and the wetland perimeter divided by the wetland area. The apparent disparity in its relationship to open water in the 2 studies may have been due the different scales of measurement that were used. The first study measured openings as small as 0.6 m within emergents. The second study measured only open water that was devoid of emergents (Fairbairn and Dinsmore 2001a, 2001b; Lederer et al. 1975; Miller 1968; Orians 1980; Picman and Isabelle 1995; Twedt and Crawford 2020; Weller and Fredrickson 1973; Weller and Spatcher 1965; Willson 1966b).

The Yellow-headed Blackbird may forage in both aquatic and terrestrial habitats, but the productivity of the aquatic habitat is the key factor in determining if a wetland is suitable for occupancy. Damselflies are an important component of the diet in most locations and the ability of a wetland to produce these insects determines whether it will be occupied. Even in terrestrial habitat, damselflies may be important in the diet. In British Columbia, it was restricted to nesting in wetlands where the conductivity was greater than 1,100 micromhos per cm. Reproductive success was much lower on a lake closer to the lower conductivity level than one much above it, with most nesting losses due to starvation. Traps captured 16.8 odonates per m along wetland edges and 15.0 per m^2 of emergent vegetation in areas with breeding Yellow-headed Blackbirds compared with 0.4 per m along edges and 0.1 per m^2 of emergents where breeders were absent. It is absent in western Washington where all lakes are low in dissolved nutrients and support few emerging aquatic insects. It was also absent in 1 highly productive British Columbia lake that lacked emergents robust enough to support nests (Orians 1980). Schroeder (1982b) concluded that the amount of submergent vegetation present in a wetland was the best measure of productivity and abundance of aquatic insects. Open water is essential for the presence of submergent vegetation and subsequent production of insects, so interspersed openings among emergents improve productivity. Dense emergents inhibit foraging by the blackbirds (Orians 1980).

In the Prairie Pothole Region of Canada, abundance of the Yellow-headed Blackbird was positively correlated with the amount of precipitation received the previous year, the annual temperature, and the amount of wetlands in the landscape. The first factor affects the amount of emergent vegetation and the amount of water under the emergents. Land-use parameters had no influence on its abundance (Forcey et al. 2007). In Iowa, there was no difference in its abundance in natural and restored prairie pothole wetlands. The difference between the 2 types of wetlands was that restored wetlands did not have low prairie or wet meadow zones between the emergent vegetation and upland habitats. This type of habitat is not used by this blackbird. Density of emergents was less on restored than natural wetlands, but this did not affect its abundance (Delphey and Dinsmore 1993).

Schroeder (1982b) prepared a habitat suitability index model for the Yellow-headed Blackbird. He considered wetlands with solid stands of emergents, those with no open water, and those with less than 15 cm of water underneath the emergents to be unsuitable. Suitability was 0 when no submergents were present and optimum when 80-100% of the wetland supported submergents. The amount of edge between open water and emergents was an important factor. All water depths of 15 cm or more were considered optimum, although excessive water depths will kill emergents. The percentage of emergents robust enough to support nests was another factor, with 100%

optimum and 0% unsuitable. Another important criterion that was not included in the model was wetland permanence. Most odonate nymphs require a year to develop into an adult, so they require permanent or semipermanent water bodies. Wetlands that regularly dry up are unsuitable for production of damselflies, one of the most important food items.

The Yellow-headed Blackbird and the Red-winged Blackbird frequently nest in the same marshes, but their territories rarely overlap. This is due in part to interspecific territoriality, but also because the Red-winged Blackbird is more of a habitat generalist. The Yellow-headed Blackbird is confined to robust emergents in deeper water and lower densities than areas used by the Red-winged Blackbird, and it requires wetlands to be more nutrient-rich. The Red-winged Blackbird nests in emergents with no standing water beneath them, in much less robust emergents, in trees and shrubs at margins of wetlands or on the upland shore, and also in grasslands and other non-wetland habitats. In the absence of the Yellow-headed Blackbird, the Red-winged Blackbird occupies the habitats that the Yellow-headed Blackbird uses (Campbell et al. 2001; Miller 1968; Orians 1980; Weller and Spatcher 1965).

The Yellow-headed Blackbird is not an area-sensitive species. In the core of its breeding range, it prefers smaller than large wetlands and even very small wetlands may support substantial colonies. In Washington, colonies occurred in wetlands 0.2-2.4 ha (Miller 1966). British Columbia colonies occur in sloughs, ponds, marshes, or small lakes 0.5-5 ha (Campbell et al. 2001). In Iowa, Brown and Dinsmore (1986) considered it area independent. It occurred in 67% of marshes smaller than 1 ha and in all larger wetlands. It is not confined to small wetlands, nesting in marshes 160 and 182 ha in Iowa (Brown and Dinsmore 1986; Weller and Fredrickson 1973). Highest densities often occur in the smallest wetlands: 30 pairs in a 0.4-ha marsh and 12 in a 0.25-ha marsh. In Iowa, it frequently nests in wetlands as small as 0.2 ha (M. Brown 1988; Schroeder 1982b).

At night, adults roost among emergent vegetation in their territories. During the day, they may loaf among wetland vegetation, in shrubby areas, and in small woodlots (Orians 1980; Twedt and Crawford 2020).

All Ontario nests were over water in emergent vegetation consisting of cattails, bulrushes, or common reed. The supporting vegetation was often dead growth from the previous year, but sometimes was living or a combination of the two. Nests were 0.2-1 m above water with most 0.3-0.7 m up (Peck and James 1987). Harris (1989) reported a nest in a dense stand of big bur-reed at Thunder Bay. It was approximately 20 m from shore where the water was 50 cm deep and was 30 cm above water.

All reported Yellow-headed Blackbird nests were over water, typically in robust herbaceous emergent plants but rarely in shrubs such as willow and saltcedar. The most common emergents used are cattails, bulrushes, and common reed. Only the larger and sturdier species of bulrushes are used such as river bulrush and hard-stemmed bulrush. It rarely nests in wild rice. The Thunder Bay nest appears to be the only one reported in bur-reeds. In a California marsh, some nests were in rushes and the weaker stems of these plants collapsed at 37% of nests. Early season nests are in dead vegetation from the previous year; cattails are preferred because they are less likely to be flattened by ice and snow. Later nests may be in green growth. Nests have been in water depths of 15-120 cm. Nests in shallower water are at risk of predation or desiccation underneath them; water deeper

than 120 cm may not support any emergent vegetation. Nests in emergents have been reported 0-90 cm above water, mostly 30-60 cm up. In shrubs, nests may be as high as 3.0 m above water. Reuse of nests is rare and occurs only within the same season after a predation event. In Washington, 7 of 1,161 nests (0.6%) were reused (Bent 1958; Campbell et al. 2001; Lederer et al. 1975; Miller 1968; Orians 1980; Picman and Isabelle 1995; Roberts 1909; Twedt and Crawford 2020; Weller and Spatcher 1965).

The Yellow-headed Blackbird typically nests colonially. Single nests are rare and usually occur at the fringes of its range or in suboptimal habitat. One Ontario colony contained 20 nests and as many as 600 nests have been reported at British Columbia colonies. In Iowa, the number of nesting pairs at 1 marsh was estimated at 5,000. Within a marsh, colonies are not always continuous and may be scattered in groups where the vegetation is most suitable for nesting. Breeding occurs in grouped territories when most food is obtained in the territory. It is loosely colonial when most food is obtained outside the territory (Bent 1958; Campbell et al. 2001; Peck and James 1987; Twedt and Crawford 2020; Weller and Fredrickson 1973). The primary function of colonial nesting appears to be to reduce predation. If a male leaves his territory, his neighbour temporarily assumes ownership of both territories and expels any intruding males or predators. Whenever any member of a colony emits an alarm call, all others immediately respond and often fly to where the alarm was sounded (Fautin 1940). Picman et al. (2002) studied a colony in Manitoba where predation accounted for 51% of nest losses, mostly by Marsh Wrens. They built experimental nests and placed eggs in them. Depredated nests were significantly further from an active blackbird nest and significantly closer to a wren nest than successful nests. Survival of experimental nests was significantly correlated with the number of nearby blackbird nests. Predation rates on nests placed outside colonies were significantly higher (almost 4 times greater) than at nests within colonies. Nests at the periphery of a colony suffered significantly higher predation rates than those in the centre of the colony. In colonies comprised entirely of artificial nests with no active blackbird nests, predation rates were similar near the edge and in the centre of the colony. Coloniality may facilitate certain aspects of the breeding strategy such as polygyny and extra-pair copulations. Some studies concluded that colonies act as information centres with members locating productive foraging areas by following successful foragers, especially neighbours. Other studies found no evidence to support this (Picman et al. 2002; Twedt and Crawford 2020). Gori (1988a) tested whether colonies acted as information centres for foraging Yellow-headed Blackbirds in Washington. He established artificial feeding sites that were superior to other areas used by the colony, 0.8-1.2 km from the colony. Recruitment rates to the enhanced foraging areas were significantly greater than expected. Birds departing the colony for the sites after provisioning were more likely to be followed than birds departing in different directions. Arrivals to the site were statistically clumped in time and disproportionately involved neighbours. He concluded that Yellow-headed Blackbirds can locate productive feeding areas by following successful colony members, especially neighbours.

Despite nesting colonially, the Yellow-headed Blackbird is highly territorial. Males establish territories almost immediately upon arrival but initially spend only the early morning and evening on the territory. Gradually the amount of time spent in the marsh increases with most of the day spent on the territory by the time females start to search for nest sites. Areas in the centre of the colony or at the outer interface between open water and emergents are settled first. These are the

most productive areas for aquatic insects and the safest from predators. For 2-4 weeks after territorial behaviour begins, vagrant males attempt to displace established males, usually unsuccessfully, or to establish territories between occupied areas. Most males defend their territories until they moult but some may abandon them as early as the beginning of June. When a territory is abandoned early, neighbours expand their boundaries to include it. Even at the height of the breeding season, males frequently feed outside the territory and may do so in small flocks with no aggressive behaviour (Fautin 1940; Willson 1966b). Females defend a radius of 0.6-0.9 m around the nest from other females. Intruders are expelled from the immediate vicinity of the nest but not necessarily out of the male's territory in which she is nesting. Females mated to the same male are intolerant of each other in the vicinity of the nest and frequently occupy opposite extremities of the territory. Females mated to polygynous males tend to maintain exclusive subterritories within the male's territory and frequently forage within their own areas. They do not forage on territories other than their own mate's (Fautin 1940; Willson 1966b). Lightbody and Weatherhead (1987) examined the relationships among females mated to the same polygynous males in a Manitoba marsh. Nests were neither clumped nor dispersed in time, with many females initiating their nests in the same territory on the same day. Females were least aggressive to each other during the laying stage and most aggressive during the nestling stage. There were no differences in the levels of aggression of primary, secondary, and tertiary females. It appeared as though females within polygynous relationships were not concerned with each other and did not nest either cooperatively or competitively. Male territory sizes are small but variable in size. Territory sizes of 8-5,899 m^2 (0.0008-0.59 ha) have been reported. Mean territory sizes from different areas range from 120 to 4,072 m^2 but a high proportion of territories are 100-400 m^2. Several factors may influence territory size. The most important is whether birds forage in the territory or in adjacent upland habitats. Territories where the adults forage within them are much larger than those where birds forage in terrestrial habitats. The quality of the emergent vegetation also influences territory size. Washington territories that averaged 4,072 m^2 were characterized by sparse scattered cattails that covered only 35% of the territories. Birds also foraged within these territories. Emergents in smaller territories tended to grow more sparsely or in a clumped fashion. Small territories had 55-79% coverage by emergents. Small territories supported as many females as large territories. Females on small territories fledged more young than those on larger territories. Another factor influencing territory size is breeding density. Areas with the highest population density have the smallest territories. Territories in productive marshes are smaller than those in less productive marshes (Fautin 1940; Lederer et al. 1975; Lightbody and Weatherhead 1987; Orians 1980; Schroeder 1982b; Twedt and Crawford 2020; Willson 1966b). Because of the small territory sizes and polygynous nesting, nests may be as close together as 2 m. In Manitoba, the distance between active nests was 2-33 m (averages 6.0 and 6.2 m in 2 years; Picman and Isabelle 1995). In California, mean internest distance in 2 years was 5.1 m and 8.3 m (Lederer et al. 1975). Twenty-five to 30 nests have been reported within an area of 21 m^2 (Bent 1958). Although the Yellow-headed Blackbird may have a small territory, its home range may be quite large. Those that forage outside the territory may fly 1.0-1.6 km to find food (Lederer et al. 1975; Shackford and Tyler 1987; Willson 1996b).

The Yellow-headed Blackbird defends its territory against the Red-winged Blackbird and Marsh Wren. The territories of the 2 blackbirds are mutually exclusive. Red-winged Blackbirds arrive earlier

in spring than Yellow-headed Blackbirds and often initiate territories throughout a marsh. Once Yellow-headed Blackbirds arrive, they evict Red-winged Blackbirds from the deep-water areas of the marsh and relegate them to shallow areas and areas of emergents that are not suitable nesting habitat for Yellow-headed Blackbirds. Aggression is common between the 2 species at this time. Red-winged Blackbirds frequently forage on newly established Yellow-headed Blackbird territories, but this stops once nesting begins. The Yellow-headed Blackbird is dominant to the Red-winged Blackbird at foraging areas outside breeding territories, but Red-winged Blackbirds are dominant at the periphery of marshes where their territories are established. Occasionally a Red-winged Blackbird will be able to maintain a territory within a Yellow-headed Blackbird colony. In these cases, there are usually minor habitat differences, such as the height or density of the vegetation, that make it more attractive to Red-winged rather than Yellow-headed blackbirds (Bent 1958; Fautin 1940; Miller 1968; Orians and Willson 1964; Voigts 1973; Weller and Spatcher 1965; Willson 1966b).

Marsh Wrens arrive before Yellow-headed Blackbirds. In some cases, they completely disappear once Yellow-headed Blackbirds arrive and reappear to breed once the blackbirds finish breeding. In other cases, the wrens remain but have highly compressed territories compared with when blackbirds are absent. When the 2 species remain for the breeding season, their territories are segregated. Yellow-headed Blackbirds occupy the deeper central portions of the marsh and the wrens are confined to the shallow perimeter of the marsh. Both species actively destroy the other's nests. Blackbird nests are most vulnerable in territories where females leave the nest to forage, thereby allowing wrens to sneak into the territory and destroy eggs or remove nestlings. Yellow-headed Blackbirds always challenge any Marsh Wrens they see. They may perch within 5 m of a singing wren and suddenly plunge headfirst at it, driving it into dense vegetation. They may also methodically follow a singing wren and occasionally perch above him, preventing him from singing from the top of emergents. Both males and females may perch on a wren's nest, preventing the female from returning to incubate the eggs. Rarely, male blackbirds may capture a wren and peck it vigorously. The Yellow-headed Blackbird responds aggressively to broadcast calls of the Marsh Wren indicating that it recognizes the wren as a threat (Bump 1986; Fautin 1940; Leonard and Picman 1986; Neudorf et al. 2011; Orians and Willson 1964; Picman and Isabelle 1995: Verner 1975). Yellow-headed Blackbirds spend more time attending their nests as Marsh Wren density increases (Behrens et al. 2019).

No information is available on natal philopatry. Males apparently do not breed in their first year, so it is unlikely that any breed for the first time in their natal area.

Adult male site fidelity varies depending upon the suitability of a given marsh. These wetland types may be quite dynamic with the amount of emergents and open water varying depending upon water levels. The Yellow-headed Blackbird is an excellent colonist and may appear at a marsh in the first year that the habitat becomes suitable. Occupied marshes may be abandoned if conditions become unsuitable, with blackbirds returning when the habitat improves. In 1 study, 30% of males breeding in 2 or more years skipped territory ownership in at least 1 year. Only 20% of those that skipped territory ownership were detected as floaters, indicating possible dispersal to other marshes. Over 5 years, 60% of breeding males changed marshes at least once. Males changed territories within the study area during 42.9% of between-year opportunities. There was no evidence

to suggest that males were more likely to move when territory density was low, likely to abandon territories that were deteriorating, or that they changed territories to improve reproductive success. Possible explanations for its low site fidelity are that it is a response to habitat deterioration and other factors causing population decline, migratory males make fresh settlement decisions each year when they arrive in the general vicinity of the previous year's territory, or it may be adapted to highly unstable habitats, moving frequently in response to changes in local site conditions. At 1 site, 51% of adult males and 19% of yearling males returned to breed the next year, often in the same territory. At Delta Marsh, Manitoba, 18 of 42 males (42.9%) returned in a subsequent year. Once a male established a territory there, he tended to return to the same marsh and usually to the same territory or very close to it. No information is available on adult female site fidelity (Beletsky and Orians 1994; M. Brown 1988; Picman and Isabelle 1995; Twedt and Crawford 2020; Weller and Fredrickson 1973; Weller and Spatcher 1965).

Limiting Factors

Eggs have been reported in Ontario nests from the end of May until the second week of July, with most present in the first 3 weeks of June (Peck and James 1998b). Upon arrival, females travel either singly or in small groups from territory to territory before selecting one. Nests are started as soon as the female selects a site, as early as 3 days after her arrival. The female builds the nest in 2-10 days, but mostly in 2-4 days. One to 5 days may elapse between nest completion and egg laying, but usually eggs are laid within 1-2 days of nest completion. Nesting within a colony tends to be highly synchronized. At a Manitoba marsh, 60% of nests were initiated within a 5-day period. Incubation usually begins with the laying of the second egg, but may vary from the first to fourth egg. The incubation period is 11-13 days, with most eggs hatching in 12-13 days. Hatching may be synchronous or asynchronous depending upon when incubation was initiated. Asynchronous hatching may be a strategy to allow brood reduction and ensure that some nestlings fledge during periods of scarce food supplies. Hatching of the first nestlings closely corresponds to the emergence dates of damselflies. After days 3-5, no brooding occurs. The nestling period is 7-14 days, mostly 9-12 days. Cold wet weather may prolong the nestling period; young may leave earlier if disturbed (Bent 1958; Campbell et al. 2001; Lederer et al. 1975; Miller 1968; Picman and Isabelle 1995; Roberts 1909; Twedt and Crawford 2020; Willson 1966b).

The Yellow-headed Blackbird raises a single brood in a season. Renesting may occur if a nest is lost, but few females attempt a replacement clutch. Over 2 years in Manitoba, 15% and 23% of females that lost a clutch renested. The replacement clutch is usually laid in a new nest at a different location within the territory. Only 0.6% of nests were reused for a replacement clutch. In some cases, the female may move to a different territory for her replacement clutch. Clutches of 3-5 eggs (average 3.73 eggs) have been reported in Ontario, with most containing 4 eggs. Overall, clutches of 2-5 eggs have been reported with 4-egg clutches most common. Clutch size declines with the season, with 4-egg clutches prevalent early in the season and 3-egg clutches predominating later. The decline in clutch size may be due to inexperienced yearlings nesting later or perhaps reduced food availability. Replacement clutches typically consist of 2 eggs (Arnold 1992; Bent 1958; Campbell et al. 2001; Lederer et al. 1975; Leonard and Picman 1986; Miller 1968; Orians 1980; Peck and James 1998b; Picman and Isabelle 1995; Roberts 1909; Twedt and Crawford 2020; Willson 1966b).

It is probable that all yearling females breed. Adult males vigorously challenge yearling males that enter a colony and eject them. Most studies concluded that yearling males do not breed and first initiate breeding when they are 2 years old (Bent 1958; Fautin 1940; Orians 1980; Twedt and Crawford 2020; Weller and Spatcher 1965; Willson 1966b). Yearling males occasionally breed, but are probably restricted to areas where there are no adult males, to suboptimal habitat, or areas at the extremes of the range. Sawyer and Dwyer (1968) reported a yearling male successfully breeding in the Lake St. Clair marsh in Ontario. Twedt and Crawford (2020) reported an annual return rate of 19% for yearling males, suggesting that these birds nested in their first year. Even after males begin breeding, they may occasionally skip breeding in some years and become nonterritorial floaters (Twedt and Crawford 2020).

Pair bonds are established after arrival on the breeding grounds and there is no evidence that they are maintained for more than 1 year. The mating system is predominantly polygynous. Some males are monogamous, but this is likely an indication of an inferior territory. Polygynous males may have 2-8 females nesting within their territories, but 2-5 is typical. In some cases, all females nest simultaneously on the territory but some females may settle later than others to nest. The number of females in a male's harem depends on the size of his territory, its location, and structure of the vegetation. In Washington, females were more abundant in territories with more edge. Four males had only a single mate and these had either very little edge or shallow water in their territories (Fautin 1940; Lightbody and Weatherhead 1987; Orians 1980; Picman and Isabelle 1995; Twedt and Crawford 2020; Willson 1966b). Some females move to a different territory to initiate a replacement nest, suggesting that some pair bonds may not persist for the entire season (Orians 1980). In Manitoba, half of 32 observed copulations were extra-pair, suggesting that extra-pair copulations may be a regular component of the mating system (Twedt and Crawford 2020). Roberts (1909) observed some differently coloured eggs in some nests suggesting that intraspecific parasitism may be a rare breeding strategy. In Washington, 13 of 1,161 nests (1.7%) were parasitized intraspecifically (Twedt and Crawford 2020).

Birds with small territories forage in upland areas or less frequently in undefended portions of the marsh or at a different wetland. In larger territories with open water, birds forage within the territory, but also in adjacent upland areas. Males wander much further than females from the territory and may travel to distant upland foraging areas in small groups. They do this from spring until well into the incubation period. Females may feed in areas of the marsh where emergent cover is too sparse to be suitable for nesting. Even those females that have productive territories for foraging tend to move to the shoreline or upland areas in early morning and evening to forage. In some areas, there appears to be no distinct foraging pattern, which probably depends upon behaviour of their insect prey. Preferred terrestrial foraging habitat is open and includes grassy meadows and alfalfa fields. In spring, the Yellow-headed Blackbird may follow plows to capture disturbed invertebrates. It is not very proficient at foraging in woody vegetation and tends to avoid shrubby and treed areas. An exception is at Delta marsh where birds fed on the abundant midges in a forested dune. Within wetlands, it forages predominantly near the water line by moving slowly around clumps of vegetation and searching on floating vegetation. During midday, damselflies emerge by ascending stalks of emergent vegetation and this is one of the dominant food items at most locations. It is not adept at capturing adult damselflies and relies upon recently emerged

tenerals that have not yet acquired the power of flight. It is capable of capturing some flying insects. In terrestrial habitat, it prefers to forage on the ground. It digs in the litter, sweeps with its bill, and double-scratches to uncover prey. It also uses its bill to flip over stones. When foraging in woody vegetation, it gleans mostly aquatic prey but also caterpillars. It preferentially forages near Forster's Tern nests, probably because they are in openings with a plentiful food source. Insects may be attracted to the nesting mounds by the heat of the incubating terns. Blackbirds frequently forage on and near tern nests without harming them. The terns benefit from the blackbirds' alarm calls and their displacement of Red-winged Blackbirds. When artificial feeders are provided in marshes, both sexes of the Yellow-headed Blackbird are attracted. Adult males displace females so they can access supplemental food only when males are absent. Red-winged Blackbirds and Brewer's Blackbirds are also displaced by male Yellow-headed Blackbirds (Arnold 1992; Bent 1958; Bump 1986; de Queiroz 2008; Fautin 1940; McNicholl 1981; Orians 1966, 1980; Picman and Isabelle 1995; Roberts 1909; Twedt and Crawford 2020; Voigts 1975; Willson 1996b). In Washington, Orians and Horn (1969) compared the foraging behaviours of the Yellow-headed, Red-winged, and Brewer's blackbirds and the Western Meadowlark. The Yellow-headed Blackbird foraged completely within the marsh at this study area, mostly by clinging to emergent vegetation. This behaviour was similar to that of the Red-winged Blackbird, which foraged in the same manner but mostly only during the morning. In the afternoon, it fed in adjacent uplands so there was no overlap in the foraging of these 2 blackbirds at that time. The meadowlark foraged solely in terrestrial habitat and the Brewer's Blackbird seldom fed in the marsh and was ill-adapted to clinging to stems of emergent vegetation. The Red-winged and Yellow-headed blackbirds fed predominantly on emerging damselflies. Although there was a broad overlap in their diet and foraging strategies, the damselflies were an abundant resource that was not limiting.

The female is mostly responsible for feeding the nestlings. Some monogamous males do not feed their nestlings; others do. Polygynous males tend to feed nestlings only at the primary nest, if they feed at all, but may feed nestlings at the secondary nest if the primary nest has a small brood. In Manitoba, only 7 of 67 males (10.4%) fed any of their nestlings; at some marshes, no males fed any of their nestlings. The probability of a male feeding young is much higher on unproductive than productive marshes. On productive marshes, males expend their energy on attracting additional females rather than assisting their existing mates. Males preferentially feed nestlings of females that have broods of 3 or more young aged 4 or 5 days rather than those in nests where broods have already been reduced due to starvation. Food is allocated to chicks based on their size, with larger nestlings fed more. This ensures that the largest chicks fledge but the youngest may starve if there is a shortage of food (Bent 1958; Cash and Johnson 1990; Gori 1988b, 1990; Picman and Isabelle 1995; Price and Ydenberg 1995; Roberts 1909; Twedt and Crawford 2020; Willson 1966b). In Washington, Willson (1966b) classified food items brought to nestlings as primary if they constituted 25% of all items and occurred in at least 50% of samples. Secondary food items constituted 10-24% of all items and occurred in 10-49% of samples. Tertiary items comprised less than 10% of all items but occurred in at least 10% of samples. Primary prey consisted of narrow-winged damselflies, flies, mayflies, soft-winged bugs, and lepidopterans. Secondary prey included flies, lepidopterans, other odonates, and true bugs. Tertiary prey included beetles, flies, caddisflies, mayflies, true bugs, spiders, lepidopterans, orthopterans, snails, and hymenopterans. The odonates were predominantly narrow-

winged damselflies but also included spread-winged damselflies, darners, and skimmers. The flies were mostly midges but included shore flies and house flies. The beetles were predominantly predaceous diving beetles and scarab beetles, the true bugs were water boatmen, the soft-winged bugs were aphids and spittle bugs, and the orthopterans were mostly short-horned grasshoppers. Some neuropterans and nematodes were consumed. The amount of damselflies fed to nestlings increased as they aged. There appeared to be no active selection for prey. Roberts (1909) reported a female feeding a leech to a nestling. In Iowa, the food provided to nestlings included narrow-winged damselflies, true bugs, treehoppers, aphids, ground beetles, owlet and snout moths, crane flies, midges, soldier flies, flower flies, shore flies, anthomyiid flies, spiders, and corn. Narrow-winged damselflies were the only food item that was important all day. The diet of nestlings changed as the season progressed. Before 20 June, the most important foods were narrow-winged damselflies, larval soldier flies, and adult midges. After 20 June, midges and soldier flies continued to be important, but aphids, anthomyiid flies, and flower flies from nearby hayfields became important. The overlap in diet between Yellow-headed and Red-winged blackbird nestlings was 46-49%. The 2 species selected much of the same food items, but at different times of the season. Differences in their habitat selection, foraging behaviour, and mutually exclusive territories further reduced competition for food (Voigts 1973). Orians (1966, 1980) analyzed the diet of nestling Yellow-headed Blackbirds in British Columbia and Washington. Odonates were most important in the diet at all lakes studied, predominantly narrow-winged damselflies. In 1 year when damselflies were scarce at a lake, females that continued to select for them raised fewer young than those that searched for alternate prey. Other important prey included long-horned beetles, caddisflies, and flies. Other food items included dragonfly nymphs and adults, spittle bugs, plant bugs, seed bugs, water striders, predaceous diving beetles, weevils, ground beetles, click beetles, water scavenger beetles, scarab beetles, lepidopterans, shore flies, flower flies, midges, biting midges, soldier flies, black flies, house flies, picture-winged flies, bristle flies, ants, ichneumonid wasps, braconid wasps, spiders, water mites, snails, mayflies, locusts, froghoppers, planthoppers, water boatmen, shore bugs, rove beetles, checkered beetles, snout moths, robber flies, fruit flies, amphipods, plant bugs, marsh beetles, crane flies, harvestmen, leaf beetles, and snipe flies. In 1 lake where damselflies were scarce, flies dominated the nestling diet. In Washington, Orians and Horn (1969) reported that the nestling diet consisted of 56% odonates, 1% orthopterans, 1% leafhoppers, 4% lepidopterans, 24% flies, 7% other insects, 4% spiders, and 3% other items. In Texas, nestlings were fed adult orthopterans, caterpillars, flies, and lesser quantities of beetles, odonates, spiders, and snails (Twedt and Crawford 2020). In Utah, the nestling diet was dominated by insects and spiders, with small insects provided initially and larger ones such as damselflies and grasshoppers supplied as the nestlings became older. In California, nestlings were fed snails and partially digested larvae on their first day; predigested and crushed insects devoid of wings, legs, and chitinous parts on their second day; and similar food on their third day but it was less digested and occasionally supplemented with fresh food (Bent 1958). Although the Yellow-headed Blackbird can survive where narrow-winged damselflies are scarce, they appear to be the most important food item in much of its range. Timing of egg laying or hatching of the first nestling are often timed to coincide with the emergence of damselflies (Miller 1968; Willson 1966b).

During the breeding season, adults eat mostly the same items that they provide to the nestlings. They have a high dependence on damselflies in most areas, but also capture terrestrial prey such as caterpillars, leafhoppers, grasshoppers, spiders, and probably most, if not all, of the items described in the nestling diet (Bent 1958; Orians 1980; Twedt and Crawford 2020; Willson 1966b). Fifteen stomachs collected in Utah contained 7 orthopterans (mostly grasshoppers), an ant-lion, 7 odonate nymphs, 2 true bugs, 96 beetles (including 13 ground beetles, 2 predaceous diving beetle larvae, 1 skin beetle, 1 lady beetle, 2 scarab beetles, 7 leaf beetles, and 18 weevils), 40 caterpillars (including 18 cutworms and armyworms), 13 flies that were mostly larvae plus an adult horse fly, and 10 hymenopterans (including 7 ants). They also contained 2 spiders, 109 weed seeds, 18 wheat kernels, and 6 barley kernels (Knowlton 1947). Arnold (1992) installed feeders in Manitoba wetlands and provided corn, layer diet for chickens, rabbit chow, oystershell, and grit. Both sexes visited the feeders and 1 female repeatedly fed her nestlings from the feeder. In all cases, birds selected corn, a species that otherwise is not available in southwestern Manitoba. The high-protein foods that were available were not used. From early spring through the postbreeding season and migration, the Yellow-headed Blackbird forages on agricultural crops such as sunflowers, corn, and small grains. Twedt et al. (1991) summarized its usage of these crops in the Prairie Pothole Region. Small grains (wheat, oats, barley, and rye) were the dominant crops in the provinces and North Dakota and corn dominated in Minnesota and South Dakota. The diet varied geographically and reflected the dominant crop species that were available. The diet of the sexes differed significantly. Males ate more sunflowers in North Dakota and Saskatchewan and more weed seeds in Manitoba, North Dakota, and Saskatchewan than females. Insects and, to a lesser extent, small grains and weed seeds were a large proportion of female diets in all geographic areas. The Yellow-headed Blackbird did not contribute much damage to sunflower crops. Beal (1900) summarized the contents of 138 stomachs collected in all seasons from 10 Mississippi Valley states, California, and Canada. The diet consisted of 33.7% animal matter and 66.3% vegetable matter. The diet was highly terrestrial, suggesting that most samples were collected outside the breeding season. The animal food consisted of 2.8% ground beetles, 5.0% other beetles, 4.6% caterpillars, 11.6% grasshoppers, and 9.7% other insects. The other insects were mostly ants and wasps with a few dragonflies and the occasional spider and snail. Almost two-thirds of the caterpillars were eaten in July when they formed 21.5% of the diet. Grasshoppers first appeared in the diet in May, with a peak in consumption in July and another significant increase in consumption in August. The vegetable matter consisted of 9.8% corn, 3.5% wheat, 25.6% oats, 27.1% weed seeds, and 0.3% other material. Oats were the most important grain, representing 63% of the October diet and 43.2% of the August diet. The seeds that it consumed included those of barnyard grass, panic grasses, and ragweed, with lesser amounts of smartweeds and docks. Seeds were most prominent in the diet in September when they comprised 64.4% of the diet. No fruit or garden produce was consumed.

The Yellow-headed Blackbird is rarely parasitized by the Brown-headed Cowbird, possibly because it is much larger. It readily accepts cowbird and other foreign eggs when added at an appropriate time. Eggs added 1-4 days after incubation is initiated are accepted, but those added 3 or more days before clutch initiation are rejected or abandoned. When real cowbird eggs were added to Colorado nests, there was no difference in the number of blackbirds fledged from parasitized and unparasitized nests. In most areas, cowbird parasitism is absent or very low.

Parasitism has not been documented in Ontario, no nests were parasitized in a Utah study, and 0 of 351 nests were parasitized in Colorado. In British Columbia, 2 of 357 nests (0.4%) were parasitized. The highest recorded incidence of parasitism was in Idaho where 12 of 62 nests (19.4%) were parasitized. There are no records of cowbirds fledging from Yellow-headed Blackbird nests. The cowbird has essentially no effect on this blackbird's populations (Bent 1958; Campbell et al. 2001; Dufty 1994; Fautin 1940; Ortega and Cruz 1988; Roberts 1909; Twedt and Crawford 2020).

Habitat loss probably is not a significant limiting factor for the Yellow-headed Blackbird in Ontario. In the core of its range, wetland drainage, conversion of wetlands to agricultural land, and forest encroachment on wetland edges have probably reduced populations (Twedt and Crawford 2020).

Weather significantly affects Yellow-headed Blackbirds, with precipitation dictating the quality of a marsh for it. The amount of precipitation received the previous year and prior to the current breeding season determines water depths in the marsh. Deeper water kills some emergents and tends to make marshes more suitable for this blackbird by creating open water. If water depth exceeds approximately 1.2 m, the marsh may become too open to be suitable. If water levels are low, the emergent vegetation may become too dense for nesting, or the water depth may drop below 15-20 cm in depth, becoming marginal for nesting. Nests built over water more than 52 cm deep have higher success rates than those over shallower water. In Iowa, variations in amounts of precipitation affected its habitat use. It tended to not settle and establish territories during dry years. Those that did nest failed to fledge any young. This was attributed to predation, which increased as water levels declined. Sudden changes in water levels during the nesting period are often detrimental. Rising waters may flood nests and nests may be abandoned or depredated if water beneath the nest becomes too shallow. Cold wet weather in spring may delay nesting and result in the nestling period being asynchronous with the peak emergence of damselflies. It may also delay plant maturation, resulting in fewer nest sites. This type of weather during the nestling period is more detrimental. Older nestlings are not brooded and may become chilled and die of exposure. Prey is less available during adverse weather, resulting in more runt nestlings and a higher rate of starvation. High winds may destroy nests because they are situated in more open areas of marshes (Bent 1958; M. Brown 1988; Campbell et al. 2001; Fautin 1940; Fletcher and Koford 2004; Lederer et al. 1975; Miller 1968; Orians 1966; Twedt and Crawford 2020; Willson 1966b).

Carp can destroy Yellow-headed Blackbird habitat. They stir up sediments and decrease the amount of submergent and emergent vegetation by uprooting it. This also decreases the abundance and diversity of aquatic insects. In some lakes, introduction of carp resulted in the elimination of Yellow-headed Blackbirds (Orians 1980; Schroeder 1982b).

Most marshes support muskrats and their presence may be positive or detrimental to the Yellow-headed Blackbird. The muskrat feeds on aquatic plants and small populations are beneficial. Their grazing creates openings among the emergents, enhancing habitat for this blackbird and emerging aquatic insects. The Yellow-headed Blackbird often uses their houses as singing perches and also for foraging. Muskrats occasionally cut off the emergents supporting a nest, resulting in its failure. High muskrat populations can eat almost all emergents in a marsh, rendering it unsuitable for this blackbird (Weller and Spatcher 1965).

The Yellow-headed Blackbird is frequently persecuted by humans because of its consumption of agricultural crops (Twedt and Crawford 2020). In addition to shooting, efforts are occasionally directed toward making its breeding habitat less suitable. In North Dakota, Linz et al. (1996) sprayed cattails with glyphosate to break up cattails to improve habitat for many marshland birds but make the area less favourable for blackbirds. Seventy percent of cattails were sprayed in 4 marshes and 90% on 4 other marshes. There was a slight but nonsignificant decline in Yellow-headed Blackbirds for 2 years after spraying. Their population rebounded once the cattails became re-established.

In most populations, the primary cause of nest failure is predation. This may be particularly severe in wetlands where the Marsh Wren is present. Despite the aggressive behaviour of Yellow-headed Blackbirds toward this wren, it may destroy in excess of 50% of nests (Picman and Isabelle 1995; Picman et al. 2002; Rutberg and Rohwer 1980).

In an effort to control mosquitoes, Hanowski et al. (1997a) sprayed wetlands with Bti and methoprene. There were no apparent effects on the Yellow-headed Blackbird as a result of the treatments.

There are 2 minor factors that may affect individual nests but not populations. Uneven growth of the emergents supporting nests may result in their contents being dumped into the marsh. Heavy mite infestations may contribute directly or indirectly to mortality (Twedt and Crawford 2020).

Status

The first record of the Yellow-headed Blackbird in Ontario was one near Toronto around 1885. Although the species was very rare in the province near the end of the 19th century, McIlwraith (1894) correctly predicted that it would eventually become a breeder. The first evidence of it breeding in Ontario was in 1931 when it was reported nesting near Quetico Park. Breeding was first confirmed in 1961 when 35 males were counted near the mouth of the Rainy River near Lake of the Woods; a nest with eggs was collected then. At that time, there were scattered summer records from other locations in southern Kenora and Thunder Bay districts, and in Essex, Chatham-Kent, Middlesex, Peel, Peterborough, Haliburton, and Frontenac. Breeding was not confirmed in any of these locations. In 1965, 3 territorial males were observed in the Lake St. Clair marsh complex. Two nests were found there in 1966 (Baillie 1961; Sawyer and Dyer 1968). Baillie (1967) and de Vos (1967) reported that the range of the Yellow-headed Blackbird had expanded eastward to include the Great Lakes area and Ontario, possibly due to forest clearing and damming of rivers (Austen et al. 1994). The first atlas indicated that it bred regularly in the Lake St. Clair and Rainy River areas. Nesting evidence was also obtained at Kenora and Dryden in the north and in Essex County. There was a possible breeding record from Tiny Marsh west of Barrie. Records of isolated birds were considered unlikely to represent long-term range expansions. Because it is a colonial species, sightings of individuals or even single pairs are not usually indicative of breeding (Flood in Cadman et al. 1987). Harris (1989) found a nest at Mission Island in Thunder Bay and presumed that another nest was present based on the presence of 2 females. James (1991) considered the Yellow-headed Blackbird locally uncommon at Rainy River, Atikokan, Essex County, and in Chatham-Kent; rare at Thunder Bay; and possibly occurring in Norfolk County. Summer records had been documented from Red Lake, Long Lac, and Simcoe County (Tiny Marsh) at that time. He concluded that it was slowly expanding in Ontario, with sight records north to Moosonee. Austen et al. (1994) estimated the Ontario

population at 25-56 pairs annually during the first atlas, but large colonies nesting in Lake of the Woods had been overlooked.

The second atlas revealed no significant changes in the range or probability of observation of the Yellow-headed Blackbird since the first atlas. It occurred in a few more areas in northwestern Ontario, north to the Pikangikum sewage lagoons. Small colonies previously reported at sewage lagoons at Amherstburg and Essex in Essex County and near Stoney Point on Lake St. Clair disappeared or declined between atlases. The population along the east shore of Lake St. Clair, excluding Walpole Island, was estimated at 75-100 birds (Dunn in Cadman et al. 2007).

Breeding Bird Survey data for Canada indicate annual increases of 0.841% 1970-2021 and 2.78% 2011-21. The long-term trend was highly reliable; the short-term trend was of medium reliability. There are no data for Ontario (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Upon leaving the nest, young move up the vegetation supporting it. When it bends over, they move to another stem and adeptly move about the marsh in this manner until they are capable of flight. They can fly 1-2 m 4-5 days after leaving the nest and are capable of 25-m flights by the time they are 3 weeks old. The young fledglings and female usually remain close to the nest for several days. At this time, the male may assist the female in feeding the fledglings. Eventually the female and fledglings make their way into other males' territories where they are not challenged. The male does not follow and the female assumes all responsibility for the fledglings (Bent 1958; Fautin 1940; Twedt and Crawford 2020; Willson 1966b).

Juveniles undergo a partial moult that begins in July. During this time, they and adults may congregate in large flocks where the growth of cattails or other emergents is the densest. If the natal marsh does not have dense stands of emergents, birds may begin to disperse from it by late June. While remaining in dense vegetation, flocks may segregate with males found in 1 part of the marsh and females and juveniles in another. Birds leave the marsh during the moult only in mornings and evenings to feed (Bent 1958; Picman and Isabelle 1995).

The moult is complete around the beginning of August. At this time, birds come out of hiding, spend the day foraging in fields, and roost in wetlands overnight. They leave the roost at sunrise in characteristic flight lines, often flying 10 or more km to suitable foraging areas. Near sunset, they typically follow the same flight lines to return, but may roost in different wetlands nightly (Bent 1958; Campbell et al. 2001; Twedt and Crawford 2020; Twedt et al. 1991).

Foraging flocks of Yellow-headed Blackbirds are often mixed with European Starlings, Red-winged Blackbirds, Brown-headed Cowbirds, and Common Grackles. They forage mostly in fields of small grains and corn, but often in landfills, floodplains, stubble fields, and bare, plowed, or fallow fields. They may also visit chicken runs, barnyards and manure piles, cattle feedlots, estuaries, marine beaches, lawns, and corn cribs (Beal 1900; Campbell et al. 2001; Cummings et al. 1989; Miller 1968; Twedt and Crawford 2020).

During the postfledging period, most foraging occurs in agricultural crops including wheat, oats, barley, millet, milo, sorghum, sunflowers, and corn. Once a suitable foraging site is found, flocks return to it repeatedly over several days until the crop is depleted or becomes too ripe for their

preferences. It prefers ripening grain and sunflower fields where the seed kernels are in the soft dough stage of development. After this seed stage is over, numbers of visiting birds decline rapidly. In unharvested fields, birds perch on the plants to feed on the seeds. Large foraging flocks roll over fields gleaning weed and grain seeds. Birds at the rear of the flock fly over birds foraging on the ground and land at the head of the advancing flock. Unripened grains may be milked from the hull and sunflowers are hulled before they are consumed. The conversion of vast areas of upland habitat from grasslands and forage crops to cultivation of small grains, corn, and sunflowers has created an immense food supply for postbreeders and has probably increased fledgling survival (Cummings et al. 1989; Twedt and Crawford 2020).

In some years, large numbers of juvenile birds appear in Massachusetts and on the Atlantic Coast, well away from the breeding areas. This appears to be long-distance postfledging dispersal. The numbers that occur each year on the east coast are linked to reproductive success. Large numbers on the coast coincide with years when large numbers of young are produced along the northern and eastern edges of the breeding areas, the portion of the breeding range that is closest to the coast (Veit 1997).

MIGRATION

The Yellow-headed Blackbird is a diurnal migrant that migrates in small flocks. Flocks tend to be composed almost exclusively of either adult males or females with juveniles. Flocks are often mixed with Red-winged Blackbirds, Common Grackles, Brewer's Blackbirds, and Brown-headed Cowbirds. These flocks congregate in staging areas and roost overnight in dense emergent vegetation in marshes, similar to the postfledging period. It is a rare and irregularly encountered autumn migrant throughout eastern Canada and the United States. Although it is distributed throughout this area in autumn, most records are from Atlantic Coast regions. It is a rare but increasing spring migrant in the east (Bent 1958; Twedt and Crawford 2020).

The Yellow-headed Blackbird appears to be cold intolerant and arrives in the spring later and departs in autumn earlier than the Red-winged Blackbird. The northward movement begins in the south in mid-March and continues through April, with most birds arriving on the breeding grounds by mid-May. At 1 Iowa marsh, there was little difference in the arrival times of adult males and females. In most areas, females arrive 1-2 weeks after the males. By then, males have established their territories and females can assess the quality of territories and males before selecting a site. Yearling males arrive 3-4 days after adult females and yearling females arrive about a week later. Autumn migration is usually underway by late August or early September (Bent 1958; Fautin 1940; Orians 1980; Picman and Isabelle 1995; Roberts 1909; Twedt and Crawford 2020; Weller and Spatcher 1965; Willson 1966b).

In southern Ontario, spring migrants arrive in late March and may continue to pass through until early June. Autumn migrants occur from mid-August to late October; some remain until December or January (Black and Roy 2010; Curry 2006; Speirs 1985; Weir 2008). Although some birds have been seen in winter, these appear to be late autumn migrants. There is no evidence that the Yellow-headed Blackbird has successfully overwintered in the province.

During migration, the Yellow-headed Blackbird is predominantly granivorous, eating small grains, corn, and weed seeds. The diet is similar to that of the postfledging season, particularly during

autumn migration. Preferred habitats for foraging include agricultural fields such as harvested grain fields, loose piles of hay around barnyards, cattle feedlots, along railways where there is spilled grain, in pastures and meadows, and in plowed fields. Less frequently, it may occur in wild rice stands and along roadsides and city streets. At night, it still requires marshes with dense emergents for roosting (Bent 1958; Campbell et al. 2001; Roberts 1909; Twedt and Crawford 2020).

Bobolink

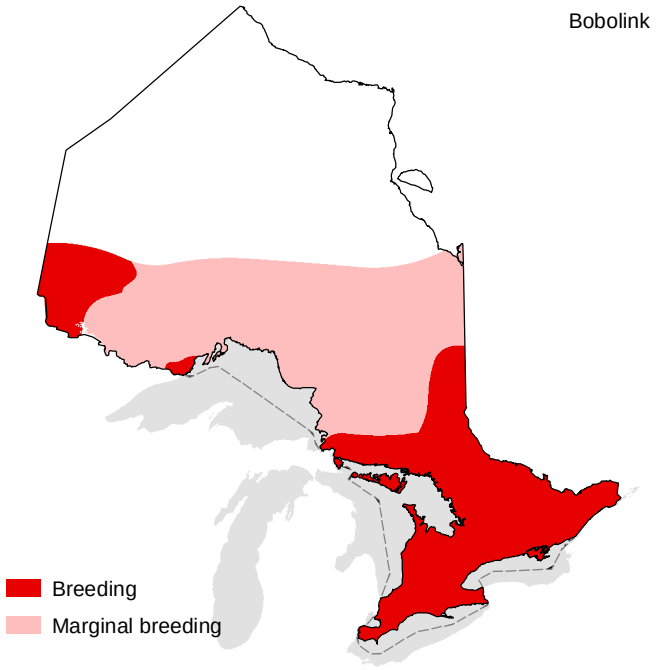
Dolichonyx oryzivorus

BREEDING SEASON

Habitat Requirements

All Ontario Bobolink nests were in open fields: 35.6% in hayfields, 35.6% in shrubby and weedy fields, 15.7% in pastures, 12.2% in marshy fields, and 0.9% in stubble fields (Peck and James 1987).

In Ontario, the Bobolink is an open-habitat species associated with agricultural landscapes with large areas of hayfields and pastures. It is an obligate grassland species that avoids areas dominated by shrubs or trees. It seldom nests in small-grain fields and avoids row crops such as corn and sorghum. Highest densities are associated with the highest densities of cattle and largest areas of hay and pasture. It still nests in some habitats that were used historically, such as remnant prairies, savannahs, and alvar grasslands. These habitats are now rare and support only a small proportion of the population. In landscapes that are extensively forested, it is confined to large openings such as blocks of agricultural land or bogs, fens, or beaver meadows dominated by grasses and sedges. It



does not nest in clear-cuts or burns. In some areas of southwestern Ontario where more suitable habitat is absent, it nests in fields of winter wheat that are at least 50 ha. It prefers fields where the grain crop is underseeded with clovers or alfalfa, or that are bisected by a wet grassy area (McCracken et al. 2013; Tozer 2012).

In Durham Region, the Bobolink showed a strong preference for old fields and hayfields with few nesting in pastures (Speirs and Orenstein 1967). At Luther Marsh, it nested in 4 habitats: monotypic reed canary grass or reed canary grass mixed with tufted vetch and bird's-foot trefoil; willow stands; mixed communities with Canada goldenrod, tufted vetch, bird's-foot trefoil, and grasses dominating; and ponds and vegetated mud mounds. Nests were placed where the vegetation, mostly Canada goldenrod, averaged 37.4 cm tall (range 33-41 cm). In addition to grasses, tufted vetch, bird's-foot trefoil, and common dandelion occurred near nests. In all cases, residual grass cover was used for nesting. Canada goldenrod was commonly used as a perch but did not appear to be an essential habitat component. The Bobolink also occurred in fields without goldenrods. It used fence posts, wire fencing, dead vegetation, and occasionally willow branches as perches, but preferred goldenrod (Joyner 1978).

The Bobolink was equally abundant on organic and conventional farms in southern Ontario. It was positively correlated with hedgerows, spring grain, hay, pastures, and habitat heterogeneity (Kirk et al. 2011).

Throughout its range, the Bobolink is restricted to grassland habitats. Where native grasslands persist, it is associated predominantly with tallgrass prairies and does not use shortgrass prairies or those containing a large proportion of shrubs. It is rare or absent in shrubsteppe communities. In native grasslands, it is most frequently associated with big bluestem and switchgrass, but it may inhabit other warm-weather grasses. Other natural habitats that it uses less frequently include graminoid fens and bogs and grassy margins of marshes (Askins et al. 2007; Norment et al. 2010; Robertson et al. 2012; Savignac 2010a; Swanson 1996). It is much more abundant in nonnative grasslands, particularly in hayfields and areas managed for waterfowl such as Conservation Reserve Program (CRP) lands in the United States and Dense Nesting Cover (DNR) in Canada. Hayfields are the largest source of nesting Bobolinks in the east; in New York, 74% nest in hayfields. In Massachusetts, 97% of territories were in hayfields that represented only 52% of available grasslands. In arid areas of the west, occupied grasslands tend to be near a source of water or be irrigated, but presence of water is not important in the east. Mesic fields are preferred to those that are dry or

flooded in the west, but drier habitat is acceptable in the east. Other grassy habitats it may use include lightly to moderately grazed pastures where shrubs are scarce, old fields and meadows, reclaimed surface mines, military bases, and airports. Less frequently used habitats include no-tillage croplands, fields of oats and winter wheat, grassy power-line rights-of-way that are at least 30 m wide and 500 m long and in rural rather than urban landscapes, and fields managed for blueberry production. Grass species that are characteristic or commonly found in fields used by Bobolinks include timothy, orchard grass, bluegrass, quack grass, and smooth brome. Other grass species that may occasionally be dominant in Bobolink habitat include reed canary grass, nonnative wheat grasses, fescues, Virginia wild rye, and meadow fox-tail. Some forbs within the grasses are desirable, especially red and white clover, bird's-foot trefoil, common dandelion, and American and tufted vetches. Many occupied fields contain alfalfa but those dominated by this species tend to be avoided. Other old-field species that are commonly present include buttercups, asters, goldenrods, and thistles (Askins et al. 2007; Banville and Gauthier in Gauthier and Aubry 1996; Beal 1900; Bollinger and Gavin 1991; Bollinger et al. 1988, 1990; Campbell et al. 2001; Dechant et al. 2001; Ells 1995b; Giroux et al. 2000; Graber and Graber 1963; Graves et al. 2010; Hartley 1994; Leston and Koper 2017; Nocera and Forbes 2010; Nocera et al. 2007b; Patterson and Best 1996; Renfrew and Ribic 2008; Renfrew et al. 2020; Renken and Dinsmore 1987; Savignac 2010a; Shustack et al. 2010; Swanson 1996; Vickery et al. 1994; Walk et al. 2010; Wiens 1969; Wittenberger 1978; Wootton et al. 1986).

The presence and abundance of the Bobolink are affected by several habitat features at the landscape level. These are related predominantly to the openness of the landscape and the abundance or proximity of forest cover. During the arrival and egg-laying periods in New York and Vermont, more birds occurred in fields where open habitats dominated the landscape within 2,500 m. During the incubation and early fledging periods, the amount of potential nesting habitat within 500 m became more important. The overall openness of the habitat was more important during settlement than the amount of habitat. This suggested that hayfields or pastures in landscapes with high proportions of row crops may provide suitable habitats. It was recommended that grassland reserves should be in mostly nonforested and undeveloped landscapes of 2,000 ha with subsets of areas of 80 ha with as much grassland and late-cut hay as possible (Shustack et al. 2010). In the same area, it avoided habitat that was not open, using open habitat more than expected even when only those nests within 50 m of edge were considered. Nest densities were reduced when the angle to the horizon was as low as 10° above horizontal; the minimum observed openness at a nest was 20° (Keyel et al. 2013). In Wisconsin, its abundance was associated predominantly with landscape characteristics. Densities were highest in landscapes with low cover diversity to a distance of 800 m. Low-diversity landscapes were characterized by large amounts of hay and grassland. Density was also higher where the area of woodlots was lower and where there were fewer wooded patches within 800 m. Density was lower when woody vegetation or larger wooded patches were closer to the transect (Ribic and Sample 2001). The amount of grassland within 1,200 m was important when Bobolinks were making settling decisions (Renfrew and Ribic 2008). In North Dakota, it reached its maximum probability of occurrence (more than 90%) in open, treeless grasslands; this declined to 40% at 10-25% woodland cover. The percent of woodland cover within 500 m was the most important predictor of its occurrence, which dropped to 0% at 40% woodland cover within this distance. Its probability of occurrence also declined with increasing coverage by tall shrubs. It was a

woodland-sensitive species that was negatively affected as woody plant height increased from brush to tall shrubs and trees. Even nominal increases in woody vegetation compromised the use of grasslands (Grant et al. 2004). In the Great Plains of the United States, the Bobolink's presence and abundance were positively correlated with grassland and herbaceous species, pastures, hayfields, CRP lands, alfalfa, and emergent herbaceous wetlands. It was negatively correlated with open water, forests, shrubs, and developed areas. Its probability of occurrence was high with 0-20% tree coverage in the landscape, moderate at 30% coverage, and 0 at 69% tree coverage (Niemuth et al. 2017). On Ohio reclaimed surface mines, the amount of woody vegetation within 100 m negatively affected its abundance (Graves et al. 2010). In Minnesota prairies, it was positively correlated with increasing grass extent at scales of 100, 500, and 1,000 m, plus litter depth and grass height. Density increased slightly with increasing visual obstruction. It was negatively associated with all woody vegetation including number of trees and shrubs within 50 m and percent tree cover within 100, 500, and 1,000 m. It was more strongly affected by the negative influence of woody vegetation than the positive effects of grass quality or quantity (Thompson et al. 2014). In North Dakota, it was restricted to landscapes with 0-13% tree cover (Cunningham and Johnson 2019).

Numerous studies examined microhabitat requirements of the Bobolink. It is associated with areas dominated by moderately dense and tall grasses with some forb coverage, a high grass-to-legume ratio, and moderately deep litter. In New York, it was most abundant in hayfields 8 or more years old. These fields were characterized by low amounts of total vegetative cover, low alfalfa cover, low legume cover, high litter cover, and a high grass-to-legume ratio. Most younger hayfields were planted to legumes or legume-grass mixtures, especially alfalfa. Alfalfa grows too densely and it usually avoids pure stands of it. Fields with the least amount of alfalfa had more than 15 times the density of Bobolinks than fields with the greatest amount of alfalfa. Maximum densities occurred at 55-64% total vegetation cover, 10% or less total legume cover and alfalfa cover, 26-50% litter cover, and a grass-to-legume ratio greater than 5. Densities were greatest in old hayfields followed by pastures, fallow fields, old fields, and young hayfields. It occurred at very low densities in heavily grazed pastures and brushy fields and was absent in oat fields. Densities declined by 50% 3 years after fields were abandoned due to the establishment of woody vegetation. Densities in hayfields were 3 times those in prairies. In old hayfields, densities were 4 times greater than in prairies (Bollinger and Gavin 1992; Bollinger et al. 1990). In Nova Scotia, abundance of males was positively correlated with percent coverage of vegetation and abundance of true bugs and orthopterans. Abundance was negatively correlated with alfalfa, forb coverage, and cordgrass. Vegetation height and density were the most important variables; average vegetation height was 36 cm (range 10-75 cm; Nocera and Forbes 2010; Nocera et al. 2007b). In New York, average habitat conditions were 13.6-15.2% grasses, 7.3-9.8% dandelions, 5.3-6.0% clovers in the genus *Trifolium*, 2.3-3.6% buttercups, 0.4-3.1% bird's-foot trefoil, and 43.3-48.1% coverage by all vegetation. Vegetation within the field was homogenous and there was no difference in vegetation within territories of bachelors or monogamous and polygynous males. Females appeared to settle randomly into high-quality habitat without being influenced by vegetation characteristics or food abundance (Wootton et al. 1986). In DNC near Montreal, accumulation of dead vegetation reduced the attractiveness of habitat to the extent that Bobolinks avoided it. Without periodic light grazing or mowing, this habitat gradually becomes unsuitable (Giroux et al. 2000). At Minnesota and North Dakota nest sites, habitat

consisted of 3.4% bare ground, 13.9% grasses, 6.0% forbs, 74.2% litter, and 0.7% shrubs with 67.1% vegetation coverage at the nest. Within the vicinity of the nest, cover included 0.3% bare ground, 35.3% grasses, 22.6% forbs, 38.6% litter, and 2.6% shrubs. Litter depth averaged 4.8 cm, mean vegetation height was 39.1 cm, visual obstruction was 20 cm, and the nest was an average of 4.7 m from the nearest shrub and 30.6 m from the nearest tree (Winter et al. 2004). Grass height should be above 25 cm at the start of the breeding season (McCracken et al. 2013). In North Dakota, Arnold and Higgins (1986) reduced shrub coverage by wolfberry and silverberry from 30-80% to 5%. Bobolinks were 5 times more abundant on the shrubless plots. Of 127 Wisconsin nests, 83.5% were beneath tall forbs, 11% were in sedge growth containing smaller forbs, 3.1% were beneath a woody overstorey, and 2.4% were arched over by dead vegetation. No nests were found where grass provided the major concealment despite 63.8% grass coverage. The vertical density was higher at nest sites than random areas and sun penetration was lower at nest sites (Renfrew et al. 2020). In shrubsteppe habitat, Rotenberry and Wiens (1980) found the Bobolink at only 1 site where its occurrence was correlated with percent litter cover. In Wisconsin, it preferred vegetation at the taller end of the spectrum in terms of grassland structure. Vegetation structure was an important predictor of its abundance and this changed annually in response to precipitation. It was least abundant in cool dry years when the vegetation was less dense, shorter, and had lower coverage by live vegetation (Renfrew and Ribic 2008). In North Dakota, it was most abundant in plots with a dense litter layer and taller, more lush vegetation that was often dominated by smooth brome, quack grass, and sweet clover (Grant et al. 2004). In Iowa CRP lands, its abundance was positively correlated with grasses and negatively with forbs. It tended to be more abundant where litter cover was higher, but not significantly. Density increased by 9.2 times over 3 years, probably because the grass-to-forb ratio increased from 2.5 to 4.4 (Patterson and Best 1996). Mean vegetation characteristics of nesting habitat in Wisconsin included 2% woody cover, 78% herbaceous cover, 16% litter cover, 5% bare ground, and 22 cm vegetation-height density (Swanson 1996). In Wisconsin, vegetative parameters at nest sites averaged 97% coverage by grasses, 20% coverage by forbs, 0% coverage by dead vegetation, 22% coverage by vegetation 10-20 cm tall, 10% coverage by vegetation 20-30 cm tall, 0% coverage by vegetation 30-40 and 40-50 cm tall, and 0% bare ground. The mean distance from territory boundaries to a woodlot was 100 m (range 40-220 m), 0 m to a fence line, and 59.4 m (range 0-170 m) from a cultivated field. All territories contained fence posts and fence lines, 50% contained trees, and 25% contained a bale or tangle of wire. Territories were nearly completely covered with grasses that were predominantly narrow and very narrow-leaved forms. Foraging occurred predominantly in cover 6-15 cm tall. It used tops of grasses for singing. Use of forbs was not high but heavy-stemmed species were important for singing and medium-stemmed species were used as lookouts. Posts and trees were used for singing and wires and posts were important as lookout perches. Maximum litter depth in territories was 9 cm, with areas of deeper litter avoided (Wiens 1969). In Illinois, its abundance was positively correlated with mean vegetation height, mean grass height, and mean number of vegetation contacts. It was negatively correlated with within-transect heterogeneity (Herkert 1994a). In North Dakota, its abundance was positively correlated with grass coverage, litter depth, density of low-growing shrubs, vegetation density, and plant communities dominated by Kentucky bluegrass, wiregrass, and grama grass. It was negatively correlated with clubmoss coverage, bare ground, and plant communities dominated solely by native grasses. The strongest predictors of its presence were

decreasing bare ground, increasing litter, and increasing vegetation density. In Nebraska CRP lands planted to cool-season grasses, it was positively correlated with percent litter cover and negatively with the vertical density of vegetation (Dechant et al. 2001).

Some studies compared the habitat characteristics of unoccupied areas and territories; of territories and nest sites; of bachelor, monogamous, and polygynous males; and identified where birds settled first at the beginning of the breeding season. In North Dakota, areas where the Bobolink was present had significantly deeper litter, taller vegetation, less live vegetation, fewer shrubs taller than 1 m, less open woodland within 100 and 500 m, and more smooth brome–quack grass community within 100 m than areas where it was absent. There were no differences in shrub coverage, amount of bluegrass, or amount of sweet clover within 100 m in occupied and unoccupied areas (Grant et al. 2004). In Wisconsin, occupied and unoccupied areas were generally similar but different in several manners. Forb coverage and density were similar but forb height was significantly greater in occupied areas. Grass cover was similar but very narrow-leaved forms dominated unoccupied areas. Vertical vegetation density was similar but the density of low (0-10 cm) vegetation was significantly greater in unoccupied areas. Litter depth was similar inside and outside territories. Litter coverage was 63% in territories, 66% in unoccupied areas, 58% within 1 m of a nest, and 100% at nests. Areas selected for nesting were markedly different from the rest of the territory. Forb coverage was somewhat less at nest sites and a higher proportion of grasses were of the narrow-leaved type. Forb heights were similar at nests and throughout the territory. Vertical vegetation density at nests was significantly greater both near the ground and over the entire height range than in the entire territory. Light penetration to lower levels was correspondingly reduced. Litter in areas about nests was more compact, deeper, and of greater coverage than in the remainder of the territory, and these differences were accentuated at the nest (Wiens 1969). In Oregon, territories of bachelors had significantly lower forb coverage than those of mated males. Forb cover differed significantly between territories of polygynous and monogamous males, but only in 1 of 3 years. Territories of polygynous males were in wetter areas than those of monogamous or unmated males and had higher coverage by sedges. Adjacent territories of polygynous and monogamous males often did not differ in vegetation characteristics and differed only in the number of females they attracted. Territories of polygynous males contained significantly higher densities of caterpillars from 31 May to 6 June and significantly more grasshoppers after 12 June than those of monogamous males. Polygyny occurred on territories containing high abundance of nestling food; unmated males had territories with low food abundance. Females selected territories based upon food resources and not vegetation characteristics (Wittenberger 1980a). In the same study area, males settled first in mesic habitats with low sedge coverage and high forb coverage. Later arrivals established territories in wet habitats with high forb cover and either high or low sedge cover. Flooded areas and dry areas distant from water were avoided. Female habitat preferences were less reliant on moisture condition and depended more upon food availability, so their settling pattern differed from those of males (Wittenberger 1978).

Other studies compared the Bobolink's habitat preferences to those of other grassland species. McCracken et al. (2013) compared the habitat requirements of the Bobolink and Eastern Meadowlark. In Ontario, habitat is often created with the objective of attracting both species, so it is important to be aware that their habitat requirements are not identical. Compared with the

meadowlark, the Bobolink prefers larger fields and tolerates or even prefers wetter portions of fields; the Bobolink tends to avoid field edges whereas the meadowlark does not; the Bobolink is associated more with hayfields and less with pastures than the meadowlark; the Bobolink prefers more forbs in fields (22.6% compared with 11-15% for the meadowlark); the Bobolink tends to nest in patches of denser and taller vegetation; and the Bobolink has a lower tolerance of woody vegetation (maximum of 25% coverage compared with 35% for the meadowlark). Winter et al. (2004) compared nest sites of the Bobolink and Clay-colored and Savannah sparrows in Minnesota and North Dakota. Clay-colored Sparrow nest sites differed significantly from the other 2 species, nesting most frequently in or near shrubs. The Bobolink and Savannah Sparrow nested most frequently within dense clumps of litter. Bobolink nests were in taller vegetation, had a lower percentage of cover at the nest, and less bare ground around the nest than those of the Savannah Sparrow. The authors concluded that, due to differences in habitat preferences, a single species cannot be used as an indicator species for the conservation of grassland birds. In Wisconsin, Wiens (1969) compared the habitat preferences of the Bobolink with those of the 2 species of meadowlarks and the Vesper, Savannah, Grasshopper, and Henslow's Sparrows. Density of forbs within 1 m of a Bobolink nest was considerably greater than for the other species. The height of forbs was somewhat taller than at Eastern Meadowlark nests, slightly lower than at Grasshopper Sparrow nests, and the same as at Savannah Sparrow nests. When entire territories were considered, height of forbs was significantly greater on Bobolink territories than in territories of all other species except for the Henslow's Sparrow, which occupied areas with significantly taller forbs. Density of forbs in Bobolink territories was higher than in Henslow's Sparrow territories; lower than in Vesper Sparrow, Grasshopper Sparrow, and Eastern Meadowlark territories; and considerably lower than in Western Meadowlark territories. Vertical vegetation density in Bobolink territories was significantly greater than in Vesper Sparrow territories, significantly less than in Henslow's Sparrow territories, and similar to that of other species. The mean vertical vegetation density 0-10 cm from the ground in Bobolink territories was significantly less than for all species except the Henslow's Sparrow. The mean effective height of vegetation in Bobolink territories was significantly less than in Henslow's Sparrow territories and significantly higher than in Vesper Sparrow, Savannah Sparrow, Grasshopper Sparrow, and Western Meadowlark territories. Coverage by low lawn-like vegetation with an effective height of less than 5 cm in Bobolink territories was the least of all species except the Henslow's Sparrow. Litter depth in Bobolink territories was shallower than in Henslow's Sparrow territories; deeper than in Vesper Sparrow, Eastern Meadowlark, and Western Meadowlark territories; and similar to the territories of other species. Bobolink territories were closer to woods than territories of all other species. The habitat continuum included sparse low vegetation for the Vesper Sparrow, dense low vegetation for the Western Meadowlark, and dense tall vegetation for the Bobolink and Henslow's Sparrow. The ranking of species based on increased richness of the habitat, including vegetation density and height and litter coverage and depth, was Western Meadowlark, Vesper Sparrow, Savannah Sparrow, Grasshopper Sparrow, Eastern Meadowlark, Bobolink, and Henslow's Sparrow. The range of differences among the rankings was low.

The Bobolink may avoid nesting near edges of grasslands, but this is not always the case. Whether it avoids edge may depend upon factors such as the amount of grassland in the landscape and the type of edge. Even where edge avoidance occurs, avoidance is manifested predominantly

by a lower density of nests near edge rather than by complete avoidance. In Wisconsin, Renfrew et al. (2005) found no relationship between nest density and distance to edge. The type of edge (wooded or nonwooded) was not a significant predictor of nest density within 50 or 100 m of edge. Nest density increased 50-200 m from edge, but not significantly. In Iowa, Fletcher and Koford (2003) examined the location of territories relative to edges created by row-crop agriculture, gravel roads with row-crop agriculture on the opposite side, and closed-canopy deciduous woodlands at least 30 m wide. Nest density increased with distance from edge and was 2 times greater near agricultural edges and 1.5 times greater near roads than near woodland edges. Habitat differed among edge types: litter depth was lowest near woodland edges and greatest near agricultural edges; total vegetation cover was greatest at agricultural edges and least at roads. Territory positioning was inconsistent with active avoidance of agricultural edges, marginally consistent with avoidance of roads but within the measurement error of the GPS used, and consistent with active avoidance of woodland edge. The Bobolink tended to settle closer to edges where territory densities were higher. One territory extended to within 10 m of a woodland edge. The authors concluded that the habitat differences among the edge types did not explain its distribution. Bollinger and Gavin (2004) studied 375 nests at 3 sites in New York and found that the Bobolink consistently avoided forest edges. Nest numbers within 25 m of forest edge were 0-8% of those expected based on field area. The degree of avoidance varied at sites beyond 25 m from edge. At 1 site, very few nests were 50-100 m from edge but at another site, the number of nests was 98% of those expected 25-50 m from edge. Wooded hedgerows were avoided at 1 site but not at another although the number of nests was lower than expected within 25 m of hedgerows. Road edges were avoided. At 1 site, nest densities were 0% of expected 0-15 m from roads, 57% of expected at 26-50 m, and 235% of expected 50-100 m from edge. At another site, road avoidance appeared to extend 100 m from edge, with nest numbers only 65% of expected 50-100 m from road edges. Old-field and pasture edges were not avoided with nest numbers 0-25 m and 26-50 m from these edges greater than expected. Daily nest survival within 50 m of forest edges was significantly lower than for areas more than 100 m from all edges. Survival was particularly low within 25 m of forest edge and was also lower within 50 m of wooded hedgerows. After nest failure, females tended to move further from forest edges but not hedgerows. Edge avoidance may contribute to area sensitivity in the Bobolink. Grasslands smaller than 10 ha may be poor habitat if they are near a wooded area. Larger fields may be poor habitat if they are bisected by wooded hedgerows. Fragmentation of grassland by agricultural crops, pastures, and old fields is not as detrimental as fragmentation by wooded habitats or roads. In Vermont and New York, it avoided both roads and wooded areas, including hedgerows (Keyel et al. 2013). Perkins et al. (2013) examined edges defined by agriculture, forests, hedgerows, human development, roads, and wetlands in the same area. Areas within 50 m of edge were used significantly less than expected: 60% of habitat was within 50 m of edge but only 17.0% of nests were within that band. Only 31% of habitat was 50-100 m from edge but this area contained 45.5% of nests. Nest survival and nestling mass were unaffected by distance to edge. The Bobolink nested closer to a forest edge more frequently than other edge types. The percent of nests nearest an edge type was 24% for wetlands, 21% for roads, 3% for human development, 1% for hedgerows (significantly less than expected), 42% for forests, and 9% for agriculture. Overall, 652 nests averaged 94.5 m from edge.

The Bobolink is usually considered an area-sensitive species, but this is not always the case. In some areas, it exhibits no sign of area sensitivity. In some regions, it may be area sensitive in some landscapes but not in others. The more grassland and open habitat there is in a landscape, the less likely it is to be area sensitive. In Massachusetts, Ells (1995b) found no evidence of area sensitivity, with it nesting in small scattered fields that were only 1.8-8.1 ha. As many as 30 occurred in a 1.2-ha field during the postfledging period. In Wisconsin, its abundance was positively correlated with the amount of field habitat 25 m from edge when there was a high percentage of tree cover in the landscape. When there was a low percentage of tree cover in the landscape, there was no relationship between field size and its abundance. Renfrew and Ribic (2008) concluded that patch size may be influential on the abundance of the Bobolink in fragmented landscapes. In another Wisconsin study, Ribic and Sample (2001) concluded that field size was not an important variable. In the Prairie Hardwood Transition Bird Conservation Region of the United States, Thogmartin et al. (2006) concluded that it was sensitive to grassland patch size at landscape scales of 800 ha and 8,000 ha. It was more abundant in grasslands surrounded by forest when grassland patches were large. In Minnesota and North Dakota, Winter et al. (2006) found no evidence of area sensitivity. The patches they examined were large with a mean size of 226.1 ha, so they may all have been larger than its minimum size requirements. Another study they completed using grasslands exclusively 65 ha or smaller also found no evidence of area sensitivity. In Ohio, grasslands occupied by the Bobolink averaged 12 ha (range 5-26 ha; Swanson 1996). In fields managed for blueberry production on Maine, its abundance was positively correlated with patch size. Many of the sites were unsuitable for it and Vickery et al. (1994) concluded that their results were probably not applicable to other grassland systems. Johnson and Igl (2001) examined grasslands 2.2-270.5 ha in Montana, North Dakota, and South Dakota. Bobolink abundance and presence was unrelated to size in 2 counties, was positively influenced by size in 4 counties, and negatively affected by size in 3 counties. They concluded that it generally favoured large patches and considered it area sensitive. In New York, its abundance increased exponentially with field size, but it occurred in fields as small as 1.5 ha, with maximum densities occurring in 30-ha fields, the largest examined (Bollinger and Gavin 1992). In Illinois, Herkert (1994a) studied native and restored grasslands 0.5-600 ha. It was significantly associated with larger grasslands, occurring in 88% of grasslands larger than 100 ha and 7% of grasslands smaller than 100 ha. The area at which its probability of occurrence was 50% of its maximum was 50 ha. The Bobolink occurred infrequently in this area, so birds may have occupied only the larger parcels. Seventy-four percent of transects in grasslands contained suitable habitat, but only 7% were occupied. He concluded that the Bobolink was area sensitive and most likely to occur in large grasslands. In Ontario, it is generally thought that the Bobolink prefers fields larger than 10 ha, and that fields as small as 5-10 ha in fragmented landscapes can provide suitable habitat, but the quality of the habitat is diminished if it is surrounded by forest (McCracken et al. 2013). Frei (2011) concluded that patches smaller than 4 ha were unlikely to attract the Bobolink. To compensate for lost Bobolink habitat in Ontario, it is recommended that created grasslands be a minimum of 4 ha with a minimum field width of at least 200 m. There have been no studies on area sensitivity of the Bobolink in Ontario and it is likely to vary geographically. It will probably use smaller patches in agricultural than forested or developed landscapes, and will probably require larger patches where it is less common.

Several studies provided recommendations for creating or managing Bobolink habitat. Habitat must be managed to prevent woody vegetation from invading fields. This may be accomplished by regular mowing outside the breeding season, periodic burning, or grazing at low to moderate intensities. In extensive grasslands, mowing, burning, and grazing should be done rotationally to provide a variety of successional stages. The periodicity of management should be site specific depending upon how quickly woody vegetation becomes established. Habitat should be dominated by grasses with scattered clovers (Bollinger and Gavin 1992; Dechant et al. 2001; McCracken et al. 2013).

During the nesting season, males roost on the ground at night and females remain on the nest until the young fledge (Renfrew et al. 2020).

Almost all (96.8%) Ontario nests were on the ground; 2 were 15 cm from the ground supported by grass stems and another was 30 cm up in vetch. Most were very well concealed under grasses, forbs, and sometimes shrubs, and were woven into surrounding grass and forb stalks; 3 nests were unconcealed. Some nests (13.8%) were in shallow depressions (Peck and James 1987).

Renfrew et al. (2020) stated that nests are always on the ground, but this is not the case. Three Ontario nests were elevated and Bent (1958) reported one 15 cm from the ground. The female selects a small depression for the nest site or scrapes one out. The nest is usually open but is occasionally under cover of heavy litter, usually where forbs are scarce and the litter is deep. New nests are built for replacement clutches; there is no evidence of nest reuse.

The Bobolink is territorial, but tends to nest in small groups of pairs. Single pairs may occur in small or marginal habitat patches. In Nova Scotia, males tended to strongly select territories based on the presence of conspecifics, and yearlings and older males tended to aggregate within their own age class. Presence of conspecifics appeared to be an indicator of habitat quality. The tendency to nest in groups may be a response to its mating systems that include polygyny and extra-pair copulations. Grouping may also explain its tendency to be area sensitive. Males establish territories soon after their arrival on the breeding grounds with territorial defence ending abruptly once the male begins feeding the nestlings. At this time, floater males may successfully establish territories and attract a mate. Territories are used for courtship, nesting, and the initial stages of fledgling rearing. Foraging may occur either on or off the territory. Territory boundaries may fluctuate throughout the season with no apparent relationships to singing perches, foraging sites, or any other features. Early arriving, usually older, males establish large territories but these become compressed as later arrivals squeeze among the established territories. The result is an area of contiguous non-overlapping territories. Females exhibit little aggression toward each other and do not defend a subterritory within the male's territory. Active nests have been found as close as 5 m together on the same male's territory (McCracken et al. 2013; Nocera and Forbes 2010; Renfrew et al. 2020; Savignac 2010a; Wiens 1969). Territory size varies depending upon habitat quality and density of nesting birds. Larger territories are associated with lower-quality habitat and lower nesting densities. Territory sizes of 0.33-4.90 ha have been reported with most averaging 0.4-0.75 ha. In Oregon, territories averaged 0.74 ha in good habitat and 1.46 ha in lower-quality habitat. In a lush Wisconsin field, territories averaged 0.45 ha. In low-quality fields, territories averaged 2.55 ha (range 1.09-4.90 ha). Territories in New York hayfields and pastures were 0.33-0.75 ha at 1 site and

averaged 0.4 ha at another. Territories were 0.45-0.69 ha in Wisconsin hayfields and averaged 0.43 ha in the St. Lawrence Valley of Quebec. Territories averaged 1.4 ha in a Michigan hayfield. In Washington, territories of polygynous males (1.2 ha) were significantly larger than those of monogamous males (0.95 ha). In Iowa, territory sizes increased near road edges, decreased near woodlands, and showed no changes along agricultural edges compared with territories distant from edge. Average territory sizes were similar along different types of edges: 0.34 ha at agricultural edges, 0.34 ha at roads, and 0.35 ha at woodlands (Bollinger and Gavin 1992; Dechant 2001; Fletcher and Koford 2003; Renfrew et al. 2020; Savignac 2010a; Wiens 1969; Wittenberger 1978; Wootton et al. 1986). Because adults often forage outside their territory, home ranges may encompass the territories of several males. The home range becomes even larger once the nestlings fledge (Renfrew et al. 2020).

Natal philopatry rates vary, with some birds returning to their natal area and others dispersing moderate to long distances. In Vermont, Perlut and Strong (2016) recaptured 83 of 759 nestlings (12.5%). Of these, 18 (21.7%) returned to their natal field. Mean and median dispersal distances were 1,267.2 and 1,037.1 m, respectively. Birds that fledged late in the season with below average body mass were most likely to return. Heavier birds that fledge earlier in the season have a longer period to disperse and may exhibit greater dispersal rates. In New York, 6 of 337 nestlings (1.8%) returned to breed (Renfrew et al. 2020). In Wisconsin, 7 nestlings returned to breed the next year; they were all females (Martin 1974). In Oregon, 1 of 8 yearling males (12.5%) established a territory within 1,000 m of its natal territory and 3 settled more than 2,000 m from the natal territory. Zero of 9 returning yearling females nested within 200 m of their natal territory but 6 (66.7%) nested within 1,000 m. Significantly fewer females than males dispersed further than 1,000 m from the natal territory. Females dispersed a mean distance of 810 m (range 290-2,200 m) compared with a mean of 1,610 m (range 120-3,350 m) for males (Wittenberger 1978, 1980a). In New York and Vermont, mean natal dispersal distance was 1,552 m (median 975 m, maximum 8,424 m). Approximately 30% of natal dispersal events resulted in birds breeding in the field in which they were hatched. Most dispersal was less than 300 m or more than 900 m. Birds either returned to their natal field or moved a substantial distance from it. There was no difference in dispersal distances of the sexes, with medians of 361 m for males and 1,033 m for females. Birds were most likely to disperse to a field with the same management practices as their natal field, but chose fields at random with respect to habitat quality. There was a high return rate of yearlings at this site and suitable habitat was patchily distributed so philopatry may have been unavoidable. Young did not make favourable decisions regarding habitat during natal dispersal. Fajardo et al. (2009) concluded that their data did not support the hypothesis that recently fledged young use the presence of conspecifics as a cue to assess potential breeding sites in subsequent years. Brewer et al. (2018) reported longer dispersal distances of juveniles banded in Ontario. Three banded in August at Mountsberg were recovered in a subsequent June in Newmarket, Carlisle, and Maine, having dispersed distances of 19-742 km. These birds were banded in August, so it is possible that they had already dispersed from the natal area.

Adult site fidelity is high and birds nesting in high-quality habitat usually return to the same area every year (Wittenberger 1978). Adult return rates may be influenced by the previous year's breeding success, with successful breeders remaining faithful. Birds that were unsuccessful tend to return to

high-quality habitat but may disperse from low-quality habitat. In New York, 22 of 56 females (39.3%) returned to nest. All settled significantly closer (67 m) to their previous year's nest than the expected distance of 217.3 m (Wootton et al. 1986). In Oregon, males often returned to the same territory but females usually did not. An average of 56.9% of males returned each year. Ninety-six percent of males and 92% of females settled within 1,000 m of where they had nested the previous year. Adult site fidelity was lower in years when areas that were inhabited the previous year dried out. Ten of 27 adult males (37.0%) established territories within 50 m of their previous year's territory. Males dispersed a mean of 205 m (range 0-1,450 m). Four of 13 adult females (30.8%) nested within 50 m of their previous year's nest, 9 (69.2%) within 200 m, and all but 1 within 2,000 m. Females dispersed a mean distance of 315 m (range 0-2,250 m; Wittenberger 1978, 1980a). In New York, significantly more males (44.1%) than females (25.4%) returned to breed in a subsequent year. Return rates were strongly influenced by the previous year's nesting success and by habitat quality. Significantly more returning males had been successful the previous year than birds that did not return, and returning males had significantly more mates the previous year than those that did not return. Females that returned hatched significantly more eggs and fledged more young than those that did not return. Five of 69 former residents (7.2%) that did not return settled 6 km away. Breeding success in the previous year influenced the choice of nesting sites by both sexes. Significantly more birds (70% of males, 49% of females) returned to a high-quality site than to lower-quality sites (44% of males, 25% of females). The return rate of birds that nested successfully the previous year did not differ between high- and low-quality sites. At low-quality sites, successful birds were 3-5 times more likely to return than unsuccessful birds. Unsuccessful birds were more likely to return if they had nested more than 1 year previously than were novice breeders. At high-quality sites, males dispersed a mean of 46 m, significantly less than for females (65 m). Birds dispersed significantly further at low-quality sites (93 m for males and 110 m for females). Unsuccessful birds were more likely to return to high-quality habitat. Females that lost their nests in poor habitat did not return. When birds dispersed between nesting seasons, they moved to higher-quality habitat and areas where the density of breeders was higher (Bollinger and Gavin 1989; Gavin and Bollinger 1988). In New York and Vermont, site fidelity also depended upon nesting success and habitat quality. Adults consistently returned to breed at the previous year's site and more than 80% nested in the same field. The mean dispersal distance was 370 m (maximum 10,637 m). There was no difference in the median dispersal distances of males (129 m) and females (108 m). When birds dispersed, they exhibited strong selection for sites with similar management practices as their previous year's site. Only 4 of 103 dispersal events (3.9%) involved a bird moving to a field with different management practices. Of birds that nested successfully, 93.7% returned to nest in the same field; 79.2% of unsuccessful nesters returned to the same field. Of those that moved, 86.2% made a favourable decision by remaining in or moving to higher-quality fields (Fajardo et al. 2009). In New York and Vermont, high-quality habitats produced more fledglings, had stable populations, and adults living in them survived longer and had higher site fidelity. Return rates in early cut hayfields were 43% for males and 27% for females compared with 63% for males and 46% for females in late-cut hayfields. There was a greater turnover of birds in more disturbed fields. Females that selected high-quality fields either returned or dispersed outside the study area. Some males appeared to disperse regardless of habitat and breeding success. First-time breeders and immigrants settled more frequently in low- and medium-quality fields than in high-quality fields. High-quality fields were at capacity and offered few open territories

(Perlut et al. 2008). In the same fields, the sex ratio of nestlings was 1:1 but male return rates were 35% higher than for females. This suggests that females have a lower survival rate or that a higher proportion of them disperse (Perlut et al. 2014). In Wisconsin, 62.8% of males and 33.9% of females returned. Unsuccessful females had a strong tendency to not return in the following year (Martin 1974). In Indiana, Scheiman et al. (2007) banded 143 males and monitored their movements within and between seasons. Thirty (21.0%) returned in a subsequent year and 24 (80%) were site faithful. Ten males (9.5% of the 105 that were resighted) moved as far as 14.2 km (mean 7.4 ha) to a different population from the one they were banded in, either within or between years. The probability of an individual dispersing from 1 habitat patch to another within a breeding season was 24%. Dispersal was frequent, which functionally linked the spatially separated groups of individuals into a single population.

Limiting Factors

Eggs have been found in Ontario nests from mid-May to mid-July, with most present in the first 2 weeks of June (Peck and James 1998b). In Algonquin Park, eggs and young occur in late June and dependent fledglings have been observed from mid- to late July (Tozer 2012). Egg laying typically begins during the last week of May in Ontario. Most eggs hatch in mid-June and most young have fledged by early July. Second nests hatch around 21-30 June with fledging occurring 1-12 July (McCracken et al. 2013).

Females returning to the same grassland patch often select a male within hours of returning. Females unfamiliar with the site move around the habitat for about 2 days before pairing. After the second day of courtship and by the first day of copulation, the male attempts to attract additional females. Pairing and other mating activities within a given field are highly synchronous. In an Oregon population over 3 years, all primary females selected mates over periods of 5, 7, and 10 days. Secondary females selected their mates later and did so over periods of 7, 10, and 10 days. Polygynous males obtain their second mate 3-8 days after the first. The female constructs the nest in 1 or 2 days and egg laying begins 1-2 days after the nest is complete. In Oregon, the average interval in 3 years between pair formation and laying of the first egg was 5.6, 6.1, and 7.3 days (range 2-17 days) for primary females. This interval averaged 5.8 days over the 3 years for secondary females (range 3-17 days). Early pairing females had longer intervals between pairing and egg laying. Eggs are laid at the rate of 1 a day. Incubation usually begins with the laying of the penultimate egg. The incubation period at 1 Ontario nest was 11 days. The incubation period is 10-13 days with most clutches hatching asynchronously; the last egg usually hatches 20-30 hours later than the others. In Ontario, more than 80% of clutches hatched asynchronously. Young usually leave the nest when they are 10 or 11 days old but may remain as long as 14 days. Young that are disturbed may leave when they are 8 days old, but mostly at age 9 days (Bent 1958; Bollinger and Gavin 1991; Gavin and Bollinger 1988; Martin 1974; Renfrew et al. 2020; Wiens 1969; Wittenberger 1978, 1980a).

The Bobolink typically raises a single brood each year, but there are confirmed records of second broods. At a New York site, 6 of 20 females (30.0%) laid a second clutch after successfully rearing a brood. None were successful in rearing their second brood. At a nearby site, 0 of 21 females were double-brooded. In Vermont, 58 of 798 females (7.2%) attempted a second nest after their first nest either fledged young or failed. One case of a double brood has been reported in Wisconsin. In

Vermont, 10 females attempted to raise a second brood and 6 were successful. Renesting may occur if the first brood is lost but most females do not attempt a replacement nest; 1 female attempted to renest after 2 failures. In a New York hayfield, 5 of 21 females (23.8%) attempted a second nest after the first one failed. After a nest is destroyed, females may disperse 10-15 km (range 0.5-60 km). Only 25-30% of females that disperse attempt to renest (Bent 1958; Bollinger and Gavin 1991; Bollinger et al. 1990; Gavin 1984; Gavin and Bollinger 1988; McCracken et al. 2013; Renfrew et al. 2020; Winter et al. 2004). Clutches of 3-7 eggs have been reported in Ontario, with most containing 5 eggs (average 4.95 eggs). Replacement nests have smaller clutches averaging 4 eggs. Clutches of 1-7 eggs have been reported with most containing 4-7 eggs; 5 eggs is the most frequent clutch size. Clutch size varies with the female's age, whether she is a primary or secondary female, whether it is a replacement clutch, and with the season. As a female ages, the number of eggs she lays increases from an average of 3.8 eggs in her first year to 5.9 eggs in her fourth year. Older females arrive earlier and become primary birds and lay more eggs than later-arriving and younger females that attain only secondary status. One female laid 7 eggs in her first year as a primary bird, became a secondary bird the next year and laid 5 eggs, and was once again a primary female the following year and laid 7 eggs. Secondary females may lay smaller clutches because they receive less or no assistance from the male in rearing the young. Females laying replacement clutches usually lay 1-2 fewer eggs than in their first nest and often become secondary females. Clutch size declines with the season. Mean clutch sizes reported elsewhere include 5.2 and 4.99 eggs in New York, 5.1 eggs in Wisconsin, and 4.7 eggs in Vermont (Bent 1958; Bollinger and Gavin 1991; Martin 1974; McCracken et al. 2013; Norment et al. 2010; Peck and James 1998b; Renfrew et al. 2020; Winter et al. 2004).

Both sexes are capable of breeding when they are 1 year old. It is probable that all yearling females breed, but some yearling males remain bachelors. Territories of unmated males may be drier than those of mated males, support lower densities of insects, or be inferior in other manners. Some unmated yearling males do not establish a territory and remain as floaters. In high-quality habitat in Oregon, only 2% of males were unmated; 27% were unmated in low-quality habitat. In Quebec, 26% of males failed to attract a mate and 8% did not establish a territory. Once a bird has bred, it probably breeds in all subsequent years (Giroux et al. 2000; Nocera and Forbes 2010; Renfrew et al. 2020; Wittenberger 1980a; Wootton et al. 1986).

The pair bond dissolves after the young reach independence. Females that renest may retain their mate or select a new one. When both members of a pair return the following year, they occasionally remate. In New York, 5 of 14 females (35.7%) whose previous mate returned paired with them again. They settled a mean of 31.5 m from their previous year's nest, significantly closer than the mean of 77.3 m for other returning females (Gavin and Bollinger 1988; Renfrew et al. 2020; Wootton et al. 1986).

The Bobolink is strongly polygynous. Polygynous males typically have 2 mates and rarely 3; 1 male had 4 mates. Although polygyny is the norm, monogamous and bachelor males also occur in populations. Polygyny is regulated by females who select territories, rather than males, based on habitat quality and abundance of insect prey. Primary females do not mate until territorial disputes among males are resolved. All males within a population are mated with a primary female before any mate with a secondary female. Females mated to the same male settle randomly with respect

to each other, with internest distances not varying from random, and exhibit little to no aggression toward each other. Females engaging in polygynous relationships do not settle asynchronously as is the case with many other polygynous species. When nests of females within a single territory are asynchronous, males might be more likely to assist at nests of secondary females if the primary nest was near completion. The rate of polygyny at a site is strongly governed by habitat quality. In Oregon, 43.7% of males were polygynous in high-quality habitat compared with 20.2% in lower-quality habitat. Overall, 28.8% of males were polygynous, 49.6% were monogamous, and 21.6% were unmated. Fewer males were polygynous in a dry year when habitat quality was lower. No yearling males attracted a second mate, possibly because their territories were not in the best habitat. Females choose to mate polygynously in high-quality habitat rather than monogamously in lower-quality habitat. The presence of high-quality habitat and more abundant food resources apparently outweigh the potential disadvantages of males contributing less to the rearing of nestlings in nests of secondary females (Bollinger and Gavin 1991; Martin 1974; Renfrew et al. 2020; Wittenberger 1978, 1980a; Wootton and Bollinger 1992; Wootton et al. 1986).

In New York, Gavin and Bollinger (1985) analyzed the nestlings in 7 nests genetically. In 2 nests, all nestlings were not sired by the attending male. Bollinger and Gavin (1991) collected DNA data for 840 nestlings from 191 families. Thirty-six nestlings (4.3%) exhibited genotypes that were consistent with extra-pair fertilizations. The frequency of extra-pair young was 36% for novice males, 10% for males that had nested at the site previously, 11% for novice females, and 22% for females that had nested previously. Frequency of extra-pair nestlings was highest when novice males were paired with experienced females and lowest when experienced males were paired with novice females. Frequencies were highest for primary females (24%), intermediate for monogamous females (12%), and lowest for secondary females (4%). For males, frequencies were similar for polygynous (16%) and monogamous (15%) birds. Bachelor, monogamous, and polygynous males sired extra-pair young at rates similar to their frequency in the population, but no nestlings were sired by nonterritorial floaters. Nearby residents sired most, if not all, the extra-pair young. It was uncertain if females solicited extra-pair copulations or if males actively pursued older primary females. Population density did not affect the rate of extra-pair copulations. As a result of extra-pair copulations, even unmated males may contribute to the population. In Vermont, 42% of 120 nestlings were sired by extra-pair males. Evidence of extra-pair paternity occurred in 57.5% of 40 nests. Extra-pair nestlings were more common in nests of polygynous males (49%) than those of monogamous males (33%), but not significantly (White et al. 2021).

At 4 New York nests, more adults than the parents fed the young. At 1 nest, 2 males and a female fed the nestlings. At 2 nests, 2 females and a male attended the young, and 3 males and a female attended the fourth nest. The reason for helpers at the nest was unclear (Beason and Trout 1984; Bollinger et al. 1986).

In New York, adults tended to forage outside the territory, frequently more than 150 m from the nest. Only 10 of 42 pairs (23.8%) foraged more than 60% of the time within their territories; 60.5% of foraging trips were to areas outside the territory (Wootton et al. 1986). In Wisconsin, adults foraged mostly in their territories early in the season. Later when they were feeding nestlings, most foraging occurred outside the territory, especially in adjacent oat and alfalfa fields and a marsh 1 km away.

Males travelled further for food for nestlings than females. When adults foraged within the territory, the sexes usually did so in different locations (Wiens 1969). In Oregon, both adults often foraged in flooded areas when provisioning the nestlings (Wittenberger 1980a). The Bobolink gleans arthropods from the mid-growth of vegetation and at bases of forbs, grasses, and sedges. It perches atop herbaceous plants interspersed within expanses of grasses or sedges, and eats their seeds. It occasionally forages for invertebrates in trees and shrubs near the nesting habitat. It feeds while walking very slowly on the ground or as it ascends into the lower levels of vegetation. It may jump from the ground to grasp dandelion seeds and those of other plants too limber to permit perching. During the breeding season, the Bobolink forages singly (Renfrew et al. 2020).

Females time their nesting activities and select their territory in relation to the availability of food for nestlings. In Oregon, secondary females showed no preference for areas based on densities of tiger moth caterpillars but settled preferentially in areas with higher owlet caterpillar densities. Females do not select territories until the abundance of caterpillars can be assessed. Primary females begin nesting shortly after caterpillars first emerge in the spring. The nestling period coincides well with peak caterpillar densities unless adverse weather interrupts their emergence. Caterpillar densities decline considerably by the time nestlings fledge (Wittenberger 1978, 1980a). In Nova Scotia, prey availability did not affect where Bobolinks settled, but its abundance was associated with bugs, particularly plant bugs, one of the top 4 prey groups fed to nestlings; spiders were also important prey (Nocera et al. 2007b). Most monogamous males help feed the nestlings but some do not. In Wisconsin, polygynous males fed nestlings at primary nests but not those at secondary nests. In Oregon, almost all polygynous males fed nestlings in secondary nests, often at the same rate as at primary nests. Females that receive male assistance spend more time brooding the young and less time feeding them than those without assistance. When food is scarce, males preferentially feed young in the primary nest and the larger chicks which are most likely to survive. Primary females spend more time feeding and less time brooding when food is scarce and the weather is good. When food is scarce and the weather is poor, primary females do not reduce the amount of time spent foraging but brood less. When food is scarce, males deliver food faster and bring more prey items and a higher biomass of food each trip. When food is scarce, brood reduction may occur with the youngest and smallest chicks starving. Brood reduction rates are higher in secondary than primary nests (Martin 1974; Wiens 1969; Wittenberger 1978, 1980a, 1980b, 1982; Wootton et al. 1986). Food items fed to nestlings in Wisconsin consisted of 57 geometer moth caterpillars, 46 other caterpillars, 17 dragonflies, 7 beetle larvae, 4 spiders, 4 damselflies, 3 adult beetles, 3 adult lepidopterans, and 2 harvestmen (Wiens 1969). The 1,575 food items fed to nestlings by 13 females in Oregon consisted of 44.4% caterpillars, 13.6% grasshoppers, 10.8% tiger moth caterpillars, and 4.1% owlet moth caterpillars. At a low-quality site, the 780 food items a female fed her nestlings consisted of 48.2% caterpillars, 29.0% grasshoppers, 10% owlet moth caterpillars, and 0.8% tiger moth caterpillars (Wittenberger 1980a). In another study in the same area, the major food items delivered to nestlings were lepidopterans and sawfly larvae, with males bringing a significantly higher proportion of each of these than females in every year. Small numbers of beetles, flies, spiders, bugs, adult hymenopterans, neuropterans, mayflies, odonates, and annelids were brought to nestlings. The proportion of caterpillars in the diet of nestlings varied annually and ranged from 54.2% to 65.6% (Wittenberger 1980b, 1982).

In Oregon, adults fed extensively on dandelion seeds in May and early June. In June, the Bobolink ate seeds of other forbs, but less frequently than earlier. These included seeds of cinquefoils, yarrow, Canada thistle, curly dock, and dwarf mallow, although these were not important components of the diet. Other forbs that were present whose seeds were not eaten included yellow sweet clover, hop clover, red clover, American vetch, groundsel, starry false solomon's-seal, and pepperweed. Most of these were host to sawfly larvae and caterpillars of tiger and owlet moths, and butterflies such as whites, sulphurs, common wood-nymph, ladies, and coppers that were fed to nestlings (Wittenberger 1978, 1980a). Bent (1958) reported that the diet of New England birds consisted of 70-90% insects in May, June, and July. In May, the Bobolink consumed a small but quickly dwindling amount of grain and more grain in July, with grain constituting 35% of the August and 3% of the September diets. Forb seeds constituted 8% of the diet in May, June, and July, but increased rapidly in August to 90% of the diet in September. Weevils were an important component of the diet, representing as much as 68% of food items at times. Beal (1900) reported that the Bobolink ate corn, grubs, caterpillars, beetles, grasshoppers, crickets, spiders, and seeds of wild rice, wheat, barley, and other grasses. He analyzed the contents of 291 stomachs. The diet consisted of 57.1% animal matter and 42.9% vegetable matter. The animal diet included 19% beetles (8.9% weevils plus some ground and June beetles), 13% caterpillars that were mostly cutworms (17.6% of the May diet and 28.1% of the June diet), and 11.5% grasshoppers (23.2% in June and 25.8% in July). It also consumed a few flies, bugs, mayflies, spiders, and millipedes. It began to switch to a vegetable diet in August, when oats constituted 31.4% of the diet. Rice was also commonly consumed; other grains such as wheat, barley, and buckwheat were eaten sparingly. In the north, wild rice is more important but cultivated rice is important in the south. It ate forb and grass seeds mostly in August when they represented 36.9% of the diet compared with 16.2% overall. Seeds that were most prevalent in the diet included those of barnyard grass, panic grass, smartweed, and ragweed.

The Bobolink is an occasional host for the parasitic Brown-headed Cowbird and readily accepts its eggs and raises cowbird nestlings. In Minnesota and North Dakota, clutches of parasitized nests were 0.5 egg smaller than unparasitized nests. The number of young fledged from parasitized nests was significantly lower than for unparasitized nests, averaging 1.4 fewer overall. Winter et al. (2004) concluded that the effect of parasitism was insignificant in these populations because the rate of parasitism was low. Cowbirds may destroy Bobolink eggs at nests that are both parasitized and unparasitized, and they may also kill nestlings in unparasitized nests. This may prompt the Bobolink to renest, potentially providing another opportunity for parasitism (Granfors et al. 2001). Habitat may affect parasitism rates. In Minnesota, nests within 45 m of wooded areas were parasitized at a greater rate than those further from edge (Renfrew et al. 2020). In predominantly grassland habitat in North Dakota, parasitism rates declined with increasing tree cover. For every 1% increase in tree cover within 2 km, the odds that Bobolink nests would be parasitized decreased by 5%. Odds of parasitism occurring were 35% at 0% tree cover within 2 km, 25% at 10% tree cover, 19% at 20% tree cover, 10% at 30% tree cover, and 8% at 40% tree cover. The availability of alternative hosts in woodland habitats may reduce the risk of parasitism. Bird densities are higher in woodlands and nests may be easier to find. Cowbirds are less likely to target grassland species in landscapes with sufficient tree cover to provide alternate hosts (Pietz et al. 2009). In Ontario, 8 of 149 nests (5.4%) were parasitized.

Parasitism rates are low in the east: 0 of 422, 0 of 81, and 1 of 375 nests (0.3%) in New York and 1 of 1,025 nests (0.1%) in Vermont; low to moderate in the Midwest: 0 of 57 and 1 of 62 nests (1.6%) in Illinois, 1 of 85 nests (1.2%) and 5-20% in Wisconsin; and higher in the west: 38 of 315 nests (12.1%) in Minnesota and North Dakota, 11 of 36 (30.6%) and 42 of 108 nests (38.9%) in North Dakota, 430 of 839 nests (51.3%) in Nebraska, and 0 of 11 nests in British Columbia (Bollinger and Gavin 2004; Campbell et al. 2001; Granfors et al. 2001; Norment et al. 2010; Peck and James 1998b; Renfrew et al. 2005, 2020; Winter et al. 2004).

The original clearing of forests to create agricultural land was highly beneficial for the Bobolink, resulting in large increases in its numbers and large range expansions. Modern agricultural practices coupled with other land-use changes now represent one of the greatest limiting factors for it. Reductions in habitat quantity and quality are the most significant threats. Based upon a literature review and modelling exercise, Ethier and Nudds (2017) concluded that habitat quantity better defined its population trend than habitat quality.

Habitat conditions were probably ideal for the Bobolink around the end of the 19th century. Prior to European settlement, there were only about 66,500 ha of grasslands in Ontario, mostly tallgrass prairie. There are only 300 ha of this habitat remaining in the province now. This habitat and much of the southern Ontario woodlands were converted to anthropogenic grasslands such as hayfields and pastures. The Bobolink readily adapted to this nonnative habitat. Subsequent habitat loss was related directly to a decrease in the number of livestock and consequently the requirement for hay and pasture. The amount of land planted to hay decreased strongly from 1930 to 1940, due the replacement of horses by tractors and other mechanized machinery. A second sharp decline occurred from 1965 to 1975 related to a decline in the number of cattle as farmers switched from raising livestock to planting crops such as corn and soybeans. The amount of improved and unimproved pasture decreased by 77% and 38% since 1966 and 1971, respectively (McCracken et al. 2013). The decline in the number of cattle, and therefore pastures and hayfields, continues. In 2001, there were 2.141 million cattle in Ontario but only 1.624 million in 2016 (Statistics Canada 2018), a decrease of almost 25%. In addition to changes in the crops grown, habitat was lost due to abandonment of farms, natural succession, tree planting, and conversion to urban areas and other land uses (Cadman et al. 2016; Ethier and Nudds 2017; Frei 2011; Savignac 2010a). Declines in the Carden Plain between the 2 atlases were related mostly to conversion of grasslands to row crops, but habitat in some fields changed from pasture or hayfield to shrublands and became unsuitable habitat (Merondun et al. 2024).

The remaining habitat is of lower quality than it was formerly due to the species that are planted for hay and the intensity of grazing. Hay originally consisted of timothy mixed with moderate amounts of clovers which provided ideal nesting habitat. This hay mix has been widely replaced by monocultures of alfalfa which grow too tall and dense to be attractive to Bobolinks. Until the 1950s and 1960s, most farmers had a few head of cattle, resulting in fairly low grazing intensity. Now limited numbers of farmers raise cattle and grazing intensity is much higher, usually making pastures unsuitable for nesting. The habitat trends that are occurring in Ontario are occurring in much of the Bobolink's range, particularly in the northeastern United States. It is anticipated that current habitat

trends will continue and Bobolink populations will continue to decline in the east (Askins et al. 2007; Bollinger and Gavin 1992; Bollinger et al. 1990).

Next to direct habitat loss, mowing of hayfields during the breeding season is the second most important limiting factor for the Bobolink. This is a direct result of conversion of most hayfields from grass-dominated forage crops to alfalfa crops. Hay is now cut 2-3 weeks earlier than formerly and usually 3 times a year instead of twice. The period between cuts must be 65 days or longer to provide enough time for vegetation to regrow and the Bobolink to complete a nesting cycle. This seldom occurs in alfalfa fields. Near Peterborough, typical hay management resulted in little to no reproductive success and early harvested sites were abandoned for the season. High reproductive success occurred in fields where the harvest was delayed until 14 July, but hay quality fell below ideal protein levels for most cattle before harvest. Delaying cutting from the last week of June until the end of the first week of July can increase fledging rates from 0 to 70%; cutting is rarely delayed this late in Ontario. Not all hayfields are cut every year or during the peak nesting period, and these contribute to the population (Cadman et al. 2016; Diemer 2014; Frei 2011; McCracken et al. 2013; Savignac 2010a). Tews et al. (2013) determined that the greatest losses of Bobolinks due to mowing in Canada occurred in the Carolinian Zone. Losses to the autumn flight due to the death of birds that would have fledged successfully in the absence of mowing were estimated at 321,000 annually in Canada, including 36,000 in the Great Lakes–St. Lawrence Forest Region and 154,000 in the Carolinian Zone of Ontario. Nest losses due to early mowing are high in other areas in the east, typically resulting in 80-100% mortality of eggs, nestlings, and young fledglings. Older fledglings occasionally survive if they are able to move to nearby uncut areas. Mortality occurs from 3 sources: the initial cutting of the hay; predation by gulls, corvids, and other predators on exposed nests and young fledglings; and by raking of the hay prior to baling. When a field is cut, all adults that were present abandon it and typically no birds colonize it later. These birds disperse and most do not attempt replacement nests; their entire reproductive effort for the year is lost (Bollinger and Gavin 1992; Bollinger et al. 1990; Ells 1995b; Fajardo et al. 2009; Nocera et al. 2007b; Perlut et al. 2006; Shustack et al. 2010). In New Jersey, the effects of leaving 5 uncut refugia of 0.25 ha in a 23-ha hayfield were studied. Bobolinks used the refugia more often than the cut areas. Their density increased only slightly in the refugia after mowing, with most differences in densities resulting from lowered densities within mowed areas. Birds completely abandoned fields that were entirely mowed. Although the refugia resulted in some birds remaining after harvest, there was no evidence of renesting (Allen et al. 2019). Mowing every few years later in the season is necessary in most fields to prevent them from becoming invaded by woody vegetation. Wolcott et al. (2023) recommended that grassland management be deferred until August to protect both nests and fledglings.

Light to moderate grazing or grazing on a rotational basis in areas of large pasturelands can be beneficial by preventing natural succession to woody vegetation. Heavily grazed areas where the grass is cropped close to the ground are unsuitable habitat. In most areas, ungrazed meadows support higher densities than those that are grazed. Its preference for moderate to tall vegetation means that grazing has to be low intensity in order to maintain habitat quality. In addition to altering the structure of the vegetation, cattle often trample nests and actively depredate them by feeding on the eggs and nestlings, possibly incidentally. Grazing may also expose nests, making them vulnerable to predation. Grazing appears to be beneficial only when stocking densities are less than

0.198 cows per ha per day. Average stocking density in Ontario is 7 times this rate (Ethier and Nudds 2017; Frei 2011; Giroux et al. 2000; Kim et al. 2008; McCracken et al. 2013; Perlut et al. 2006; Renken and Dinsmore 1987; Savignac 2010a; Swanson 1996). Campomizzi et al. (2019) studied the effects of rotational grazing of cattle on Bobolink breeding success in the Ottawa Valley of Ontario. Some fields were ungrazed in 1 of 2 years during the breeding season; they were grazed normally in the other year. In another experiment, some fields were grazed for 4-8 days between 21 May and 3 June at stocking rates of 31-40 cattle per ha per day and not again until the Bobolink breeding season was over. Over 2 years, 13% and 28% of nests were trampled by cattle; 77% of trampled nests were in fields with 50 or more cattle-days per ha. In the year when fields were ungrazed, young fledged from 54% of territories, significantly more than when the same fields were grazed (16%). In the light spring grazing experiment, 67% of territories fledged young. The probability of a territory fledging young decreased with grazing intensity: 53% at 0 cattle-days per ha and 4% at 174 cattle-days per ha. Fields that were rotationally grazed provided suitable Bobolink habitat and production of fledglings. Favourable conditions for Bobolinks include keeping fields ungrazed until 15 July or grazing fields lightly after territories are established. In Grey County, fields were rotationally grazed beginning in late May. Bobolink abundance decreased 73% after grazing and it was more abundant in ungrazed than grazed fields. It dispersed from grazed fields. Few remained after the first round of grazing and they remained in fields where the vegetation was taller than in grazed fields (Campomizzi and LeBrun-Southcott 2022).

Prescribed burning to reduce woody growth can be beneficial for the Bobolink, provided that it is done either after the breeding season or early enough in spring that vegetation can grow to a suitable height. In North Dakota, it was absent in unburned mixed prairie, reached its highest abundance 2 years after fire, and declined considerably by 5 years after fire. In Minnesota, it was most abundant 1 year postfire at 1 site and at the other site it was absent 1 year after fire but present 2 years postfire (Dechant et al. 2001; Madden et al. 1999).

In the west, abundance and survival of the Bobolink are strongly linked to weather factors such as precipitation and temperature. It is uncertain if these are important in Ontario. In most studies, it was less abundant in dry years. Its abundance was positively correlated with mean annual precipitation, the amount of precipitation in the previous year, and early spring moisture indices. It was negatively correlated with drought indices and the differential between the previous year's precipitation and the long-term average. An exception occurred at a Nebraska site where it was more abundant in dry than wet years. In that location, wet riparian wetlands may have provided a refuge from drought. Nest survival may be lower when June to August weather is wetter than usual. In the Great Plains of the United States, its abundance was positively correlated with maximum August temperatures. Nestling mortality may increase due to exposure to long-term rainstorms, hailstorms, and nights with temperatures near freezing. Adult return rates in Oregon were lower in a year when both sexes encountered both snow and rain storms before arrival, suggesting that these events increased mortality rates (Kim et al. 2008; Niemuth et al. 2008, 2017; Thogmartin et al. 2006; Wittenberger 1978, 1982; Zuckerberg et al. 2018).

Herbicides are unlikely to be a limiting factor for the Bobolink, but pesticides may have adverse effects. Neonicotinoids are a concern due to potential toxicity to pollinators and birds. High

concentrations in surface water have been linked to declines of local populations of farmland-breeding passerines and have negative impacts on nontarget invertebrates that may provide prey. The Bobolink is routinely exposed to pesticides on its wintering grounds in South America where it feeds in treated rice fields. It may be intentionally poisoned there and in the southeastern United States where it may significantly damage rice crops (Cadman et al. 2016; Frei 2011; McCracken et al. 2013; Renfrew et al. 2020).

At 1 Ontario wind farm, the Bobolink was among the top 10 species killed by turbines. It may be vulnerable to being struck by turbine blades because of its high aerial flight displays (McCracken et al. 2013). In North and South Dakota, Bobolinks were attracted to the area encompassing turbines and the area within 0.8 km of them in the first year. After 2-5 years, Bobolinks exhibited an avoidance reaction at 2 of the 3 sites. At 1 site, displacement occurred at all distance categories (0-100 m, 100-200 m, 200-300 m, and more than 300 m), but only within 200 m at the other site. The delayed response may have been due to site fidelity (Shaffer and Buhl 2015).

Grasslands planted for agrofuels have some potential to be beneficial, particularly if cornfields are converted to grasslands, but the high-density planting tends to favour habitat generalists only. Management of these fields to maximize biomass and homogenize vegetation structure is likely to reduce species richness and abundance of grassland birds (Robertson et al. 2012).

Fragmentation of grasslands by forests and other land uses has the potential to reduce nesting success. In Minnesota tallgrass prairies, nest parasitism and depredation decreased with distance from edge; similar results were obtained in Wisconsin. Productivity was greatest in nests more than 45 m from edge. Nest depredation rates were significantly lower on large (130-480 ha) than small (16-32 ha) grasslands (Dechant et al. 2001; Renfrew et al. 2005).

Human disturbance may have low to moderate effects on the Bobolink. Nests discovered early in construction are often abandoned immediately (Renfrew et al. 2020). In Wisconsin, Renfrew and Ribic (2003) placed video cameras at nests to study predation. Nests with cameras were abandoned more frequently than those without cameras. Nests with cameras were more likely to be trampled by cattle. In Massachusetts, Keyel et al. (2012) measured the flight-initiation distance when observers walked toward a male Bobolink. Males flushed at an average distance of 21.8 m and flew an average of 33.5 m. A buffer of 28 m would prevent 75% of males from flushing, 40 m would prevent 95% from flushing, and 59 m would prevent 99% from flushing.

Nixon et al. (2016) predicted the response of the Bobolink to climate change in Alberta. They concluded that 100% of the existing habitat would remain suitable and that there would be a 42% expansion in Bobolink habitat to the north based on more favourable climate in this area. They predicted a large increase in habitat by 2050 and even more suitable habitat in 2080. Price (2004) predicted that the breeding range of the Bobolink might contract in southern Ontario if the average summer temperature increased by 2°C. Unlike Alberta, its range cannot expand northward in Ontario because of the largely forested habitat on the Canadian Shield.

Status

Prior to European settlement, the Bobolink was probably rare in Ontario. Its primary range at that time consisted of the prairies and Great Plains where it was predominantly associated with tallgrass

prairies. It was not very common in this habitat, probably because the grass was taller than it prefers. It may have nested in Ontario in native prairies, savannahs, alvar grasslands, meadow marshes, beaver meadows, burns, and areas cleared for agriculture by First Nations. It was known to breed in natural meadows along the north shore of Lake Ontario in the early part of the 19th century. Settlers deforested large areas and converted them to pastures, hayfields, and other agricultural crops. They also converted most of the native grasslands to croplands and nonnative grasslands. The Bobolink responded positively and expanded its core range both eastward and westward into what had formerly been forested landscapes. The grasses that were planted in hayfields and pastures were an optimum height for it, and it became much more abundant in nonnative than native grasslands (Banville and Gauthier in Gauthier and Aubry 1996; Bent 1958; Cadman et al. 2016; de Vos 1964; Frei 2011; Mayfield 1988; Renfrew et al. 2020). Anecdotal declines were reported early in the 20th century with large declines beginning in the 1930s and 1940s due to changing agricultural practices (Frei 2011; McCracken et al. 2013).

In the Kingston area, the Bobolink was very common by the late 19th century, particularly on Wolfe, Simcoe, and Amherst islands which are agricultural habitats (Weir 2008). In Elgin County, it was a very common summer resident in 1891 and an abundant breeder in 1954; in 2000, it was locally common (Lancaster et al. 2004). In Niagara Region, Sheppard et al. (1936) considered it a common breeder that appeared to be increasing; Black and Roy (2010) considered it a local and uncommon breeder. In Algonquin Park, it formerly nested in old fields and extensive sedge meadows but decreased drastically beginning in the 1980s due to forest succession (Tozer 2012). Baillie and Harrington (1937) reported that it was a common summer resident in the south, breeding north to at least Sudbury and Ottawa. They concluded that it probably bred in Nipissing District and the Thunder Bay area. The first atlas revealed a somewhat broader range for the Bobolink, but confirmed that it was associated predominantly with agricultural lands. It was widespread south of the Canadian Shield; had a spotty distribution in the Shield portion of the Great Lakes–St. Lawrence Forest Region, including the area from Thunder Bay to Kenora; and occurred in the agricultural areas of the Clay Belt. It also probably bred along the James Bay coast north of Moosonee. It was most abundant south and east of the Shield. Within this area, it was less abundant southwest of Chatham-Kent (where hayfields and pastures were less common) and around Lake Ontario from Niagara Region to Prince Edward County (Weatherhead in Cadman et al. 1987). James (1991) considered the Bobolink a common breeder in southern agricultural areas, rare in the north to Dryden and Kapuskasing, and a vagrant north to Big Trout Lake and Moosonee.

The second atlas demonstrated that there had been no significant change in the range of the Bobolink since the first atlas. It was not detected north of Moosonee and in some of the more northern areas where it was observed during the first atlas. Its probability of observation declined significantly province-wide and in all regions. The greatest decline occurred in the Shield portion of the Great Lakes–St. Lawrence Forests Region, probably due to natural succession. Declines south of the Shield were probably due to continuing losses of hayfields and pastures and to increasing use of alfalfa for hay. It was most abundant in the Great Lakes–St. Lawrence Forest Region south of the Shield. Highest densities were in Grey and Bruce counties, around Peterborough and Kingston, and between the Ottawa and St. Lawrence rivers in southeastern Ontario. These areas were associated with lower-intensity farming practices and grazing of small herds of cattle was still common. Despite

its decline, the Bobolink remained a very common species in the agricultural south. On point counts, it was the 12th most abundant species in the Great Lakes–St. Lawrence Forest Region south of the Shield and 24th most abundant in the Carolinian Zone (Gahbauer in Cadman et al. 2007).

The Bobolink has declined significantly throughout its range. According to Breeding Bird Survey (BBS) data, it declined in North America at a rate of 1.7% per year 1966-2004 (McCracken 2005). For 1968-2008, the rate of decline was 5.2% in Canada and 2.6% in Ontario (Savignac 2010a). Ontario supports approximately 13% of the global population of the Bobolink. The sharpest declines in Canada since 2000 occurred in Ontario. Annual rates of decline in the province were 3.3% 1970-2010, 3.6% 1980-2010, 3.7% 1990-2010, and 4.0% 2000-2010 (Frei 2011; McCracken et al. 2013). BBS data indicated annual decreases of 3.06% in Canada and 3.08% in Ontario 1970-2021. The 2011-21 trends were annual decreases of 3.37% in Canada and 4.59% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

The Bobolink has been designated threatened in Canada (McCracken 2022) and Ontario. A strategy for its recovery in Ontario was prepared (McCracken et al. 2013). The long-term goal is to maintain stable self-sustaining populations. The goal for 2013-23 was to slow the annual population decline to an average of no more than 1.0% per year. The long-term goal is to achieve a stable population of approximately 90% of the 2013 population. Maintaining the 2013 population was not considered feasible due to existing trends in agriculture, urbanization, human population growth, and the changing dairy and beef production sectors.

Ethier and Nudds (2015) analyzed BBS data for southern Ontario for 1967-2011 and 1998-2011. Of 35 survey regions, only 5 had positive population trends and 6 had significant negative trends. These were mostly in the southwest and included Brant, Perth, Oxford, Middlesex, and Huron counties and an isolated area in the Kawartha Lakes region. They concluded that the trend estimates exceeded the goals of the recovery strategy and that the outlook for the Bobolink might be more optimistic than analyses obtained at broader scales indicated.

POSTFLEDGING PERIOD

Young are unable to fly when they leave the nest and remain in dense vegetation until they attain the power of flight about 13 days of age. Some fledglings remain near the nest for as long as 5 days. Others disperse as far as 70 m from the nest in the first day. In Oregon, a fledgling from a primary nest was found in one of the male's secondary nests 23 m away. The young and adults usually leave the territory within a week and interfamily flocks may begin to form as early as 6 days after the young fledge (Bent 1958; Renfrew et al. 2020; Wittenberger 1980a, 1980b; Wootton et al. 1986).

Brood division occurs a few days after the young fledge with each adult feeding half the brood. In Oregon, every male continued to feed its primary fledglings while attending secondary nestlings. Within interfamily flocks, adults continue to feed their own young for as long as 28 days after fledging (Renfrew et al. 2020; Wittenberger 1980b).

As soon as the fledglings are capable of flight, usually by mid-July, adults and young form flocks mixed with other families. These often disappear from the breeding fields and move to more secluded locations such as marshes, stream margins, and interfaces between wetlands and

agricultural lands. These flocks feed mostly on weed seeds, but also on grain and wild rice if it is available (Beal 1900; Bent 1958; Campbell et al. 2001; McCracken et al. 2013).

MIGRATION

The Bobolink migrates in flocks, mostly at night but some diurnal movements occur. In spring, flocks are composed of a single sex with flocks of males moving northward first. Autumn flocks contain both sexes as well as adults and juveniles. It makes one of the longest migratory flights of North American passerines, travelling 19,000-20,000 km during a round trip. The flight path is complex and includes transoceanic flights. The autumn migration is protracted and takes 3-4 months, although it may fly as far as 1,200 km a night while flying over the ocean. Some birds flew nonstop between North and South America. Spring migration is more rapid and takes 5-6 weeks (Bent 1958; Hamilton 1962; Perlut 2018; Renfrew et al. 2020).

Renfrew et al. (2019) analyzed the migration of the Bobolink using geolocators for 4 birds in Ontario, 1 in British Columbia, and 15 in the western United States. The Ontario birds were captured at Luther Marsh. Results indicated that most of the global population uses a single migration corridor. Individuals from eastern populations tended to stage more than 250 km from their breeding locations for 1-3 weeks before making consistent southbound flights. The duration of southbound migration was 20 weeks compared with 10 weeks for the northward flight. Two Ontario birds flew from the Colombia-Venezuela border 2,500-2,600 km to Florida within 2 days. A female from Ontario carried out her moult in western Brazil.

Males may initiate northward migration fairly synchronously and arrive on the breeding grounds in flocks. Female arrival is more diffuse. Females arrive 4-10 days after males, averaging about 10 days later in the Kingston area. Yearling females may arrive 1.5-2 weeks later than adult females. Yearling males arrive after adult males (Bent 1958; Martin 1974; Renfrew et al. 2020; Wittenberger 1980a, 1982). Most Bobolinks return to Ontario in the first 30 days of May (McCracken et al. 2013), but some arrive in the last week of April (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004).

Some Bobolinks leave the breeding grounds in late July and early August and congregate in freshwater or coastal marshes while they complete the moult. Others remain on the breeding grounds until mid-August. From mid-August to mid-September, large concentrations occur along the Atlantic Coast from Nova Scotia to Florida (Hamilton 1962; Renfrew et al. 2020). Based on banding at Long Point Bird Observatory, most autumn migration in Ontario occurs between mid-August and 20 September (McCracken et al. 2013). Most leave the southern Shield in late July or early August, but some may persist until mid-October (Mills 1981; Tozer 2012). Autumn migration is underway in southern Ontario by late July or early August with most birds gone by mid-September; birds rarely remain until early November. In Hamilton Harbour, individuals and flocks migrate westward along the Lake Ontario shoreline from the end of July through August and early September (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

During spring migration, birds may first appear on the breeding grounds in typical breeding habitat. The Bobolink may also occur in in grassy fields, oat fields, newly sown rice fields in the south, pastures, sorghum fields, idle fields, and margins of crop fields (McCracken et al. 2013; Meanley 1953). During autumn migration, it may spend several weeks in staging areas where it may

concentrate in large numbers. Certain staging areas are used traditionally and are important in its life cycle by providing abundant food resources for building energy reserves prior to transoceanic flight. Before European settlement, it probably congregated in autumn in wild rice stands along coastal shores and in large rivers in the southeast. These were largely replaced by cultivated rice and the Bobolink exploited this rich food resource. The creation of agricultural land has resulted in more suitable migration habitat. It has become more opportunistic and may concentrate wherever food is plentiful. This may include weedy fields, cornfields, small grain fields, grassy wetlands, and hayfields (Beal 1900; Meanley 1982; Renfrew et al. 2020; Savignac 2010a; Watts 1997).

The Bobolink may roost nocturnally in large numbers during autumn migration. In Virginia, approximately 6,000 roosted in a field of foxtails in scattered dense patches of amaranths 1.2-m tall (Meanley 1982). Two other autumn roosts in Virginia were in dense monocultures of common reed 31 and 70 ha in area. The smaller area was the primary roost, and most birds settled within an area smaller than 1 ha near the centre of the vegetation. Average density of birds within the roost was more than 5 per m^2, but sometimes reached densities several times that. Individuals appeared to roost at night and make most of their southward movements during early morning and late afternoon. Groups of a few to several hundred could be heard flying high and out over Chesapeake Bay, primarily in early morning hours (Watts 1997).

During migration, the Bobolink feeds in flocks. Sentinels sit atop plants while the remainder of the flock feeds, predominantly while they are on the ground. It may feed nocturnally on moonlit nights in rice fields while it is building fat reserves during autumn migration. During spring migration in Pennsylvania, 18 of 27 birds fed exclusively on beetles, larvae, ants, and a few earthworms; others fed on seeds. Historically, autumn migrants fed almost exclusively on wild and cultivated rice, eating the grain when it was still milky. It visits cornfields, tearing open the tops of the husks and eating the milky grain. It also eats large amounts of grass and weed seeds. At a Virginia roost site, seeds of foxtails and goosefoots were favoured foods. Thirty stomachs collected in autumn in an Arkansas rice field contained 76.0% rice, 14.3% paspalum grass seeds, 2.9% barnyard grass seeds, 2.4% panic grass seeds, 1.2% foxtail seeds, 0.5% ragweed seeds, 0.1% smartweed seeds, 2.7% beetles, and traces of soft-winged bugs, stink bugs, locusts, and weevils (Beal 1900; Bent 1958; Meanley 1953, 1982; Renfrew et al. 2020).

Habitat loss is occurring in migration habitat and particularly in wintering areas (Cadman et al. 2016; McCracken et al. 2013).

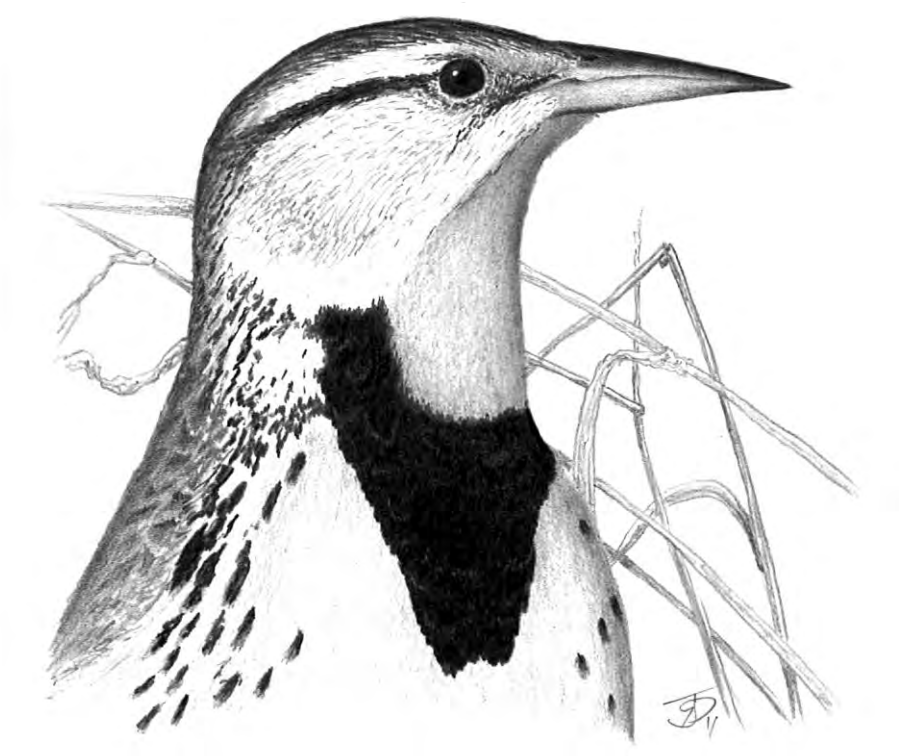
Human persecution during autumn migration was formerly a significant limiting factor. The Bobolink was highly esteemed for its flesh and vast numbers were killed by market hunters. Populations were thought to have been greatly reduced by this activity but numbers rebounded after proclamation of the *Migratory Birds Convention Act*. Bobolinks caused extensive damage to rice crops in the southeastern states and these were also killed in large numbers. There are records of individual landowners killing 45,000-60,000 in a single autumn. Some birds continue to be killed in the southeast, but at a fraction of former rates. Shooting and poisoning of Bobolinks on the wintering grounds still continues (Beal 1900; Bent 1958; McCracken et al. 2013).

During migration, the Bobolink occasionally strikes tall structures such as buildings, communication towers, and lighthouses. This does not appear to be a significant threat (McCracken et al. 2013). Weir (2008) reported that 33 were killed at the Lennox generating station chimneys and that an additional bird was killed by a car.

James (1991) considered the Bobolink a common to locally abundant migrant in Ontario.

Eastern Meadowlark

Sturnella magna

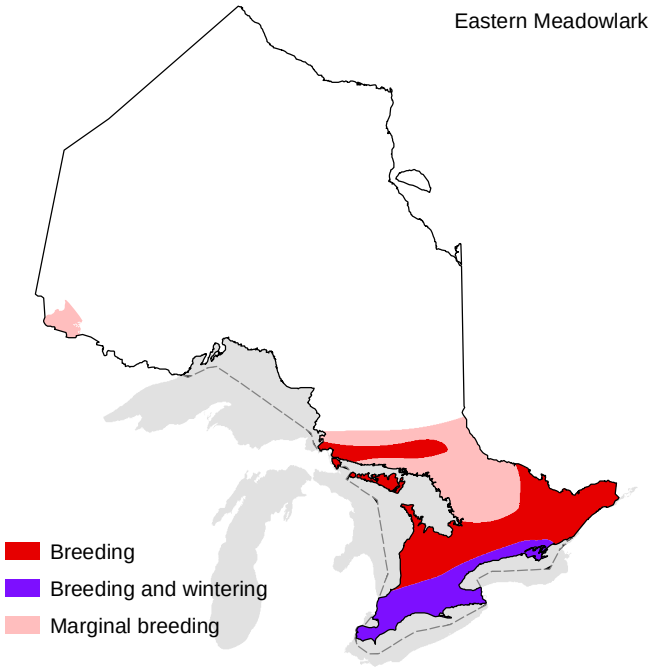


BREEDING SEASON

Habitat Requirements

Ontario Eastern Meadowlark nests were in open grassy fields, pastures, and occasionally golf courses (61.0% of nests); in shrubby and overgrown grassy fields, partially wooded city ravines and parks, young conifer plantations, and orchards (33.9% of nests); in treed sand-dune areas (4.7%); and on road allowances (0.4%). Areas of tall grasses were preferred to those with short grasses. Dry areas were selected more often than wet sites (Peck and James 1987).

The Eastern Meadowlark is an obligate grassland species. In Ontario, it still nests in native grasslands such as remnant prairies, savannahs, and alvar grasslands, but these habitats are rare in the province. It nests predominantly in anthropogenic grasslands, particularly in hayfields and pastures dominated by nonnative grasses such as timothy and Kentucky bluegrass and various



broad-leaved forbs such as clovers. It is most common in pastures followed by hayfields, native grasslands, and savannahs. It also nests in weedy meadows, young orchards, golf courses, grassy roadsides, young plantations, grain fields, herbaceous hedgerows, and grassy airports. It rarely nests in row crops such as corn and soybeans, except perhaps when grassed waterways are present. It is most abundant in agricultural landscapes in areas of high cattle density and with the largest amounts of pasture and hayfields (McCracken et al. 2013). McIlwraith (1894) reported that it nested in agricultural regions throughout the province and was associated with clover fields and freshly mowed hay. In Parry Sound and Muskoka districts, it is restricted to large open areas (Mills 1981). In Durham Region, it nested in a young pine plantation that was still dominated by shrub willows and meadowsweet; in an abandoned grassy field with scattered hawthorns and apple trees 1.2-m tall; in an old field dominated by grasses, goldenrods, and asters; and in hayfields of clover, timothy, and alfalfa (Speirs and Orenstein 1967, 1975). In Niagara Region, it nested in old fields dominated by grasses and in abandoned vineyards with grasses and forbs growing among rows of old posts and dead cultivated grape stalks. The fields were crossed by several old fence lines that were used as song perches (Knapton 1987, 1988b).

The Eastern Meadowlark was equally abundant on organic and conventional farms in southern Ontario. It was positively correlated with fences and negatively correlated with hedgerows, woods, spring grain, and road and utility rights-of-way (Kirk et al. 2011).

Throughout its range, the Eastern Meadowlark is associated with open grasslands. In the northeast, it uses a wide range of grassland types, often in association with the Bobolink. In addition to native grasslands, it nests in pastures and hayfields dominated by nonnative grasses. In the Midwestern and eastern states, it is common on reclaimed surface mines planted to grasses. In the central portion of the continent, it inhabits tallgrass prairies where it prefers vegetation of moderate height. It also nests in Conservation Reserve Program (CRP) fields. It tends to avoid short-grass prairies (Askins et al. 2007). A variety of nonnative grassy areas may be used for nesting. These include old fields and meadows, CRP lands, hayfields, young orchards, golf courses, restored surface mines, grassy roadsides, pastures, young plantations still dominated by grasses, grain fields, herbaceous fencerows, Dense Nesting Cover (DNC) established for waterfowl, grassy patches within plowed fields, fields of grain stubble, cranberry and blueberry fields, wet meadows, grassed waterways, farmstead shelterbelts, fallow fields, weedy borders of croplands, airports, shrubsteppe communities, grassy areas along railways, large woodland clearings, no-tillage corn and soybean

fields, and oak and pine barrens (Galligan et al. 2006; Granfors et al. 1996; Graves et al. 2010; Hull 2002; Jaster et al. 2020; Lanyon 1956a; Mossman et al. 1991; Norment et al. 2010; Roseberry and Klimstra 1970; Rotenberry and Wiens 1980; Savignac 2011b; Swanson 1996; Vickery et al. 1994). Native grasses that the Eastern Meadowlark nests in include big bluestem, little bluestem, grama grass, switchgrass, broomsedge, and Indian grass. Common forbs include sunflowers, milkweeds, and dense blazing star (Askins et al. 2007; McLaughlin et al. 2014; Shugart and James 1973; Winter and Faaborg 1999). It may use a variety of nonnative grasses for nesting: timothy, orchard grass, redtop, smooth brome, Kentucky bluegrass, quack grass, tall ryegrass, meadow fescue, and Virginia wild rye. Timothy, orchard grass, and bluegrasses tend to be the dominant grasses in northeastern areas. These fields may contain forbs such as thistles, clovers in the genus *Trifolium*, bird's-foot trefoil, alfalfa, wild carrot, and milkweeds (Norment et al. 2010; Renfrew and Ribic 2008).

The Eastern Meadowlark is less affected by habitat variables at the landscape scale than many other grassland species. In Quebec, it is associated with open agricultural landscapes and is patchy in distribution and rare in more northern forested landscapes (Rail in Gauthier and Aubry 1996). In Wisconsin, it was associated only with variables at 200 m and 400 m and not by characteristics of larger landscapes. There was a tendency for it to be more abundant where grasslands were more abundant within 200 m. Densities were higher further from woodlots or where overall hedgerow length was greater in the landscape. Densities were higher in areas with more hedgerows or where hedgerows were closer. Hedgerows were important because they were used as singing perches (Ribic and Sample 2001). In the same area, it was negatively correlated with the amount of woody cover within 200 and 1,200 m. Its abundance was affected by the amount of core grassland area more than 25 m from edge. When the percent coverage by grasslands within 200 m was low, its abundance increased with increasing core area. In landscapes with a high percentage of grassland within 200 m, the pattern was reversed. Interactions between microhabitat variables and landscapes were important only where grassland cover was low (Renfrew and Ribic 2008). In Nebraska and Kansas, its abundance and presence were positively correlated with grasslands, pastures, hayfields, CRP lands, emergent herbaceous wetlands, minimum temperatures, and long-term precipitation. It occurred mostly in moister portions. It was negatively correlated with forest cover and developed areas. As tree cover increased in the landscape, its occurrence declined. It had a high probability of occurrence at 0% tree cover, moderate at 30% tree cover, and low at 100% tree cover (Niemuth et al. 2017). In the Prairie Pothole Region of the United States, it was positively associated with grasslands, particularly at the 800-m scale. It had the highest niche breadth of all grassland species, indicating that it was a habitat generalist (Murray et al. 2008).

The Eastern Meadowlark exhibits distinct preferences for types of grasslands. It prefers grasslands with moderately tall vegetation with abundant litter cover, a high proportion of grass coverage, moderate to high forb density, and low coverage by woody vegetation. Nonnative grasslands are often preferred to native grasslands. Grasses in tallgrass prairies and other native grasslands may be taller than it prefers. In Missouri and Ohio CRP fields planted to switchgrass or nonnative grasses, it was more abundant in nonnative grasses probably due to their lower height. In Nebraska, it was found only in native grasslands and not in sorghum fields or CRP fields planted to either nonnative or native grasses. This was probably because CRP vegetation was tall and dense and did not provide adequate perch sites. In Oklahoma, densities were higher in moderately grazed

heterogeneous tallgrass habitats than in ungrazed homogeneous tallgrass. In Kansas, abundance was highest in CRP fields with the greatest abundance of forbs (Hull 2002). In Illinois, pasture was the preferred nesting habitat followed in order by hayfields, CRP fields, winter wheat fields, idle fields, and fallow areas. Alfalfa fields were the least preferred type of hayfield. Fully stocked alfalfa fields lacked sufficient grass cover at ground level to provide suitable nesting habitat and the vegetation was probably denser than it prefers. Grass-invaded fields of sparse alfalfa provided appropriate nesting cover. In hayfields, density was highest in mixes of orchard grass, meadow fescue, timothy, bluegrass, and downy brome. Few birds used dense uniform stands of meadow fescue with some orchard grass and bush-clover. Density was higher in this habitat where planted grasses had died out and were replaced by bush-clover, panic grasses, and other invading species. Fallow fields were seldom used because of an absence of sufficient grass cover. One to 2 years after termination of cultivation, there were still too few dead stems available for nesting. Idle lands received little usage because they supported numerous shrubs and small trees and a variety of forbs mixed in with the grasses. Areas with suitable ground cover for nesting were avoided if woody cover was extensive. Idle areas that received moderate use were recently idle and had a better cover of grasses than fallow areas, but supported little to no woody vegetation (Roseberry and Klimstra 1970). In North Carolina, Moorman et al. (2017) investigated a variety of field types, including wildlife fields planted to native grasses and forbs. It was absent in wildlife fields. They contained the dense litter and dense ground cover that it prefers but lacked the vertical structure of vegetation that it requires. It used both hayed and grazed native grasslands, but at lower densities than in fields of nonnative grasses. The height of the native grasses was too tall to be attractive. It was most abundant in grazed nonnative grasslands followed by hayed nonnative grasslands. The grazed nonnative grasslands were larger than other field types and this may have partially explained why density was highest in these fields. These grasslands had short grass heights, a moderately dense litter layer, no woody vegetation, and high coverage (50%) by forbs. In New York, nest survival was higher in hayfields and pastures than in fallow fields (Norment et al. 2010).

Numerous studies examined microhabitat preferences of the Eastern Meadowlark. It prefers vegetation 25-50 cm in height, but may use areas with vegetation 2.5-75 cm tall provided that other conditions are ideal. Best foraging habitat is 10-30 cm tall. Effective vegetation-height density of nesting habitat ranges from 6-30 cm and is mostly 20-30 cm. It avoids areas of very sparse or dense vegetation. Percent litter cover in occupied areas ranges from 7-70% and averages around 30%. Areas with sparse litter are avoided. Litter depth is typically 2-5 cm in territories. Very dense litter may inhibit movement and tends to be avoided. Ideally, grasses occupy 80% or more of the habitat; areas with less than 20% grass coverage are unsuitable. It may tolerate forb coverage as high as 50%, but prefers less than 20%. Areas completely dominated by grasses without forbs may provide excellent habitat. The coverage by bare soil within territories varies from 0% to 42%, but less than 8.5% appears optimum. Less than 5% woody vegetation is preferred and once woody cover exceeds 35% the habitat becomes marginal or unsuitable (Kerschner et al. 2004a; McCracken et al. 2013; Schroeder and Sousa 1982; Wiens 1969). In Ohio, Graves et al. (2010) studied the influence of woody cover on reclaimed surface mines on the Eastern Meadowlark. Its abundance was negatively correlated with woody cover. Daily nest survival was significantly negatively correlated with the amount of woody vegetation surrounding the nest. Woody vegetation may attract predators and reduce nest survival.

Mean vegetation parameters were 1.5% woody vegetation within 100 m, 1.9 woody patches within 100 m, and 201.8 m to the nearest woodland. Nest sites had 72 times less woody cover and fewer woody patches within 100 m than random locations. On reclaimed surface mines in West Virginia, it was more abundant on areas planted to grasses than shrubby areas, but not significantly (Margenau et al. 2019). In Illinois, presence of dead grass stems at ground level and absence of woody vegetation or numerous shrubs within the immediate vicinity appeared to be prerequisites for nesting. Cover height at 204 nests was 5-76 cm (average 37.8 cm); 66.6% of nests were in vegetation 25-50 cm tall. One nest was in the mowed portion of a golf course fairway. When it nested in gently rolling or moderately hilly terrain, it exhibited a definite affinity for slopes rather than flat crests or valleys. Most (75.8%) were in areas of good to excellent drainage where they would not be flooded or washed out except possibly under torrential conditions (Roseberry and Klimstra 1970). In Nebraska and Iowa, its occurrence was positively correlated with the total number of grass hits and negatively with mean vegetation height. Its probability of occurrence was 75% at vegetation heights of 15 cm, 60% at 20 cm, 30% at 25 cm, 20% at 30 cm, and 5% at 35 cm (McLaughlin et al. 2014). In Missouri, it was most abundant where the grass was 10-30 cm tall (Jaster et al. 2020). In Kansas tallgrass prairies, it selected nest sites with higher vertical vegetation density and greater litter depth, less bare ground, and sites further from patches of bare ground 1 m^2 or larger than random sites. In West Virginia, nests were associated with greater amounts of standing dead vegetation, deeper litter, and taller vegetation than random sites (Jaster et al. 2020). In shrubsteppe communities in the Midwest, there was a clear association between its abundance and variables describing tallgrass plots with dense grass and deep litter, but it was strongly negatively correlated with bare soil and increasing horizontal heterogeneity. It was positively correlated with grass cover, litter, total vegetation hits, the maximum dm interval containing hits, effective hits, the number of hits in the first dm, and litter depth. It was negatively correlated with percent coverage by bare soil or rock, the coefficient of variation of total hits, the coefficient of variation of litter depth, the coefficient of variation of maximum-minimum forb and shrub height, the total hits heterogeneity index, and the litter depth heterogeneity index (Rotenberry and Wiens 1980). Abundance of the Eastern Meadowlark in mixed-grass prairies was greatest when red cedar coverage was less than 10% and was consistently near 0 at 25% coverage. The presence of cedar appeared to override the influence of other cover features (Chapman et al. 2004). In Arkansas, it was common to abundant in open fields but absent in fields that had been invaded by shrubs and small trees (Shugart and James 1973). In Kansas, it occurred mostly in hayfields and prairies where the grass was fairly short. An area of dense grass with a heavy accumulation of dead vegetation on the ground was not occupied, but it nested in nearby grain fields. As the grain grew taller, it provided better nesting cover than the dense stand of smooth brome (Fitch 1958). In Maine blueberry fields, it was positively correlated with grass cover and shrubs 0-60 cm tall and negatively correlated with shrubs 0.6-2 m tall. It preferred areas of extensive grass cover (Vickery et al. 1994). In Wisconsin, occupied fields were large and grassy with some elevated singing perches and some litter present of variable depth and density. Occupied areas had 96% grass coverage: 17% at grass height of 10-20 cm, 11% at height 20-30 cm, 1% at height 30-40 cm, 0% at height 40-50 cm, and 1% at height above 50 cm. Other characteristics of occupied habitat included 3% bare ground, 41% effective vegetation height below 5 cm, litter depth 2 cm, forb height 20 cm, and effective vegetation 6 cm. Litter coverage was 61% in territories and 80% in unoccupied areas, but 92% at nests (Wiens 1969).

In Missouri CRP lands, it was negatively correlated with percent canopy coverage by dead vegetation and positively correlated with percent live grass canopy, length of pasture-hayfield edge, vertical obstruction, litter cover, and area of core (greater than 50 m from edge) hay and grassland. In Nebraska CRP fields planted to nonnative grasses, it was negatively correlated with litter depth (Hull 2002). In Wisconsin, its abundance was negatively correlated with the maximum vegetation height and vegetation height-density. It was positively correlated with percent litter cover, density of prostrate residual vegetation, and woody vegetation, although occupied areas were characterized by only 4% tree and shrub coverage. Mean vegetation characteristics included 74% vegetation coverage, 29% litter cover, 5% bare ground, 66 cm maximum vegetation height, and 20 cm vegetation height-density (Swanson 1996).

Perches may be an important habitat component for the Eastern Meadowlark. Although males occasionally sing from forbs, it prefers taller perches. These include shrubs, isolated trees, fence posts and wires, hedgerows, and edges of woodlots. In Wisconsin, 67% of territories contained posts, 67% contained a fence line, 33% a bale or tangle of wire, and 58% a tree that functioned as a singing perch. Other features that may be used as singing perches include power lines, mounds of earth, and farm implements. Territories may contain several perches. One is usually selected as a favourite and becomes the centre of the territory. This may be changed by polygyny when a male selects secondary perches nearer his mates (Gross in Bent 1958; Wiens 1969). In Missouri, areas at song perches had few woody stems less than 2.5 cm diameter at breast height (DBH) and 0 larger than 2.5 cm DBH, more than 90% ground coverage by vegetation, and more than 65% litter cover (Hull 2002). In Michigan, Harrison (1977) installed perches 1.5 and 2 m tall in an alfalfa field. In 34 of 40 observations, the taller perch was selected. Significantly more 2-m tall perches and significantly fewer 1.5-m perches were used than expected.

Several studies compared the habitat characteristics of territories with unoccupied areas and nest sites with the remainder of the territory. Others studied the effects of habitat features on nest survival. In Kansas, microhabitats at nests in CRP fields and grazed grasslands did not differ, indicating that the Eastern Meadowlark had the ability to find suitable nest sites despite large differences in habitat structure. The main difference between nests, areas within 5 m of a nest, and random sites was that litter within 5 m of the nest was finer in diameter than at the nest or random sites. Habitat was more homogeneous at nests than at other locations. Areas within 5 m of nests were more similar to nest sites than random areas for all parameters except the fineness of the litter. Successful nests had more grass and standing dead cover than unsuccessful nests (Granfors et al. 1996). In Kansas, the 0.25 m^2 around the nest had significantly less bare ground than the area 1-10 m from the nest. It selected nest sites with significantly greater litter cover and depth, a higher proportion of grass cover, and more structured homogeneity than was available in random areas (Hull 2002). In Illinois, there were no significantly different nest-site characteristics between successful, failed, and subsequent nest sites except that the maximum vegetation height was taller at successful initial nests. Females that failed during their first nesting attempt selected areas with similar nest-site characteristics for their second nesting attempt (Kerschner et al. 2004a). In Wisconsin, territories had lower coverage by dead forbs, medium- and heavy-stemmed forbs, and very narrow-leaved grasses than unoccupied areas. In unoccupied areas, forb density was somewhat lower but the forbs were taller. Vertical vegetation density and mean effective height were significantly lower in territories,

but vegetation density near the ground was greater. Coverage by low lawn-like vegetation was considerably greater in unoccupied areas than in territories. Litter in territories was significantly shallower, less extensive, and less compact than in unoccupied areas. In early spring, it selected areas where the litter was significantly deeper, more compact, and more continuous than in unoccupied areas. It also selected areas with more grass cover and less bare ground. Vegetation around nests was denser and taller than in the entire territory. Vertical vegetation density was significantly greater at nest sites than in territories but there was no difference in vegetation density near the ground. Light penetration to the ground was less at nests than within the entire territory. Litter was used to form the nest dome and was substantially deeper at nest sites than in the entire territory (Wiens 1969). In Indiana, nest survival was greatest in shrub savannah habitat and lowest in open and mixed grasslands. Nest survival increased with increasing distance to forest in shrub savannah habitat (Galligan et al. 2006).

Several studies compared the habitat preferences of the Eastern Meadowlark with those of other grassland-nesting birds. McCracken et al. (2013) compared the habitat preferences of it and the Bobolink. These are important to understand because there is often a requirement in Ontario to create habitat that is suitable for both species. This meadowlark may inhabit smaller fields than the Bobolink; it prefers to nest in drier areas and will nest along field margins whereas the Bobolink prefers damper areas away from edge; it is associated more with pastures and less with hayfields than the Bobolink; it prefers a lower proportion of forbs (11-15%) than the Bobolink (more than 20%); it tends to nest in less dense and shorter vegetation; it is tolerant of higher coverage by shrubs (35%) than the Bobolink (less than 25%); and it can withstand as much as 8.5% bare ground compared with 0.3% for the Bobolink. Lanyon (1956b) compared habitat preferences of Eastern and Western meadowlarks in the zone of overlap within the United States. The Eastern Meadowlark preferred tallgrass prairies. The Western Meadowlark was better adapted to short and mixed-grass prairies. In the western portion of the overlap zone where the Western Meadowlark is more abundant, it prefers extremely dry upland areas. The Eastern Meadowlark occurs in lowland areas with lush vegetation. The Eastern Meadowlark preferred smaller fields, taller vegetation, and damper soils. The Western Meadowlark preferred larger fields, shorter vegetation, and better drainage. Where the Eastern Meadowlark was more abundant, the Western Meadowlark nested on upland ridges of prairie surrounded by Eastern Meadowlarks in a variety of habitats. Vegetation was not a dominant factor in defining the 2 species' distributions. Soil moisture was the most important factor. The differences in vegetation at sites occupied by the 2 species were a direct consequence of soil drainage. Szijj (1960) found no differences in the habitats of Eastern and Western meadowlarks in Ontario. The species were not segregated by soil moisture and exhibited no apparent differences in habitat selection. In Midwest shrubsteppe communities, habitat of the Eastern Meadowlark was most similar to that of the Dickcissel, with a 90% niche overlap, and the Grasshopper Sparrow, with a 65% niche overlap. Of the species studied, the Eastern Meadowlark was the second most specialized species. The Bobolink tends to be more specialized but was not included in the analysis. The overlap between this meadowlark and the Dickcissel was 98% on a vegetation gradient that dealt mostly with grass and litter components (Rotenberry and Wiens 1980). In northern Illinois, density of the Eastern Meadowlark appeared to vary inversely with that of the Red-winged Blackbird. This was attributed to habitat preferences rather than interspecific territoriality (Graber and Graber 1963). It is

probable that the Red-winged Blackbird nested in areas that were wetter than this meadowlark prefers. Wiens (1969) compared habitat preferences of the Eastern Meadowlark with those of the Savannah Sparrow, Vesper Sparrow, Grasshopper Sparrow, Henslow's Sparrow, and Western Meadowlark in Wisconsin. Forb density and coverage of Eastern Meadowlark territories were intermediate among values for the species. Mean forb height in this meadowlark's territories was less than for the Bobolink and Henslow's Sparrow and greater than for the Western Meadowlark, Savannah Sparrow, and Vesper Sparrow. Vertical vegetation density was similar to most species but significantly less than in Henslow's Sparrow territories. Density of vegetation on the ground in Eastern Meadowlark territories was less in areas occupied by the Western Meadowlark and Vesper Sparrow and greater than in Bobolink and Henslow's Sparrow territories. Coverage by low vegetation (effective height 5 cm) was slightly greater than in Bobolink territories and similar to Savannah and Vesper sparrow territories. The mean effective height was less than that in Henslow's Sparrow territories but greater than in Western Meadowlark and Savannah, Grasshopper, and Vesper sparrow territories. Litter in Eastern Meadowlark territories was deeper than in Western Meadowlark and Vesper Sparrow territories and shallower than in Bobolink and Henslow's Sparrow territories. Eastern Meadowlark territories were closer to fence lines than other species and not far from cultivated fields and woods. Territories averaged 165.8 m from a woodlot (range 10-330 m), 11.6 m from a fence line (range 0-60 m), and 45.8 m from a cultivated field (range 0-180 m). In early spring, the Eastern Meadowlark occupied areas with greater grass cover and less bare soil than the Savannah Sparrow, but occurred where the overall vegetation height and litter depth were lower. Substrates used by this meadowlark for singing and perching included 50.0% grasses, 41.4% posts, 7.7% trees, and 0.9% in flight. Foraging substrates included 54.8% grass 0-5 cm tall, 36.4% grass 6-10 cm tall, and 8.7% grass 11-15 cm tall. It used grass cover more than any other species, predominantly for foraging in low grasses. Half of singing activity was in grass cover but forbs were also used for singing and perching. Litter depth at nests was greater than for the Bobolink and Savannah and Grasshopper sparrows. Forbs at this meadowlark's nests were of intermediate height and widely dispersed. Forb coverage at nests was the least compared with nests of Bobolinks and Savannah and Grasshopper sparrows. Species arranged in increasing order of vegetation richness (vegetation density and height, and litter coverage and depth) included Western Meadowlark, Vesper Sparrow, Savannah Sparrow, Grasshopper Sparrow, Eastern Meadowlark, Bobolink, and Henslow's Sparrow. There were many similarities in habitat occupancy of the species, especially among the Savannah Sparrow, Grasshopper Sparrow, and Eastern Meadowlark. The range in differences in the habitat ranking was low. Differences in patterns of foraging in grasses by the species may have been sufficient to bring them into contact with different types of food items.

The Eastern Meadowlark exhibits limited to no evidence of edge avoidance, although nests near forested edges may be subject to higher rates of predation and parasitism. In Wisconsin, Renfrew et al. (2005) pooled results for the 2 meadowlark species. Nest density was lower near edges, but not significantly. Nests within 50 m of a wooded edge tended to have higher predation rates than those the same distance from nonwooded edges, but not significantly. There were no differences in predation rates 100 m from wooded and nonwooded edges. Edges were bordered by fence lines and the Eastern Meadowlark may establish territories close to them so that they can use trees as singing perches. In Illinois, nests were a median of 80 m (range 3-400 m) from cropland edges and

a median of 400 m (13-1,000 m) from a wooded edge. Results suggested that it did not avoid cropland-grassland edges but may avoid wooded edges. Significantly fewer nests were found within 100 m of wooded edges. Proximity to edge had no effect on daily nest survival (Walk et al. 2010). In Kentucky and Tennessee, there were no differences in its abundance at roads or areas 300 and 600 m from roads (Lituma and Buehler 2016). In Kansas, meadowlarks that nested within 100 m of woodland edges experienced higher rates of nest parasitism. The mean distance of nests from agricultural edges was 44 m compared with 50 m from woodlands, suggesting no avoidance of either edge type (Hull 2002).

There is little evidence that the Eastern Meadowlark is area sensitive. In Illinois, Herkert (1994a) concluded that it was positively correlated with patch area. Eight-eight percent of transects in grasslands larger than 100 ha contained suitable habitat and 100% were occupied. All transects in smaller grasslands contained suitable habitat but only 77% were occupied. The probability of its occurrence was approximately 30% in 1-ha patches, 55% in 10-ha patches, 85% in 100-ha patches, and 98% in 1,000-ha patches. He concluded that the minimum patch size for the Eastern Meadowlark was 5 ha. This was the area at which its probability of occurrence reached 50% of the maximum. It occurred less than 50% of the time in grasslands smaller than 5 ha, about twice the size of a territory. In Maine blueberry fields, it was positively correlated with patch size, but it had a low rate of occurrence (40%) even in 500-ha patches reflecting the fact that many of the sites were unsuitable habitat. Vickery et al. (1994) concluded that size was an important factor in their study area but that their results were probably not applicable to other grassland systems. This study and the one by Herkert (1994a) are frequently cited as demonstrating that the Eastern Meadowlark is an area-sensitive species. It was only mildly area sensitive in Illinois, occurring in 50% of patches as small as 5 ha. Walk et al. (2010) and Walk and Warner (1999) found it in every grassland they studied, ranging from 3-142 ha. They concluded that there was no evidence of area sensitivity or that nest survival was related to patch size. Nest survival rates were higher in small than large grasslands. Even small grasslands were important from a conservation perspective. McLaughlin et al. (2014) concluded that patch size was not an important predictor of Eastern Meadowlark occurrence or density in Nebraska and Iowa. In New York, Norment et al. (2010) found it in fields 5-98 ha in size. Grassland area had little effect on nest survival in hayfields and pastures, but survival was lower in larger fallow agricultural fields. Their results were influenced by lower survival rates in 1 large fallow field. In Wisconsin, grassland size was not an important variable influencing its presence and abundance (Ribic and Sample 2001). In Missouri, there were no effects of grassland area on its density or nesting success. The smallest prairie that Winter and Faaborg (1999) sampled was 31 ha, so their patch sizes may have been too large to detect area sensitivity. In Ohio, 10 occupied fields averaged 14 ha and 24 occupied CRP lands averaged 10 ha (range 1-26 ha; Swanson 1996).

Swanson (1996) and Hull (2002) recommended management practices for maintaining habitat for the Eastern Meadowlark. Woody encroachment should be limited by mowing every 3-5 years. This also removes accumulations of dead vegetation that may make cover too dense to be suitable. Mowing should be done later in summer after young have fledged and left the area. Light grazing that leaves 40% or more vegetative cover at least 25 cm tall is beneficial because it results in vegetation of intermediate density and height; grazing also removes woody vegetation. Tallgrass prairie should not be grazed to below 25 cm during the breeding season. Burning in early spring

can be beneficial but it is desirable to maintain a complex of burned and unburned areas. No more than 50-60% of an area should be burned at once.

The Eastern Meadowlark roosts nocturnally on the ground, usually in dense grass (Jaster et al. 2020).

All Ontario nests were on the ground, often in a depression. Most nests (88.2%) were hidden in or under grass clumps, 5.1% were under clumps of other plant species, and 2.9% were at bases of shrubs or small trees. One nest each (total of 2.9%) was under pine branches and forbs, under manure and straw, under a piece of linoleum, and under a mound of sod. One nest was within 1 m of a paved road (Peck and James 1987).

Nests are almost always in a depression in the ground. These are usually scraped out by the female, but occasionally deeper depressions caused by cattle or horse tracks are used. Nests are occasionally built in rather deep bowls or natural depressions, allowing nesting in areas with very little cover and grass heights as low as 5 cm. Unused nests are commonly built or partially built early in the season when females may not have attained the full sexual and physiological conditions required for nesting. Of 388 Illinois nests, 126 (32.5%) were not used; 32.0% of these had no canopies and only 18.0% had full canopies. Of used nests, 17.3% had no canopies and 38.2% had full canopies. Some nests have obvious runways that may be as long as 1 m leading to the entrance. Of 377 Illinois nests, 19.1% were excellently concealed, 47.8% were well concealed, 28.9% were fairly well concealed, and 4.2% were poorly concealed. There was no relationship between nest concealment and fledging success. Nests are not used more than once (Gross in Bent 1958; Jaster et al. 2020; Roseberry and Klimstra 1970; Wiens 1969). Nest orientation is nonrandom, with most nest entrances facing north or east away from prevailing winds. In Kansas and Oklahoma, nests were oriented more to the east before the median date of nest construction and more northward later in the season. The prevailing winds were from the south and shifted significantly from the southwest to the southeast as the season progressed. Nest orientation in the opposite direction of the prevailing winds has thermoregulatory advantages by being out of the wind and providing shading from the sun. Orienting nests in the direction of wind-blown grasses might confer some structural advantages in constructing nest domes. In Kansas, nests were normally oriented east to northeast, but were oriented southward in a drought year. This may have diminished morning solar radiation and increased cooling due to the prevailing southerly winds. In Illinois, most nests on slopes faced downward but a few faced upslope. An Oklahoma nest on a steep slope faced downward. A nest within 2.7 m of a busy railway faced away from it. Nest locations do not appear to be correlated with any particular position in the territory or with singing perches (Corimanya et al. 2024; Gross in Bent 1958; Jaster et al. 2020; Long et al. 2009; Roseberry and Klimstra 1970; Shackford 1990; Wiens 1969).

Males are territorial and begin defending territories as early as 4 weeks prior to the arrival of females. Territory maintenance continues until young of the first brood fledge, but the intensity of defence varies with breeding stages. Defence is most intense preceding incubation of the first clutch with secondary peaks of lower intensity preceding each subsequent nesting attempt. Males defend against intruding resident and migrant males and migrant females. Females are not aggressive toward each other even when mated to the same male. They do not establish subterritories within the male's territory. Territory boundaries and size flux considerably as a result

of changes in population density, relocation of female activity centres, and changes in habitat availability and suitability. In 1 Wisconsin study area, territories were initially small and became larger; the opposite was true at another Wisconsin site. Initial shrinkage of larger territories is probably more common as new birds arrive and attempt to establish a territory. When a male disappears, his territory is absorbed by his neighbours. Males that are unsuccessful in attracting a mate either leave voluntarily or are forced out by their neighbours. During boundary disputes, males keep between their mate and the intruder, possibly to lessen the likelihood of extra-pair copulations (Lanyon 1956a; Jaster et al. 2020; Knapton 1987, 1988b; Wiens 1969). Territory sizes of 1.1-8.1 ha have been reported, with most 2-4 ha. In 1 Wisconsin area, territories ranged from 1.2 to 6.1 ha but most were 2.8-3.6 ha. At another Wisconsin site, territories averaged 2.3 ha (range 1.7-3.2 ha). Territory size varied inversely with population density at this site. When 6 territories were present, they averaged 2.59 ha (range 1.94-3.12 ha); when 12 territories were present, they averaged 2.33 ha (range 1.50-3.08 ha). Kansas territories were 1.2-4.8 ha. Large territories were in open grazed grassland with few trees and shrubs. Small territories were in open ungrazed grassland with lush ground cover and numerous scattered trees. In New York, 15 territories averaged 2.8 ha. Two other New York territories were 3.6 ha and 8.1 ha, but the area within them that was regularly used was the same: 2.4 ha. In Kansas, 1 pair had a territory of 1.1 ha. Another male defended an area of 0.57 ha but did not attract a mate and left the area (Fitch 1958; Gross in Bent 1958; Hull 2002; Jaster et al. 2020; Lanyon 1956a; Wiens 1969).

There is almost no interspecific aggression among the Eastern Meadowlark and most other grassland species. The exception is the Western Meadowlark. The 2 meadowlarks defend mutually exclusive territories and each is as aggressive to the other species as it is to conspecifics. Interspecific territorialism may serve to eliminate competition between these 2 closely related species with similar habitat and diet requirements (Lanyon 1956a; Wiens 1969). In Ontario, Eastern Meadowlarks responded aggressively to Western Meadowlark songs where the 2 species were in close contact, but did not recognize its song as a threat elsewhere (Falls 2000). In areas of contact, males of both species have more intense black and a larger black V on their breast and a brighter yellow glow on the breast, probably to increase interspecific communication. More fighting and greater intensity of fights occur in areas of contact, with males involved in interspecific territorial disputes suffering more wounds than those engaged only in intraspecific territoriality (Jaster et al. 2020; Rohwer 1973).

Natal philopatry rates are low. In Illinois, 1 of 343 juveniles (0.3%) returned in a subsequent year. Kerschner et al. (2004b) considered it unlikely that postfledging movements were used to locate future breeding sites or to establish navigational landmarks for future use during migration. In Wisconsin, 1 of 36 nestlings (2.2%) was found in the following year, 0.96 km from the natal site. One of 2 fledglings (50%) returned the next year to a site 0.48 km from where it was banded (Jaster et al. 2020).

Adult site tenacity appears to be high in both sexes. In Wisconsin, 8 of 14 males (57.1%) returned to breed in another year; 7 (87.5%) returned to their previous territory and 1 (12.5%) returned to an adjacent territory. Twelve of 22 females (54.5%) returned to breed and 9 (75%) returned to their former territory. Of the 3 that moved, 2 were forced to do so because there was no male on the territory (Jaster et al. 2020). Lanyon (1956a) stated that both sexes exhibited a strong homing behaviour that was directed toward their former territory rather than toward a particular mate. In

Illinois, densities in individual hayfields varied by as much as 2.5-fold annually, but the total number in all hayfields tended to remain constant. This supported the theory that there may have been considerable switching among habitats from 1 year to the next (Graber and Graber 1963).

Limiting Factors

Eggs have been reported in Ontario nests from the beginning of May until the first week of August, with most present from the last week of May until mid-June (Peck and James 1987). Pairing occurs immediately once the females arrive and nest building begins about a week later. First nests take 6-8 days to construct but later nests may be built within 3-4 days. Females may spend as long as 18 days nest building, but not all at the same nest. Multiple nests may be started and abandoned. It is unknown if there is an interval between nest completion and initiation of egg laying. Material may still be added to the nest after the first eggs are laid. Eggs are laid at the rate of 1 a day. Incubation usually begins with the laying of the last egg. Incubation of 5-egg clutches may begin with laying of the third, fourth, or fifth egg, but mostly with the fourth egg. Incubation takes 13-14 days, rarely as long as 15-16 days. Incubation periods of 12-13 days have been reported in Ontario. Hatching usually occurs on the same day, but may be spread over 2 days. The nestling period is 10-12 days but young may leave the nest when they are only 8 days old if they are disturbed (Gross in Bent 1958; Jaster et al. 2020; Peck and James 1987). In Illinois, the timing of spring initiation of nesting and the duration of nesting were important to overall nesting success, determining whether there was sufficient time to renest or raise a second brood. Only 3 of 129 nests (2.3%) were initiated after 7 July and the latest nest was begun on 23 July (Roseberry and Klimstra 1970).

The Eastern Meadowlark may raise 1 or 2 broods in a year, but never more than 2. Double broods are probable in Ontario but have not been confirmed. The frequency of double broods varies considerably geographically but the reasons for this are uncertain. In 1 area of Wisconsin, females that successfully raised a brood always attempted another one. In another Wisconsin area, single and double broods were equally common. In Illinois, no obvious peak in egg laying occurred that was indicative of second broods. If second broods were initiated, it was not until mid-May or later. At another Illinois site, 7 of 19 females (36.8%) that successfully reared their first brood attempted a second brood. Only 3 of 34 females (8.8%) successfully reared a second brood. Of the 19 females that initiated a second brood, 2 (10.5%) remained on site and ceased breeding and 10 (52.6%) emigrated from the study area. Many of these were found within 10 km of the nesting area within 3 weeks of emigration and there was no indication that they attempted another nest (Kerschner et al. 2004a; Lanyon 1956a; Roseberry and Klimstra 1970; Wiens 1969). It may be a persistent renester in some areas, making as many as 5 attempts to raise a brood. Replacement nests may be uncommon in other areas. In Illinois, 8 of 14 unsuccessful birds (57.1%) renested. Thirty-four females built a total of 52 nests (mean 1.34 per season, range 1-4). Females renested an average of 9.9 days after nest loss. Successful females did not initiate their second nest until 27.7 days after the young left the nest. At this site, individuals attempted relatively few clutches within a season; females seldom attempted more than 3 clutches. Birds ceased breeding with at least 2 months still available in the breeding season. Double brooding added little to the annual productivity because second nests were significantly less successful than early nests. In other areas, replacement nests were started 2-3 days after the first nest was lost. In Illinois, the distance between successful nests was 111.5 m, similar to the distance of 79.0 m between unsuccessful nests (Gross in Bent 1958; Jaster et al. 2020; Kerschner

et al. 2004a; Lanyon 1956a). Clutches of 3-6 eggs were reported in Ontario, plus an 8-egg clutch. The mean clutch size was 4.53 eggs and 5 eggs was the most frequent clutch size (Peck and James 1987). In the Region of Niagara, Knapton (1988b) reported clutches of 3-6 eggs; 5-egg clutches were most common. Seven of the 8 6-egg clutches (87.5%) were laid by females mated to a polygynous male. There were no significant differences in clutch sizes of females in polygynous (4.70 eggs) or monogamous (4.51 eggs) relationships. Overall, clutch sizes of 3-7 eggs have been reported, with 5-egg clutches most abundant. In Illinois, the mean size of 101 clutches was 4.16 eggs. Clutch size declined as the season progressed: 4.36 eggs for clutches initiated prior to 27 May and 4.03 eggs for later nests. In Kentucky and Tennessee, there was no evidence that clutch size declined significantly with the season. Clutch size increased initially, peaked in mid-season then gradually decreased with an overall mean of 4.6 eggs. In Illinois, there was no difference in clutch size, hatch rate, survival rate, and fledging success between initial and subsequent nesting attempts. Initial nests had a mean clutch size of 4.56 eggs compared with 4.22 eggs for subsequent nests. Females laid an average of 6.8 eggs per season. Mean clutch sizes reported elsewhere include 4.76 and 4.57 eggs in New York, 4.7 eggs in West Virginia, 4.81 eggs in Wisconsin, 4.8 eggs in Missouri, and 5.2 eggs in Kansas. Mean clutch sizes range from 4.1 to 5.2 eggs (overall mean 4.4 eggs). Clutch sizes tend to increase with latitude (Giocomo et al. 2008; Gross in Bent 1958; Jaster et al. 2020; Kerschner et al. 2004a; Norment et al. 2010; Roseberry and Klimstra 1970; Suedkamp Wells et al. 2008).

Both sexes are capable of breeding when they are 1 year old (Jaster et al. 2020). It is unknown what proportion of yearling males fail to defend a territory or attract a mate. It is probable that all yearling females breed. Females select territories where the male is singing conspecific songs and copulations all occur within territories. These factors are important in minimizing the rate of hybridization with the Western Meadowlark. Mate changes within a season occur only when the original male disappears or is displaced by another male. The pair bond is maintained until the female has completed parental duties or she aborts the first nesting attempt. Mate guarding by males is a successful barrier to extra-pair copulations. No successful stolen copulations were documented in a 4-year Wisconsin study (Jaster et al. 2020; Lanyon 1956a). The mating system is polygynous, with a higher proportion of males being polygynous than monogamous. Polygynous males typically have 2 mates, rarely 3. Later-arriving yearling females often become secondary females in polygynous relationships. Different arrival times of the year classes of females and often low nesting success frequently result in asynchronous nesting by the females of a polygynous male. This allows the male to care for both nests. In New York, 50% of males were polygynous; 70-80% were polygynous in Wisconsin (Gross in Bent 1958; Jaster et al. 2020; Lanyon 1956a; Wiens 1969). Knapton (1988b) studied the nesting strategy of the Eastern Meadowlark in Niagara Region. Polygyny occurred in all 4 years of the study, but its prevalence varied annually from 38% to 56% of males (average 50%). Females in polygynous relationships hatched a significantly higher proportion of their eggs and fledged a significantly higher proportion of their nestlings than females in monogamous relationships. There were no significant differences in growth rates and mass of nestlings or in food items and delivery rates to nestlings of females in polygynous and monogamous relationships. Starvation rarely occurred and was not an important factor, suggesting that male feeding contributions were not significantly different at nests of primary and secondary females and nests in monogamous relationships. Nests of females in monogamous relationships suffered higher

rates of predation. Polygynous males appeared to be high-quality older birds that provided better parental care in the form of predator protection. Six males that returned in subsequent years switched from being monogamous to being polygynous. One male was polygynous for the first 3 years and was monogamous in the fourth year when he switched territories.

The Eastern Meadowlark forages almost exclusively on the ground, both inside and outside the territory. It obtains food from the surface of the ground, by probing beneath the soil, and searching under clods of earth, manure, and other objects. It hunts for seeds and insects through grasses and forbs, gathering them from fallen or standing stalks. It forages in grasslands as well as in grain and soybean fields. When the wind is strong, it may fly to the lee side of a field and advance across it on foot into the wind (Gross in Bent 1958; Jaster et al. 2020; Kerschner et al. 2004a).

Young were fed cutworms, grasshopper nymphs, other small insects, and spiders. By the time they were 6 days old, they were fed grasshoppers, crickets, and ground beetles (Gross in Bent 1958). Ostrand and Bollinger (2012) used esophageal ligatures to collect 29 diet samples from nestlings in 19 Illinois nests. Spiders represented the greatest volume (44%) and frequency (53%) of food items. The spiders consisted of 80% wolf spiders, 10% jumping spiders, 4% crab spiders, 4% orb weavers, and 2% sac spiders. Orthopterans were second in volume (23%) and numbers (13.5%), with the orthopteran sample consisting of 46% crickets, 31% grasshoppers, and 23% katydids. Caterpillars constituted 18% of the volume and 14.6% of the numbers of food items, including 73% cutworms and 27% sulphur butterflies; no adult lepidopterans were consumed. Other taxa by volume and numbers respectively included 10.8% and 15.6% beetles (mostly ground and scarab beetles), 2.0% and 1.0% cicadas, and 1.9% and 2.1% stink bugs. Although spiders are occasionally identified in the diet of adults, they eat mostly orthopterans, beetles, and caterpillars. In this area, adults preferentially fed their young spiders, particularly wolf spiders. These are rather large and commonly occupy the surface of terrestrial habitats. Most were females carrying egg sacs and their larger size and presence of egg sacs may have made them more conspicuous. The spiders in the sample were suggestive of the invertebrate fauna of soybean fields. Soybean fields are not usually treated with insecticides and may have abundant food resources (Kerschner et al. 2004a).

Adults eat mostly insects in the summer, particularly cutworms and other caterpillars, beetles, and grasshoppers. Later in summer and in autumn and winter, the Eastern Meadowlark eats mostly seeds, including waste grain (corn, wheat, rye, and oats). In early spring, it may pull up and eat sprouting clover, corn, and oats. This occurs mostly in the southern states during spring migration. It rarely consumes vertebrates such as lizards (Beal et al. 1916; Gross in Bent 1958; Jaster et al. 2020). In Oklahoma, Wiens and Rotenberry (1979) analyzed its diet but pooled some results for both meadowlark species. In 3 years, the diet consisted of 30%, 40%, and 76% dry weight beetles; 20%, 40%, and 16% orthopterans; and 45%, 18%, and 2% lepidopterans. It was the most highly insectivorous species they studied, with seeds never comprising more than 5% of the diet and usually less than 1%. Ground beetles and, to a lesser extent, scarab beetles made major contributions to the diet. Crickets were the most important orthopterans in 2 years. Short-horned grasshoppers were most important in 1 year. Phytophagous arthropods were the most important prey, but it also ate large quantities of predaceous and omnivorous prey. Other prey it consumed included ants, other beetles (weevils, and long-horned, leaf, lady, and click beetles), stink bugs, leaf-footed bugs,

spiders, and traces of grass and legume seeds. The dietary niche overlap of the Eastern Meadowlark was 26% with the Upland Sandpiper, 68% with the Dickcissel, and 83% with the Grasshopper Sparrow. Its dietary overlap with the Dickcissel and Grasshopper Sparrow was high in 1 year, less in the next year, and quite low in the final year. The mean size of the Eastern Meadowlark's prey was 8.66 mm, 9.42 mm, and 10.52 mm in the 3 years, larger than for the Dickcissel and Grasshopper Sparrow but similar to that of the Upland Sandpiper. Beal et al. (1916) summarized the contents of 890 stomachs collected in the southeastern United States. The diet consisted of 78.12% animal food and 21.88% vegetable matter. Orthopterans were the most important food group, comprising 27% of the overall diet. These included all types of grasshoppers plus crickets. They constituted 9% of the January diet and increased rapidly until October when they represented 56% of the diet, then declined to 40% in November; 52.4% of all stomachs contained grasshoppers. Beetles were second in abundance in the diet, peaking in May at 28%. These were mostly dung beetles, but June beetles, ground beetles, and weevils were consistent components of the diet. It ate true bugs throughout the year but they constituted only 3% of the annual diet; they were mostly stink bugs. Caterpillars comprised about 13% of the diet, peaking in May at 28%. Spiders and millipedes represented 3% of the total diet. Other animal foods included flies, earwigs, cattle ticks, snails, and small crustaceans; 3 stomachs contained bones of frogs or toads. Vegetation eaten included fruit, grain, and weed seeds. Fruit constituted less than 2% of the diet and was predominantly wild fruit. Grain totalled 9% of the diet and consisted mainly of corn with lesser amounts of wheat and oats. Most grain was consumed in winter indicating that it was waste grain gathered from fields. Weed seeds represented 7% of the diet and were eaten predominantly in winter. Seeds commonly consumed included those of ragweed, barnyard grass, smartweeds, sorrels, mustards, amaranths, and gromwell; clover seeds were rarely eaten. Gross (in Bent 1958) reported that the diet consisted of 74% animal matter and 26% vegetable matter, with orthopterans, beetles, and caterpillars forming the bulk of the food. Additional animal foods included ants, wasps, scale insects, and adult moths and butterflies, which were rarely consumed. The vegetable matter eaten was essentially identical to what Beal et al. (1916) reported. The fruit eaten included those of cherries, strawberries, and blackberries.

Near Ottawa, Picman (1992) used cameras to identify predators at artificial nests containing quail eggs. Thirty-two of 144 egg predation events (27.2%) were by the Eastern Meadowlark. It was the second-most important predator after the striped skunk and could therefore affect the reproductive success of other grassland birds such as the Savannah Sparrow, Bobolink, and Red-winged Blackbird. It did not eat the egg contents suggesting that the motive for the egg destruction was to reduce competition for food resources.

The Eastern Meadowlark is an infrequent host of the Brown-headed Cowbird. The incidence of parasitism may be higher than reported because it is a partial rejecter of cowbird eggs. In Illinois, it rejected cowbird eggs at a rate of 37.5-40%. It is one of few species with intermediate levels of rejection suggesting that it may be evolving from an acceptor to a rejecter species. Other studies noted nest desertion after parasitism. In 1 case, a second nest was built over a cowbird egg (Gross in Bent 1958; Peer et al. 2000; Rothstein 1974). In Kansas, parasitized nests had an average of 1.4 fewer eggs per clutch. Parasitism rates are low in the east and south and higher in the west. Parasitism rates are higher where cowbird densities are higher and where cattle are more abundant. Parasitism is not considered a significant limiting factor. Eleven of 390 Ontario nests (2.8%) were

parasitized. Parasitism rates reported elsewhere include 1 of 51 nests (1.9%) in Quebec; 0 of 131 nests and 6 of 38 nests (15.8%) in Wisconsin; 0 of 87 nests in Kentucky and Tennessee; 0 of 131 nests in Indiana; 0 of 50 nests in New York and Oklahoma; 0 of 246 nests, 2 of 450 nests (0.4%), and 4 of 221 nests (1.8%) in Illinois; 0 of 25 nests in New York; 5 of 31 nests (16.1%) in Nebraska; 31 of 512 nests (6.1%) in Oklahoma; and 18 of 67 nests (26.9%) in Kansas (Galligan et al. 2006; Giocomo et al. 2008; Jaster et al. 2020; McCracken et al. 2013; Peck and James 1998b; Renfrew et al. 2005; Rivers et al. 2010; Roseberry and Klimstra 1970; Savignac 2011b; Verheijen et al. 2022; Walk et al. 2010).

Hybridization between the 2 meadowlark species is rare. Although males readily mate with females of either species, females preferentially select territories where males are singing conspecific songs. In addition, males copulate only within their territories and the 2 species defend mutually exclusive territories. These mating strategies coupled with interspecific territoriality function to minimize the potential for hybridization. In Wisconsin, 1 incomplete interspecific mating occurred across territorial boundaries but over 4 years there was no evidence of interbreeding in more than 100 pair bonds where both species were common (Lanyon 1956a). The isolating mechanisms may break down at the edge of the ranges where 1 species is rare and the other is common. In southwestern Ontario over a period of 4 years, there were 9 nests built by mismatched pairs consisting of a male Eastern Meadowlark and 2 female Western Meadowlarks. It appeared as though the females were unable to find a male Western Meadowlark on territory and had to settle on an Eastern Meadowlark territory. Hybridization is likely to occur only on the very eastern edge of the Western Meadowlark's range, with the Ontario hybridization events the first documented. The hybrid young were not very viable, with fewer than 50% of eggs hatching and only about 25% of young surviving. Vocalizations of the young were atypical of both species and they demonstrated no increase in the size of their gonads despite being injected with hormones. Young of matched pairs exhibited the proper gonadal responses. Hybridization is very infrequent and does not occur where both species are common. It is not a threat to the gene pool of either species because of the low viability of the hybrids (Szijj 1966). Hybridization of the 2 species has also been documented in Quebec where the Western Meadowlark is rare (Rail in Gauthier and Aubry 1996).

The most significant limiting factors for the Eastern Meadowlark are habitat loss and degradation, and these factors are affecting it range-wide. Habitat loss is due predominantly to changes in agricultural practices. It benefitted immensely from the initial conversion of forests into agricultural fields. Originally, much farmland was devoted to raising livestock so that pastures and hayfields were prevalent in the landscape. Two major changes in farming occurred that affected cropping systems. The first was the mechanization of machinery, with tractors and other motorized equipment reducing the need to keep horses and provide pastures and hayfields for them. The second was a switch from raising livestock to cash cropping, planting row crops such as corn, soybeans, and winter wheat. Because its abundance is directly linked to the amount of grassland, these changes resulted in declines in its population. The area of hayfields in Ontario decreased strongly from 1930 to 1940 and again in 1965-75 and 2006-11. The amount of improved pasture decreased by 77% 1966-2011. The amount of unimproved pasture decreased by 38% 1971-2011. The decline in hayfields is directly linked to changes in the livestock industry and declining numbers of cattle (Askins et al. 2007; McCracken et al. 2013; Savignac 2011b). Declines in the Carden Plain between the 2 atlases were due to conversion of pastures and hayfields to row crops (Merondun et

al. 2024). Although changes in agricultural practices have had the greatest effects, several other factors contributed to habitat loss. These include natural succession of abandoned farmland and other early successional habitats, tree planting, and urbanization (Jaster et al. 2020; McCracken et al. 2013; Rail in Gauthier and Aubry 1996; Savignac 2011b; Tozer 2012).

In Nebraska and Iowa, McLaughlin et al. (2014) studied the effects of nearby urban areas on Eastern Meadowlarks breeding in tallgrass prairies. They measured its occurrence and density along a rural to urban gradient. Urbanization had a strong negative effect on it. It exhibited the strongest response of the grassland species they studied. Adjacent urban habitat negatively affected both its probability of occurrence and density. Its probability of occurrence was 75% in areas of low and moderate urban intensity and 10% at high urban intensity. Urban intensities were defined as: low, 3.7% developed; moderate, 17.5%; and high, 50.2%.

Declines in habitat quality are related mostly to changes in agricultural practices. Hayfields were traditionally planted predominantly to grasses or grass-legume mixes, with the legumes being mostly clovers in the genus *Trifolium*. Many fields are now planted to pure crops of alfalfa or alfalfa with lesser amounts of grasses. The abundance of the Eastern Meadowlark declines with increasing amounts of alfalfa in hayfields. Pure stands of alfalfa are typically unsuitable habitat because the vegetation is too dense to attract it. Lightly or moderately grazed pastures may provide quality nesting habitat, but most Ontario pastures are now intensively grazed. Originally, most farms had a few head of cattle and grazing pressure on pastures was fairly low. Now most farmers do not have cattle and those that do tend to have large herds associated with beef and dairy production. Pastures associated with these herds are typically heavily grazed, with the grass cropped to the ground. These heavily grazed pastures do not have adequate vegetation coverage to support the Eastern Meadowlark.

The conversion of many hayfields to alfalfa has resulted in faster and denser growth of crops. The higher productivity in these fields allows them to be cut earlier in spring and more frequently, usually 3 times within a growing season. Earlier cutting of hayfields is another significant limiting factor to Eastern Meadowlark populations (Gross in Bent 1958; Hull 2002; McCracken et al. 2013; Savignac 2011b). In CRP fields in Kansas, mowing caused females to desert the area. Granfors et al. (1996) recommended that mowing be conducted after 15 July and that spot-mowing be conducted to control noxious plants because meadowlarks did not abandon territories if they were only partially mowed. In Arkansas, Luscier and Thompson (2009) examined nest survival and breeding density of the Eastern Meadowlark on early hayed (26-31 May), late hayed (17-26 June), and unhayed fields. The effects of late haying were trivial but early haying had a strong negative effect on nest survival rates. Over 80% of nests in early hayed fields were destroyed. Surviving nests were in unmowed corners of fields, so no nests survived haying. There was a more pronounced effect of haying in fields closer to residences because there may have been domestic cats associated with these fields. Delaying cutting by 2-3 weeks in early hayed fields would provide sufficient time to complete a nesting cycle. In Michigan, meadowlarks successfully fledged 1 brood before mowing occurred but ceased breeding after mowing (Hull 2002). Periodic mowing at 3-5-year intervals to remove excessive amounts of woody vegetation can be beneficial (Hull 2002; McCracken et al. 2013). In New Jersey, 0.25-ha refugia left in mowed fields were not beneficial for this meadowlark (Allen et

al. 2019). Wolcott et al. (2023) recommended that grassland management be deferred until August to protect both nests and fledglings.

The response of the Eastern Meadowlark to grazing varies depending upon the intensity of grazing and the type of grassland. Low- to moderate-intensity grazing that maintains grass heights of 10-30 cm can be beneficial. Grazing is particularly beneficial in tallgrass prairies habitats where the vegetation may be taller than it prefers. It responds negatively to heavy grazing, particularly in habitats with shorter grasses, but excessive grazing can make any habitat unsuitable. In Illinois pastures, there was an inverse relationship between grazing and use by this meadowlark. In 3 years, heavy grazing occurred in 1 pasture but grazing in it was less intense in the fourth year. Nest density was 3.7-5.5 times higher in the year of lighter grazing. Another field was heavily grazed in 2 years, with no nests present in one of those years. In the third year, grazing was less intense and it was reseeded and ungrazed in the fourth and fifth years. Nest density in the year of lighter grazing was 4.3 times higher than in the 1 year of heavy grazing that meadowlarks were present. In the 2 years when the field was not grazed, nest density was 13-13.7 times greater than in the year of heavy grazing and 3-3.2 times greater than in the year of lighter grazing. Heavy grazing resulted in grass 2.5-7.6 cm tall with scattered clumps of grasses and forbs 30 cm tall. In the year of lighter grazing, there was uniform distribution of grasses and forbs 12.5 cm tall (Granfors et al. 1996; Hull 2002; McCracken et al. 2013; Powell et al. 2008; Roseberry and Klimstra 1970). In Ontario, Ethier and Nudds (2017) concluded that grazing appeared to be beneficial for the Bobolink only when cattle stocking densities were less than 0.198 cows per ha per day. Current stocking rates average 7 times greater than this. It is probable that the Ontario stocking rates are also too high for the Eastern Meadowlark. In Grey County, rotational grazing did not affect the number of meadowlark territories. Pairs attempted to renest after failure. Some territories shifted and some were abandoned. About 6 weeks between grazing periods is required to allow young to fledge from renesting attempts (Campomizzi and LeBrun-Southcott 2022). Grazing has the potential to have other adverse effects. These include direct trampling of nests by livestock and cropping of cover near the nest by cattle can expose nests and make them more vulnerable to predation (Granfors et al. 1996; Hull 2002; Roseberry and Klimstra 1970). In Wisconsin, Nack and Ribic (2005) recorded cows removing both eggs and nestlings of Eastern Meadowlarks from nests and either eating them or carrying them off.

The effects of fire on the Eastern Meadowlark vary depending upon the initial quality of the habitat. Fires every 2-4 years may be beneficial in reducing excessive coverage by shrubs and dense litter accumulations. Different responses to burns have been reported with some studies finding no difference in burned and unburned areas. Other studies have found it either more or less abundant in burned than unburned areas. Under optimum conditions, fire should be infrequent enough to allow modest levels of litter to accumulate yet frequent enough to keep woody vegetation in check. The optimum frequency of burns will vary geographically and by how quickly litter and woody vegetation accumulate. In Kansas and Illinois, it was more abundant 1-3 years postfire than in the year of the burn. In Arizona, birds responded positively to burning, especially in the second year postfire. It avoided freshly burned fields and declined on unburned plots over a period of 7 years, probably due to invasion by shrubs. At another Kansas site, its abundance was unaffected by burning in wet years but was reduced in drought years. In another Arizona study, its abundance was significantly lower 1 year postfire than in unburned native grasses. There was no difference in its

abundance in nonnative grasses. In Kansas, it had higher nest survival in annually burned and ungrazed pastures than in pastures managed with patch-burn grazing (Askins et al. 2007; Bock and Bock 1992; Hull 2002; McCracken et al. 2013; Powell et al. 2008; Swanson 1996; Verheijen et al. 2022).

The Eastern Meadowlark has the potential to be adversely affected by chemicals used in the agriculture industry. Carbofurans probably contributed to its decline prior to their being taken off the market but these continue to be used in South America. The greatest numbers are killed in the southeastern United States where pesticides are used on specialty crops such as cotton and cranberries. Mortalities have been reported due to insecticides in Kansas and it decreased in Maine after lowbush blueberries were sprayed, although this may have been related to the resulting habitat changes. It may die after ingesting grain that has been poisoned for rodent or insect control. Insecticides may have indirect effects by reducing insect prey (Hull 2002; Jaster et al. 2020; McCracken et al. 2013; Savignac 2011b).

The Eastern Meadowlark is unusually sensitive to human disturbance at the nest. Females flushed even as late as the incubation stage may desert the nest. Disturbance during the nestling period is less likely to result in desertion, but adults become wary and secretive and delay visiting the nest (Jaster et al. 2020).

Late-spring snow or ice storms may make food unavailable and result in extensive mortality. In Colorado, many were killed during a hail storm (Gross in Bent 1958; Jaster et al. 2020).

Fragmentation of grassland habitat by wooded areas, roads, and other land uses may have adverse effects on the Eastern Meadowlark, although many studies found negligible effects due to edges and woody growth. Its productivity may be greater in grasslands larger than 10 ha, so reductions in field sizes may reduce densities. Other studies found no relationships between its density and field size. In the Midwest, daily predation rates increased with increasing field size. Some studies found that predation rates were higher 50-100 m from forest edge than further from edge; other studies found no difference in predation rates close to forests. Parasitism rates may be either higher or lower near forested edges. The woody vegetation may provide perches for cowbirds to search for nests or, alternatively, cowbirds may opt to parasitize the more frequent and diverse bird species within forests rather than in grasslands (Galligan et al. 2006; McCracken et al. 2013; Renfrew and Ribic 2003; Renfrew et al. 2005; Savignac 2011b).

In the United States, nesting success was depressed by increased rain in May and June to August and was lower when May temperatures were above or below average (Zuckerberg et al. 2018). In Quebec, abundance of the Eastern Meadowlark was correlated with the mean annual degree-days 10°C or higher in May, June, and July. It was associated with warm summers. DesGranges and Morneau (2010) considered it sensitive to climate change. Price (2004) predicted that the range of the Eastern Meadowlark might expand in southern Ontario if the average summer temperature increased by 2°C. Models that suggest that it may increase are unlikely to be correct. Habitat is the limiting factor for the Eastern Meadowlark and a more favourable climate will not improve or create habitat for it.

Status

The Eastern Meadowlark probably occupied much the same breeding range in Ontario prior to forest clearing by settlers as it does now. It would have been considerably less abundant with a much spottier distribution due to rarity of suitable habitat. It would have been restricted to habitats such as prairies (there were originally approximately 66,500 ha of this habitat), burns, and openings created by First Nations. Remains dating back to 1630-1650 have been found near Brantford and Bronte Creek in Halton Region. It was documented as being present in the province in the 1770s (Curry 2006; Falls 2000; McCracken et al. 2013; Savignac 2011b).

Deforestation by European settlers and conversion of forest cover to forage crops, pastures, and small grain fields created much more habitat for the Eastern Meadowlark in the east. The native grasslands were mostly destroyed, with only about 300 ha still remaining in Ontario. Replacement of tallgrass prairies with nonnative grasslands was beneficial because these grasses grew to optimum heights for it. Although its overall range may have been similar pre- and post-settlement, its distribution in the south became continuous rather than scattered. This phenomenon occurred throughout the east, and it expanded its range westward around the end of the 19th century. It became the dominant meadowlark in much of Illinois, Michigan, and Wisconsin and became much more abundant in its previous range (Gross in Bent 1958; Lanyon 1956b; McCracken et al. 2013; Savignac 2011b; Swanson 1996).

McIlwraith (1894) stated that the Eastern Meadowlark was found in all suitable areas in the province, particularly in the southwest. It occurred north to the Manitoba border where it was replaced by the Western Meadowlark. In both the Hamilton and Kingston areas, the Eastern Meadowlark was common during the late 19th and early 20th centuries (Curry 2006; Weir 2008). It arrived in Muskoka District around 1863 and was common at Port Sydney by 1901 (Mills 1981). It arrived later in the Clay Belt and from Thunder Bay to Rainy River District in the 1940s, by which time the Western Meadowlark was well established there (Falls 2000). Despite the Eastern Meadowlark's initial rapid increase, declines in its habitat began to occur as early as 1900 due to changes in habitat and agricultural practices (McCracken et al. 2013). The subsequent decline in its population was well documented in Elgin County: in 1891 and 1954, it was a common breeder but it was uncommon and local in 2000, with only a single pair present in some atlas squares (Lancaster et al. 2004). Baillie and Harrington (1937) reported that it was common in southern Ontario north to Lake Nipissing and further north to at least Englehart and the eastern end of Lake Superior. Notable declines began in the 1940s to 1950s and still continue (Black and Roy 2010; McCracken et al. 2013; Savignac 2011b). The first atlas determined that its range was concentrated from Sault Ste. Marie east to Sudbury and just north of Lake Nipissing south to the Great Lakes. There were a few breeding records for the Clay Belt and in the vicinity of Lake of the Woods. Its distribution was continuous south of the Shield, except that it was absent from a few squares in Essex and western Chatham-Kent. These areas are intensively farmed for cash crops and have limited grass cover. Its distribution in the Shield was spotty, where it was absent in forested landscapes. It was most abundant in mixed farmlands bounded by Listowel in the west, Flesherton in the north, Lindsay in the east, and Brantford in the south (Knapton in Cadman et al. 1987). James (1991) considered the Eastern Meadowlark common in the agricultural south and rare in the north to Thunder Bay and western Rainy River District and in the extreme east to the agricultural areas of the Clay Belt.

The second atlas demonstrated that there had been no change in the range of the Eastern Meadowlark since the first atlas. Its probability of observation declined significantly province-wide and in all regions except the more northern areas where it was too uncommon to conduct meaningful statistical analyses. It was most abundant south of the Shield, particularly in a band from Lake Simcoe to Kingston and in Grey, Bruce, and Dufferin counties. Other areas of higher densities included portions of southeastern Ontario and Haldimand County. These areas correspond with regions where there are the highest concentrations of livestock and consequently more hayfields and pastures (Leckie in Cadman et al. 2007). The area of highest density was different between the 2 atlases. A high proportion of farmers within the area of concentration during the first atlas changed their farming practices to grow mostly cash crops.

Breeding Bird Survey data indicate that the Eastern Meadowlark decreased at annual rates of 3.84% in Canada and 3.53% in Ontario 1970-2021 and at annual rates of 5.23% in Canada and 5.15% in Ontario 2011-21. All results were highly reliable (A.C. Smith et al. 2023).

The Eastern Meadowlark has been designated threatened in Canada and Ontario due to declines in its population and ongoing habitat loss and degradation. The long-term goal of the recovery strategy is to maintain stable self-sustaining populations. The short-term (2013-23) goal was to slow the annual rate of decline to no more than 1% per year. Thereafter, the long-term goal is to achieve population stability at 90% of the 2013 population. Stabilizing the population at the 2013 level was deemed impossible because of the nature and number of threats to it. Habitat loss is expected to continue (McCracken et al. 2013).

POSTFLEDGING PERIOD

Fledglings are incapable of flight when they leave the nest. For their first week they are immobile and hide cryptically in the vegetation. They can run quickly when flightless, but their survival is highly dependent upon their remaining still. Distance moved when flushed averaged 1.3 m the first day out of the nest and 35.6 m on the seventh day. They hopped through the grass on days 1-3 and graduated to short-distance flights and glides as they aged. They were capable of more extended flights after their first week. Daily movements increased then, although individuals seldom moved more than 125 m from the nest. By the second week, they remained within 200 m of the nest. Fledglings were usually independent by the end of the third week out of the nest. By then, few had travelled further than 0.5 km from the nest (Jaster et al. 2020; Kerschner et al. 2004b; Seudkamp Wells et al. 2007).

In Missouri, 30 of 107 fledglings (28.0%) died and 27 of the deaths (90.0%) occurred in the first week out of the nest. The average age of death was 5.3 days out of the nest. A 1% increase in body mass of fledglings resulted in a 2% reduction in the risk of death. Heavier nestlings obtained a higher proportion of food brought to the nest and fledged 1-2 days before their siblings. Heavier birds may have been more successful at avoiding predators. In addition to predation, primarily by snakes, fledglings appeared to succumb to heat when the temperature exceeded 35°C and the humidity was greater than 80% (Seudkamp Wells et al. 2007). The highest rate of mortality also occurred in the first week out of the nest in Illinois (Kerschner et al. 2004b).

In Missouri, juveniles had slow but consistently increasing rates of movement until they had been out of the nest for approximately 28 days. After that, they had slightly longer movements, with

3 isolated peaks of movements further than 600 m around days 40, 44, and 54. Peaks of large movements corresponded with altered periods of activity when juveniles began congregating with other juveniles in roving flocks. At this time, they frequently foraged or moved into adjacent lands outside the nest field. The mean age when daily movements exceeded 300 m was 20.1 days out of the nest, with larger juveniles moving further than 300 m more frequently than smaller juveniles (Seudkamp Wells et al. 2008). In 2 years in Illinois, juveniles travelled an average of 46.2 m (range 1-105 m) and 48.8 m (range 1-108 m). Independent juveniles dispersed from the nest site over time, with maximum dispersal distances ranging from 0.4-12.8 km. Eleven of 16 birds that dispersed from the study area were relocated, and they had moved a mean of 6.0 km (range 3.6-12.8 km). After dispersal, juveniles occurred in flocks (Kerschner et al. 2004b). In Wisconsin, 12 of 14 radiotracked juveniles (85.7%) remained in the study area. One moved from a CRP field to another CRP field 8.8 km away and the other moved from a prairie to a pasture 6.6 km away. Juveniles were 2 times more likely to remain in their natal field during the fledgling period than during the independent period. The average distance moved by juveniles that remained in the study area was 499 m (maximum 526 m). Once juveniles started to leave the natal field, 66.7% did not return. They usually remained in the nest field until they reached independence and then moved to other grassy habitats (CRP fields, prairies, pastures, or cropland). Juveniles made low use of croplands and were not observed using areas with woody cover (Guzy and Ribic 2007).

Over 3 years in Missouri, home ranges of juveniles were similar: 109.4 ha, 82.7 ha, and 70.7 ha (average 80.9 ha). The density of grass cover explained a large proportion of the annual variation in home range size. Soon after juveniles dispersed, they had larger daily movements and home ranges and were among conspecific flocks. Because of the large home ranges of juveniles, the landscape context around the nesting area may be equally important as the nesting habitat. In addition to inhabiting grasslands, juveniles often foraged in agricultural crops. A field of sweet clover more than 400 m from the nesting area was a preferred foraging area (Suedkamp Wells et al. 2008). In Illinois, juveniles also occurred in flocks in grasslands and croplands. Food is probably abundant and predators scarce in croplands (Kerschner et al. 2004b).

As soon as they are done their nesting duties, females begin foraging both within and outside their former breeding territory without the presence of the male. They begin to form flocks at this time and remain gregarious until the next nesting season (Jaster et al. 2020; Lanyon 1956a). In Missouri, females repeatedly travelled more than 500 m from the nest to forage in fields planted with sweet clover. Later, these same females led their broods to this food source (Suedkamp Wells et al. 2007). In Illinois, females spent more than 90% of their time during the postfledging period in row crops, habitat that was rarely used for breeding. They used soybean fields almost exclusively. These may have abundant food resources because they are typically not treated with insecticides (Kerschner et al. 2004a, 2004b). In Illinois, 15 of 22 females (68.2%) emigrated from the study area after breeding. Both successful and unsuccessful birds emigrated. Emigration occurred more frequently by successful than unsuccessful females. Failed females emigrated almost immediately after failure but successful females remained in the nest field significantly longer. Of 15 females that emigrated, 7 (46.6%) remained within 10 km for as long as 3 weeks after dispersing. The others were not relocated and may have moved further. Females that emigrated were found in agricultural fields and were constantly moving across the landscape. Females from the study area were rarely found

in the same area again after emigration occurred (Kerschner et al. 2004a). Guzy and Ribic (2007) radiotracked females in Wisconsin during the breeding and postbreeding periods. While nesting, 21 of 22 females (95.5%) stayed in the study area. One nested unsuccessfully and was found 53 days later in a CRP field 22 km away. During nesting, females were found in their nest field 58% of the time, and this did not differ for successful (63%) and unsuccessful (49%) nesters. After breeding, most females moved out of the nest field. The average distance moved was 590 m (maximum 662 m) with no difference in distances moved by successful and unsuccessful breeders. Once females left the nest field, 11 of 18 (61.1%) did not return. Females moved to CRP fields, pastures, and croplands.

MIGRATION

Most of the Eastern Meadowlark population is sedentary but those at the northern extent of the range, including Ontario, move southward for the winter. Birds migrate to the eastern and southeastern states. An adult banded in Agincourt, Ontario was recovered in winter in South Carolina, 1,021 km from the banding site. Of 2 juveniles banded in Minnesota, 1 wintered in Alabama and the other in Oklahoma, suggesting that migrants from a given population do not share the same winter range. Migration occurs during the day, with birds travelling together in loose flocks in both spring and autumn. During spring migration in Ohio, flocks containing as many as 60 individuals flew over Lake Erie. Near the shore, flocks of 5-100 flew short distances and began to feed. Those in the rear rose and flew over the flock, alighting in front of it to forage again. When they reached an obstruction such as a woodlot, marsh, or lake, they flew over it in a long loose column (Brewer et al. 2018; Gross in Bent 1958; Jaster et al. 2020).

Adult males arrive first in spring with females arriving 2 weeks or as many as 4 weeks later. Young birds continue to arrive throughout April and May and even into June or July (Gross in Bent 1958; Jaster et al. 2020). In southern Ontario, birds start to arrive in mid-March but migrants are most abundant in early April. Spring migration extends through much of May and birds may arrive as early as late February (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; McCracken et al. 2013; Mills 1981; Tozer 2012; Weir 2008).

In Muskoka District, migrants are most likely to move south in September with movement continuing well into October and stragglers remaining until mid-December (Mills 1981). In the south, migrants become obvious in mid-September. Peak movement occurs in late September and continues through October, with most birds leaving by early November (Curry 2006; LaForest 1993; Lancaster et al. 2004; McCracken et al. 2013; Weir 2008).

Migration habitat is similar to that used during the breeding and postfledging periods. In spring, this meadowlark inhabits mostly grasslands. First arrivals in Algonquin Park initially seek areas that are free of snow, including road margins, forest clearings, old fields, and abandoned sawmill sites. It may visit bird feeders at this time. Autumn migrants may visit croplands in addition to grasslands. Marsh habitats may be used in autumn and some birds visit margins of gravel roads. It exhibits no territoriality during migration and occurs almost exclusively in flocks (Gross in Bent 1958; Jaster et al. 2020; McCracken et al. 2013; Tozer 2012).

Robertson et al. (2012) stated that the Eastern Meadowlark may use fields dominated by switchgrass during migration. They concluded that fields planted to this grass for the purposes of agrofuel production would be less likely to support it than natural grasslands.

Because this meadowlark visits road margins during migration, it is vulnerable to being struck by vehicles. It is a diurnal migrant, so collisions with tall structures are not a limiting factor (Gross in Bent 1958; McCracken et al. 2013).

James (1991) considered the Eastern Meadowlark a common migrant in Ontario.

WINTER

The Eastern Meadowlark winters where the annual precipitation exceeds 61 cm. It avoids areas where the average minimum January temperature is below –9°C. Densest winter populations occur where the minimum January temperature is above –1°C. High densities of Western Meadowlarks appear to exclude the Eastern Meadowlark, but the opposite is not true (Root 1988).

In winter, the Eastern Meadowlark uses habitats similar to those used during the breeding season and migration, particularly grasslands and cultivated croplands. It may also inhabit feedlots, marshes with tall grasses, and salt marshes along the Atlantic coast. In Illinois, it preferred hand-picked cornfields in 1906-07 (a habitat that no longer exists), hayfields, fields of small-grain stubble, and mechanically picked cornfields. Elsewhere, it may use cotton fields and old fields grown up with weeds (Graber and Graber 1963; Gross in Bent 1958; Jaster et al. 2020; McCracken et al. 2013; Savignac 2011b). In Texas, Saalfield et al. (2016) examined the effects of management practices such as grazing, burning, and mowing on Eastern Meadowlarks wintering in prairie habitats. Fields where these activities occurred were characterized by short sparse vegetation with fewer shrubs and reduced litter coverage. Two or more years after management, sites had taller, denser vegetation and increased litter depth, and shrubs were more common. A mosaic of prairies in 2-4-year burn rotations provided suitable vegetation characteristics. It occurred equally frequently in disturbed sites as in other management regimes, with its density positively influenced by the percent coverage by flatsedge. In Arkansas, Mississippi, and Kansas, it was more abundant in fields with a buffer of native warm-weather grasses and forbs. There was no difference in its abundance in fields with buffers wider than 23 m and those with narrower buffers (Evans et al. 2015).

During winter, the Eastern Meadowlark may roost in hayfields and cropped fields. It may also roost in tall grasses in marshes and occasionally in trees with grackles (Gross in Bent 1958).

The Eastern Meadowlark is gregarious in winter. It exhibits no signs of territoriality and there is no evidence of dominance hierarchies within flocks (Jaster et al. 2020).

This meadowlark exhibits low site tenacity in winter. It may make short-distance movements in response to changes in food and habitat availability due to snow cover. It may also make random longer-distance movements. A bird banded in South Carolina was reported 350 km distant in Georgia 11 days later (Jaster et al. 2020).

In winter, the Eastern Meadowlark eats a mix of vegetable matter that is predominantly waste grain and weed seeds, and insects if they are available. During snow and ice storms, it may move into atypical habitats where it may scavenge food or even prey upon other bird species. Beal et al. (1916) examined 6 stomachs collected in the southeastern United States in winter. These birds had eaten mostly insects, including many species of beetles, true bugs, grasshoppers and crickets, and a few wasps, caterpillars, spiders, and millipedes. Other winter food items include corn, oats, cutworms, weed seeds, and earthworms. When snow or ice cover traditional food sources, it often

feeds at manure piles or fields where manure has been spread, in barnyards to feed alongside the livestock, and in vacant lots in towns where it forages with the House Sparrow and European Starling. It has been reported feeding in alleys during severe snowstorms. Almost all these features are now scarce and unlikely to be sufficient to support it during severe storms. More frequently, it visits shoulders of highways that have been cleared of snow and tracks through the snow cleared by vehicles. It has been documented eating the flesh of flickers, other meadowlarks, sparrows, Horned Larks, Mourning Doves, cotton rats, domestic cats, cottontails, and jack rabbits. One killed and ate 2 American Tree Sparrows (Gross in Bent 1958; Hubbard and Hubbard 1969; Krutzch 1950; McIlwraith 1894; Schorger 1954; Terres 1956; Tyler and Choate 1990). The Eastern Meadowlark is not a regular visitor to bird feeders, but may visit them in desperation when normal food sources are scarce or covered with ice or snow. It may use raised feeders in addition to feeding on the ground. Its favourite feeder food is black oil sunflowers but it occasionally eats mixed seeds and cracked corn. It has been documented killing and eating Pine Siskins and American Goldfinches at feeders (Dunn and Tessaglia-Hymes 1999; Tozer 2012; Waters 1990).

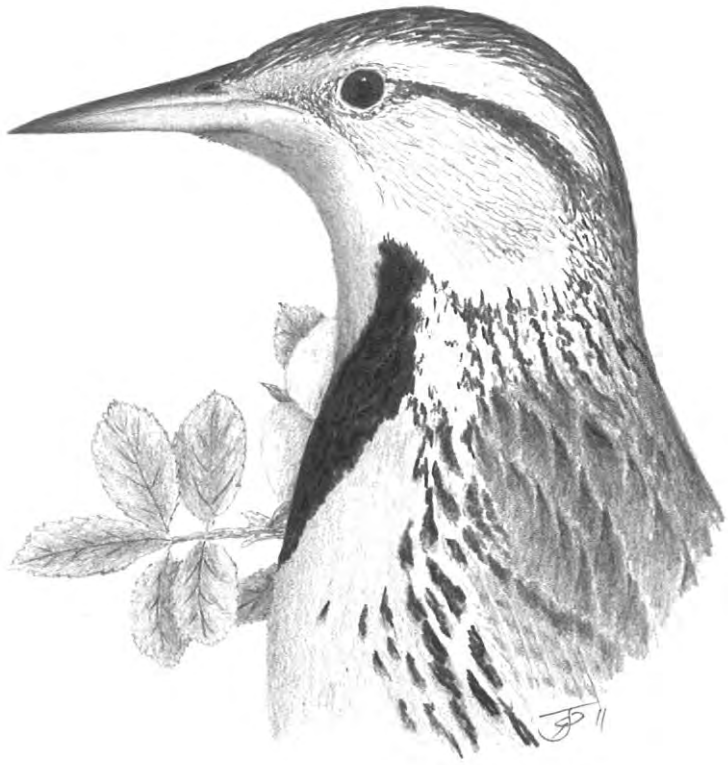
Severe winter weather can be a significant limiting factor for the Eastern Meadowlark. Widespread mortality may occur when snow covers food supplies for prolonged periods. Winter mortality is occasionally significant enough to result in drastic declines in breeding populations. Declines in populations in the late 1970s were partially attributed to severe winters in the southeastern United States during 1976-77 and 1977-78. Snowstorms force meadowlarks to visit roadsides. The birds quickly acclimatize to traffic and large numbers may be killed by vehicles. Over a 2-month period of prolonged sleet and snow in Kansas, birds foraging along roads were not obtaining adequate food. They became weakened and could scarcely fly 9 m. Each day, fewer remained and more dead birds were found (Gross in Bent 1958; Hubbard and Hubbard 1969; Jaster et al. 2020; Krutzch 1950; Robbins 1995; Tyler and Choate 1990).

Wintering habitat has declined over the past half century or more due to changing agricultural practices. In the southeastern states, the Eastern Meadowlark is among the most frequent visitors to rice fields. These are typically baited with an avicide that results in direct mortality (Gross in Bent 1958; McCracken et al. 2013).

James (1991) considered the Eastern Meadowlark a rare winter resident in the south to Kingston, with records of vagrants as far north as Dorion. In the Hamilton area, high numbers occurred in the 1950s and 1960s, with counts of 60 on 21 January and 44 on 2 February. Since the turn of the 21st century, only a few have been seen in winters with declines attributed to changing agricultural practices (Curry 2006). In Elgin County, flocks of 50 were common in the 1950s. It is now rare with usually only single birds seen (Lancaster et al. 2004).

Western Meadowlark

Sturnella neglecta

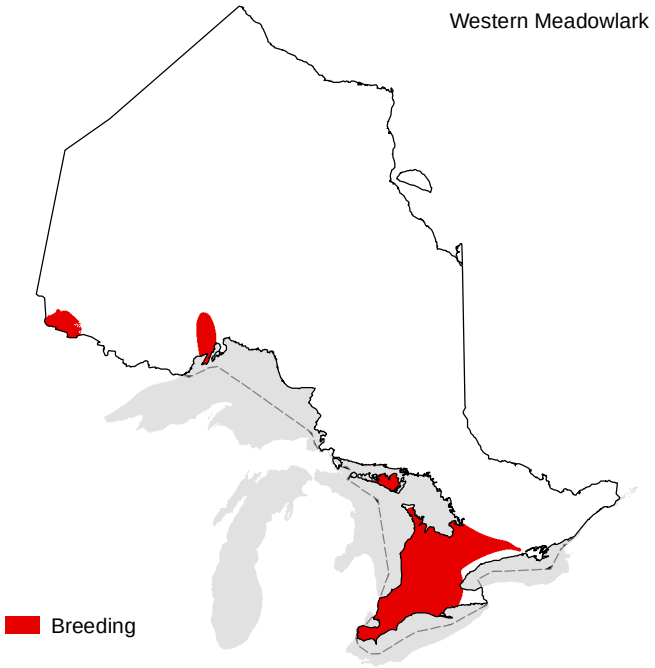


BREEDING SEASON

Habitat Requirements

Ontario Western Meadowlark nests were in grasslands, hayfields, and an orchard (Peck and James 1987). It was more abundant in southern Ontario in the drier climatic strip north of Lake Erie and Lake Ontario in the late 1950s and early 1960s. Within this area, it was found mostly in rough pastures (Falls 2000).

The Western Meadowlark is an obligate grassland species, with presence of grass an essential habitat component. It occupies a variety of grassland types including native and planted grasses. In native grasslands, it prefers short-grass and mixed-grass prairies to tallgrass prairies. It nests less frequently in shrubsteppe habitat. It inhabits undisturbed and grazed native grasslands. Nonnative grasslands that it regularly inhabits include pastures, hayfields, Conservation Reserve Program (CRP)



lands, Dense Nesting Cover (DNC) planted as waterfowl nesting habitat, meadows, and old fields. Less frequently, it nests in grassy and weedy roadsides, no-tillage cropland, weedy borders of agricultural fields, orchards, alfalfa fields, pine and oak barrens, wheat fields, airports, golf courses, large urban parks, open forests and aspen parkland areas with a grassy understorey, montane meadows, wetlands with grass or sedge cover, sand dunes, hydro corridors at least 30 m wide with reaches at least 500 m long of grassland, oak savannahs with a grassy understorey, and grassed waterways in agricultural fields. It formerly nested on vacant lots in towns and villages (Askins et al. 2007; Bent 1958; Camp and Best 1994; Campbell et al. 2001; Dancey 1990; Davis and Lanyon 2020; Dechant et al. 2002j; Earnst et al. 2009; Jones and Bock 2002; Jones et al. 2010; Leighton et al. 2002; Leston and Koper 2017; Mossman et al. 1991; Renken and Dinsmore 1987; Rotenberry and Wiens 1980; Sutter and Brigham 1998; Swanson 1996; Wood et al. 2013). Native grasses it is associated with include Mexican feathergrass, June grass, wheat grasses, grama grass, fescues, mountain bunch grass, and little bluestem (Camp and Best 1994; Davis 2003; Owens and Myers 1973; Pylypec 1991; Rotenberry 1980; Wilson and Belcher 1989). It is commonly associated with nonnative grasses including timothy, orchard grass, downy brome, smooth brome, quack grass, redtop, Kentucky and Canada bluegrasses, panic grasses, foxtails, and crested wheat grass (Dancey 1990; Davis et al. 2016; Dickinson et al. 1987; Earnst et al. 2009; Sutter and Brigham 1988; Wilson and Belcher 1989). In no-tillage croplands, it prefers fields where corn was planted into sod residue to fields where corn or soybeans were planted into corn residue (Dechant et al. 2002j).

Some studies considered Western Meadowlark habitat at the landscape scale. Its occurrence is positively correlated with the amount of grassland in the landscape and negatively correlated with tree and wooded cover. In South Dakota, its density increased but its occurrence decreased with the amount of grassland within 3,200 m. The study area was in a landscape averaging 70% coverage by grasslands. Its probability of occurrence decreased when there was woody vegetation adjacent to a plot. Its probability of occurrence was 70% where there were no wooded patches at the edge of a grassland but dropped to 20% when woody vegetation occupied 70% of the patch edge. It was negatively correlated with nonnative grasses. Its probability of occurrence was 80% when less than 5% of the grassland was covered by introduced grasses and declined below 50% where introduced grass coverage was greater than 80%. Greer et al. (2016) concluded that it was selecting for large expanses of grasslands rather than individual large patches. In Minnesota, its abundance was affected by the amount of grassland in the landscape, increasing by an average of 12 birds per

Breeding Bird Survey (BBS) route for each 10% increase in the amount of grassland in the landscape (Davis and Lanyon 2020). In Washington, its abundance was positively correlated with the amount of shrubsteppe habitat within 1 km. This was the most important variable explaining its abundance (Vander Haegen et al. 2015). In Saskatchewan, its abundance was influenced by the amount of cropland within 400 m. It was most abundant in grasslands where the surrounding landscape was composed of 40-50% cropland. Its abundance at this level of cropland was 5 times greater than where the surrounding area contained 0% or 100% cropland (Davis et al. 2016). In North Dakota, Grant et al. (2004) considered it sensitive to the presence of woodlands. Its occurrence was 50% where there was 0% woodland cover within 500 m, less than 10% at 20% woodland cover, and 0% at 40% woodland cover. In Manitoba, the amount of grassland within 100 m was an important determinant for presence of the Western Meadowlark. Its probability of occurrence decreased with the amount of woodland and urban cover within 100 m (Leston and Koper 2017). In the Prairie Pothole Region of Canada, its abundance was positively correlated with the amount of native and nonnative grasslands and wetlands within 3,200 m, but it was negatively correlated with coverage by trees and shrubs at this scale (Fedy et al. 2018). In Colorado, it was less abundant in grasslands at urban edges than in grassland interior (Jones and Bock 2002). In North Dakota, its probability of occurrence was 18% at 0-10% tree cover, dropping off quickly to 8% at 20% tree cover and almost 0% at 40% tree cover. Its favoured range of tree coverage was 0-13% (Cunningham and Johnson 2019).

The Western Meadowlark exhibits preferences for grassland types, although this may vary geographically. In native grasslands, short-grass and mixed-grass prairies are highly preferred to tallgrass prairies (Askins et al. 2007; Dechant et al. 2002j; Rotenberry and Wiens 1980). Many studies concluded that it prefers taller grasses, but this is within the context of grasses that are short compared with those in tallgrass prairies and in many nonnative grasslands. It prefers native to nonnative grasslands. This is probably because native grasslands tend to have shorter grass and the vegetation is often less dense with greater heterogeneity than nonnative grasses. In Saskatchewan, its abundance was positively correlated with vegetation height in both native prairies and nonnative grasslands. There was no significant difference in vegetation height in the 2 grassland types and both were short, averaging 18.9 and 20.5 cm. It was twice as abundant in native grasslands than planted grasslands (Davis et al. 2016). In Saskatchewan, it occurred in 66.7% of idle native grasslands, 6.3% of DNC fields, and 5.3% of wheat fields (Hartley 1994). In Manitoba, it was positively correlated with native vegetation. It was twice as abundant in native prairie than in nonnative grasslands (Wilson and Belcher 1989). In Washington, Vander Haegen et al. (2015) compared the Western Meadowlark's abundance in native shrubsteppe habitat and old and new CRP lands. Old CRP lands were planted in the 1980s with a mix of native and nonnative grasses and forbs. It was significantly more abundant in shrubsteppe habitat than either type of CRP habitat. Shrubsteppe differed significant from the CRP lands, having more shrub cover (15.8% compared with 5.0% and 2.0%) and taller shrubs (103.0 cm compared with 64.7 cm and 29.5 cm). Shrubsteppe habitat had significantly shorter grasses (42.5 cm) than new CRP lands (56.8 cm) and visual obstruction was significantly greater in shrubsteppe than in old CRP lands (11.1 compared with 5.4). In Alberta landscapes dominated by prairies and nonnative grasslands, it was more abundant in native grasslands and

prairies but differences were not significant from nonnative habitats. Fallow fields and row crops were unsuitable habitat (Owens and Myers 1987).

Several studies examined microhabitat preferences of the Western Meadowlark. It is strongly associated with grass cover, prefers dense cover near the ground and sparser cover at greater heights, low to moderate litter cover, moderate amounts of forbs, and little or no woody cover. It prefers open treeless areas (Davis and Lanyon 2020; Dechant et al. 2002j). In California, it occurred in 79% of oak savannahs with a grassy understorey, significantly different from 10% in savannahs with a shrubby understorey and 2% in montane hardwoods (Wood et al. 2013). In Wisconsin, it selected areas with less than 1% woody cover (Swanson 1996). In North Dakota, its abundance decreased significantly as coverage by shrubs increased (Grant et al. 2004). In grassland habitats becoming invaded by eastern red cedar in Oklahoma, it was less abundant in areas with greater cedar canopy cover (Chapman et al. 2004). Rotenberry and Wiens (1980) concluded that the Western Meadowlark had the broadest ecological niche of species inhabiting shrubsteppe areas. Nonetheless, it was negatively correlated with forb and shrub height but positively correlated with vegetation density. In Montana, it was the only species that avoided nest patches with high forb coverage (Dieni and Jones 2003). In Saskatchewan introduced grasses, its abundance was positively correlated with litter depth, the number of plant contacts below 10 cm, high grass and sedge coverage, and vegetation height. In native prairies, it was positively correlated with grass and sedge coverage but negatively correlated with the number of plant contacts below 10 cm and vegetation height. In both habitats, it was associated with dense vegetation. In short-grass prairies in Colorado, it was associated with taller grasses interspersed with forbs and low shrubs (Conrey et al. 2016). In Montana shrubsteppe habitat, it was significantly more abundant in areas without rock outcrops. Outcrops supported a plant community of more mesic shrub species that was unattractive to the Western Meadowlark (Rumble 1987). In a Wisconsin territory, grass coverage was high, especially by very narrow-leaved species, vegetation was about 15 cm tall, coverage by litter was low and of loose composition, and the vegetation resulted in little reduction in sun cover even at ground level (Wiens 1969). In Iowa, it was negatively correlated with vertical vegetation cover but positively correlated with vertical patchiness. It responded favourably to sites with a wide range of vertical vegetation densities (vertical patchiness) because it is within these plots that it can find the shorter vegetation it prefers (Patterson and Best 1996). Swanson (1996) reported that it was negatively correlated with coverage by legumes and summarized a Wisconsin study that stated its mean vegetation characteristics included less than 1% woody cover, 81% coverage by grasses and forbs, 14% litter coverage, 5% bare ground, and 8 cm vegetation height-density. It was positively correlated with coverage by prostrate residual vegetation and negatively correlated with the maximum height and density of vegetation. In mixed-grass prairie pastures in Saskatchewan, nest sites were significantly correlated with density of live grasses shorter than 30 cm, density of dead vegetation less than 30 cm tall, density of shrubs and forbs 20-39 cm tall, and density of forbs 50 cm or taller. It was also associated with increased litter depth and decreasing coverage by bare soil, but not significantly (Davis 2005). In North Dakota mixed-grass prairies, its abundance was positively correlated with percent grass cover, litter depth, density of low-growing shrubs such as snowberry and silverberry, and maximum and average vegetation heights (Dechant et al. 2002j). In Colorado, it was most abundant in grasslands with multilayered vegetation containing a fine-scale mixture of mid-height grasses that

provided tall vegetation structure, abundant dead vegetation from previous years, and a short-grass understorey (Davis et al. 2021).

Perches may be an important habitat component for the Western Meadowlark. It prefers to sing from an elevated perch but occasionally sings from the ground. Trees are not as important to it for perches as they are for the Eastern Meadowlark. Often Western Meadowlark territories do not include any trees. It frequently uses sturdy forb stems, shrubs, and fence posts as perches (Dancey 1990; Wiens 1969).

In Wisconsin, there were significant differences in vegetation between territories and unoccupied sites. In territories, the mean effective height of vegetation was lower, forbs were shorter, and the litter was not as deep as in unoccupied areas. Vertical vegetation density was similar in occupied and unoccupied areas, but the density at low levels was significant greater in territories (Wiens 1969). In North Dakota, occupied areas had deeper litter, less aspen woodland within 100 m, taller vegetation, shorter shrubs, more Kentucky bluegrass within 100 m, and higher coverage by legumes within 100 m than unoccupied areas (Grant et al. 2004). In Montana, it selected nest patches with greater visual obstruction, vertical vegetation density and height, grass cover, and litter cover and depth than random sites. It avoided areas with significant coverage by clubmosses (Dieni and Jones 2003).

Other studies compared the habitat preferences of the Western Meadowlark to those of other species. Lanyon (1956b) compared the habitat preferences of the 2 meadowlark species in their zone of overlap in the United States. Where they are both common, the Western Meadowlark preferred larger fields, shorter vegetation, and well-drained upland areas. The Eastern Meadowlark was more common in lowland areas in stream valleys, marshy areas, and poorly drained areas. The Western Meadowlark preferred short- and mixed-grass areas. The Eastern Meadowlark preferred tallgrass areas. Both species had a wide tolerance for varying habitat conditions and the Western Meadowlark occupied the lush lowland grasslands that the Eastern Meadowlark preferred when the other species was absent. Despite these different habitat preferences, the 2 species often nest in the same field. In Ontario, Szijj (1966) could find no differences in the habitats of the 2 meadowlark species. There were no differences in their habitat selection according to vegetation or moisture gradient. In Montana, the Western Meadowlark occurred in areas with more herbaceous and grass cover and with more widely dispersed shrubs than the Lark Sparrow (Walcheck 1970). In Wisconsin, Wiens (1969) compared the habitats of the 2 meadowlark species, Bobolink, and Vesper, Savannah, Grasshopper, and Henslow's sparrows. Coverage and density of forbs was highest for the Western Meadowlark of any species, but the mean height of forbs was significantly less than in areas occupied by other species. Coverage by broad-leaved forbs was high but heavy-stemmed forbs were sparse. Vertical vegetation density differed significantly only from that of the Henslow's Sparrow, which preferred denser areas, but density in the 0-10 cm height interval was significantly greater in Western Meadowlark territories than in areas occupied by all other species; coverage by vegetation less than 5 cm tall was the highest of all species. Its mean effective height of vegetation was significantly lower than for all other species except the Vesper Sparrow. Litter depth was significant less in Western Meadowlark territories than for all species except for the Savannah, Grasshopper, and Vesper sparrow. Species in order of increasing habitat richness based on

vegetation density and height and litter coverage and depth were Western Meadowlark, Vesper Sparrow, Savannah Sparrow, Grasshopper Sparrow, Eastern Meadowlark, Bobolink, and Henslow's Sparrow. The range of differences within the ranking was small with many similarities in habitat occupancy by the species. In Saskatchewan mixed-grass prairie, Davis (2005) compared the habitat preferences of the Western Meadowlark with those of the Sprague's Pipit, Chestnut-collared Longspur, Savannah Sparrow, and Baird's Sparrow. The Western Meadowlark was the only species strongly associated with the highest densities of tall shrubs and forbs, and it preferred tall dense vegetation. It selected the tallest and densest vegetation of all species.

The Western Meadowlark does not exhibit a strong aversion to edges and may be attracted to some edge types. An exception was in Colorado where it was significantly more abundant on plots 200 m from edges between suburban development or upland and lowland habitat than on plots closer to edge (Dechant et al. 2002j). In Wisconsin, nest density was lower near edges, but not significantly. The type of edge (wooded or nonwooded) was not a significant predictor of density within 50 or 100 m of edge and there were no differences in predation rates relative to distance from edge. Nests within 50 m of a nonwooded edge tended to have lower predation rates than those within 50 m of a wooded edge, but not significantly (Renfrew et al. 2005). In South Dakota, its density was influenced by patch shape and decreased with the complexity of patch shape as the edge-to-area ratio increased (Greer et al. 2016). In Alberta, the Western Meadowlark exhibited no response to roads. It decreased with increasing distances from wetlands and croplands indicating that it was attracted to wetlands and possibly to croplands (Sliwinski and Koper 2012).

The Western Meadowlark does not appear to be area sensitive. In Nebraska, the minimum patch size it was found in was 5 ha and territory sizes may occasionally be larger than this. In Idaho shrubsteppe, there was no relationship between its occupancy and patch size (Dechant et al. 2002j). In South Dakota, patch size was not a significant predictor of its occurrence or abundance (Greer et al. 2016). In Saskatchewan, it appeared to be area insensitive and showed some signs of inverse area sensitivity. It tended to occur more often in smaller patches, but not significantly (Davis 2004; Davis et al. 2006). Johnson and Igl (2001) studied its area sensitivity in Michigan, North and South Dakota, and Minnesota. Their results were inconclusive with no overall evidence for area sensitivity. Davis and Lanyon (2020) stated that the evidence for area sensitivity was weak and no effect of habitat size on occurrence of the Western Meadowlark had been determined. They noted that, in 1 Wisconsin study, it was not found on any lowland pastures smaller than 20 ha, but concluded that this was a function of habitat and not size. Swanson (1996) stated that it was considered mildly area sensitive in Illinois because it did not reach 50% occurrence until grasslands were at least 5 ha in size. Because some territories may be larger than that, this is not a valid indicator of area sensitivity.

Some studies provided recommendations for creating or managing habitat for the Western Meadowlark. Dechant et al. (2002j) concluded that keys to its management included providing a variety of grassland types and heights, sparse woody cover, and high coverage by grasses and forbs. They recommended avoiding burning, mowing, grazing, tilling, and chemical spraying during the breeding season, but spraying weeds on a spot-by-spot basis. Large tracts of grasslands should be provided and native grasslands and wet meadows should be protected from conversion to cropland. Management (burning, grazing, and mowing) should be done on a rotational basis to

provide a variety of habitats in different stages of succession. Mixed-grass prairie should be burned at varying intervals (2-3 years, 4-7 years, or 8-10 years) and tallgrass prairie and CRP lands should be burned every 4-5 years. Grazing can be used to improve habitat of tallgrass habitats and CRP lands. Dry short-grass prairies should be protected from grazing but wet short-grass prairies may be grazed. Patterson and Best (1996) recommended spot mowing on CRP lands in Iowa to open up dense vegetation and increase its use of this habitat.

The Western Meadowlark roosts on the ground in dense grass (Davis and Lanyon 2020), often under clumps of grass; as many as 12 may roost together (Bent 1958).

Ontario nests were all on the ground, hidden under grasses and other vegetation. They had a domed tunnel to the nest entrance (Peck and James 1987).

The Western Meadowlark invariably nests on the ground. The female excavates a depression in the ground as the first step in nest construction. Existing depressions may be used; 1 nest was in a hole in the ground 20 cm deep. In Manitoba, nests initiated before 10 May were in significantly deeper (6.0 cm) depressions than later nests (4.2 cm). Nests of primary females were in deeper depressions than those of secondary females. Many nests have a grass dome over them and some appear to be a round ball of grass. Some have tunnels constructed through the vegetation into the nest entrance; these may be as long as 75 cm. Most nests are well concealed beside a clump of vegetation or among tall grasses. They may also be at the base of a tree or beside a rock. One nest was in a plowed field with sparse oats, and the female was visible sitting on it from a distance of 30 m. In Manitoba, there was no consistent relationship between nest orientation and the direction of the prevailing winds. Nest orientation appeared to be such that it provided the most direct access through the vegetation. In Wisconsin, nests faced north or east. The prevailing winds during rain and sleet storms depressed the vegetation in these directions. Nests deteriorate rapidly and are not reused (Bent 1958; Campbell et al. 2001; Dancey 1990; Davis and Lanyon 2020; Dickinson et al. 1987; Wiens 1969).

Males establish territories as soon as they arrive, long before any females are present. They vigorously defend their territories against resident and migrant males and migrant females. Defence is most intense preceding incubation of the first clutch with secondary peaks of lesser intensity preceding each subsequent nesting attempt. Territories are defended until the last brood fledges. Although it has been stated that females are nonterritorial, females respond aggressively to the female rattle call. This response is strongest before incubation begins and declines rapidly thereafter, suggesting that this may be an attempt to delay the male's acquisition of another mate. Aggression by resident females may result in some high-quality territories not reaching their potential to support 2 females (Davis and Lanyon 2020; Dickinson et al. 1987; Lanyon 1956a). Territorial boundaries change considerably over the breeding season. Prior to the arrival of females, boundaries are dictated by the pressures of neighbouring males. Initial territories decrease in size with the subsequent arrival of additional males and an increase in density. If a bird disappears, boundaries change because neighbours annex the territory. Late in the season, the nest site and locations of females have a major influence on territorial boundaries. Males are flexible enough to alter territorial boundaries to ensure that they encompass the nests and female activity centres (Lanyon 1956a). Territory sizes are variable, with breeding density and habitat quality being major

factors influencing size. Territories in Indiana were 4-6 ha (Dancey 1990). Four Iowa territories were 4-13 ha (Davis and Lanyon 2020) and territories averaged 3.4 ha in Iowa alfalfa fields (Frawley and Best 1991). Two Wisconsin studies reported territory sizes of 1.2-6.1 ha, with most 2.8-3.1 ha (Lanyon 1956a) and 1.8-3.4 ha (mean 2.4 ha; Wiens 1969). In Manitoba, territories averaged 7 ha (Schaeff and Picman 1988). Dechant et al. (2002j) reported territory sizes of 3-13 ha in tallgrass prairies, 2-7 ha in short- and mixed-grass prairies, 3 ha in Iowa hayfields, 2.2 ha in idle shrubsteppe, 2.3 ha in shrubsteppe pastures, and 1.2 ha in Colorado. Bent (1958) reported territory sizes of 4, 8.5, 9.7, and 12.9 ha.

The Western Meadowlark tolerates most other grassland species and its territories may overlap broadly with theirs. The exception is the Eastern Meadowlark. Both species respond equally aggressively to the songs of both species. Territorial males challenge all male meadowlarks regardless of their species. This results in the 2 meadowlark species having mutually exclusive territories (Falls 2000; Lanyon 1956a; Rohwer 1973; Wiens 1969). In the main area of regular sympatry, the 2 meadowlarks have evolved to change their behaviour and body morphology. The incidence of fighting among males is much higher in the area of sympatry, and more serious wounds are inflicted. Male, but not female, Western Meadowlarks have larger and darker Vs on their chests. Female Eastern Meadowlarks showed a decrease in the size of the V but there was no change for males. Male Western Meadowlarks had brighter yellow chests and were significantly larger in areas of sympatry than where the Eastern Meadowlark was absent (Rohwer 1973).

Natal philopatry rates are low. In Wisconsin, 0 of 51 nestlings were found in a subsequent year within a radius of 1.6 km around the natal area. Three of 19 juveniles (15.8%) were observed in the following year 0.32-0.65 km from the banding sites (Davis and Lanyon 2020).

Adults appear to exhibit high site fidelity. In Wisconsin, both sexes showed strong site fidelity to their previous year's territory rather than toward a particular mate. Twelve of 21 males (57.1%) and 10 of 19 females (52.6%) returned. Only 1 male and 1 female failed to return to their former territory (Dechant et al. 2002j; Lanyon 1956a).

Limiting Factors

Eggs are likely to be present in Ontario nests from mid-May until the first week of July (Peck and James 1987). Pairing occurs almost immediately after the females arrive. It may take as long as 6 days to build early nests. Late nests may be built in a single day. Females may begin egg laying as soon as the nest lining is complete. Eggs are laid at the rate of 1 per day. Incubation begins with the laying of the penultimate or last egg. In Montana, the incubation period averaged 12.9 days (range 8-15 days). Elsewhere, incubation periods of 13-16 days were reported, with longer periods associated with long spells of cold wet weather. Hatching occurs over a 1- or 2-day period. In Montana, the average nestling period was 12.7 days (range 9-16 days). Others reported a nestling period of 10-12 days. Young may fledge as early as 8 days if they are disturbed (Bent 1958; Davis and Lanyon 2020; Dickinson et al. 1987; Jones et al. 2010; Lanyon 1956a).

Double broods have been reported in Ontario. In 1 Wisconsin study, all females that successfully raised a first brood attempted a second brood. A later study at the same site found that females laying 1 and 2 broods were equally abundant. It is likely that only females that initiate nesting early in the season raise a second brood. No more than 2 broods are raised in a season (Bent 1958; Davis

and Lanyon 2020; Jones et al. 2010; Lanyon 1956a; Peck and James 1987; Wiens 1969). The Western Meadowlark may be a persistent renester if initial nests fail. In Wisconsin, 5 females built at least 3 nests in a season and one built 6 nests in each of 2 successive years. Only birds that initiate nesting early in the season are likely to fledge young from a replacement nest (Davis and Lanyon 2020; Dickinson et al. 1987; Lanyon 1956a). Clutches of 4 and 5 eggs have been reported in Ontario (mean 4.42 eggs), although the sample size was only 7 nests (Peck and James 1987). Elsewhere, clutches of 3-7 eggs were reported, mostly 5 eggs. In Saskatchewan, mean clutch size was 5.1 eggs for unparasitized nests. Mean clutch size in Montana was 4.4 eggs, but this included parasitized nests that contained 0 meadowlark eggs. In Alberta, mean clutch size was 5.4 eggs (range 3-7 eggs, mode 6). In Saskatchewan, mean clutch sizes were 4.6 eggs in native pasture, 5.1 eggs in planted pasture, and 4.7 eggs in hayfields; in British Columbia, 58% of clutches contained 5 eggs (Bent 1958; Campbell et al. 2001; Davis 2003; Davis and Lanyon 2020; Davis et al. 2016; Gaudet et al. 2020; Jones et al. 2010; Ludlow et al. 2014). In Montana and Saskatchewan, clutch size decreased as the season progressed (Davis 2003; Jones et al. 2010), but it remained constant in Alberta (Ludlow et al. 2014). In Manitoba, clutches initiated before 1 May were smaller (5.10 eggs) than those initiated 1-10 May (5.77 eggs), with clutch size dropping to 5.00 after 10 May. Resources for egg production may be limited early in the season and may have prevented females from nesting earlier. Because secondary females began nesting when clutch size was higher, some were able to raise as many or more young than females that nested earlier. Clutches of secondary females were slightly larger (5.60 eggs) than those of primary females (5.29 eggs). Those that nest earlier may have the opportunity to raise a second brood or renest, but this increases the likelihood that their males will attract another mate (Dickinson et al. 1987).

Both sexes are capable of breeding when they are 1 year old and it is probable that all yearling females breed. Some males are unsuccessful in attracting a mate, and it is likely that these are yearlings. In a Manitoba population, 3 of 33 males (9.1%) failed to attract a mate. Males that remain unmated abandon their territories or are displaced (Davis and Lanyon 2020; Dickinson et al. 1987; Lanyon 1956a).

The mating system is polygynous, with polygynous males typically having 2 mates, rarely 3. Of 33 males in Manitoba, 10 were monogamous (30.3%), 9 mated with 2 females sequentially (27.3%), and 11 paired with females that had overlapping nest cycles (33.3%). Males' success in obtaining a second mate was related to the date when their primary females began nesting. All males that mated before 1 May subsequently mated with a second female and most of their females nested simultaneously. Most males whose females began nesting after 10 May mated with a single female; those that mated with a second female did so sequentially. Most secondary females became active on the territory after the primary female had begun incubation or fledged her young. Secondary females that were attracted while the first female was still nesting were more frequently recruited during the second half of incubation than during the first half. The staggered arrival of females may be a result of younger birds returning later than experienced females. Some females may become available if their first mate is abandoned or disappears. Unmated males were present, so some females chose to mate with an already mated male rather than entering into a monogamous relationship. When a primary female lost her nest, there was a high probability of the secondary female improving her status to become the primary female. Primary females fledged slightly more

young than secondary females, but the difference was not significant. There was no great disincentive to being a secondary female. Bigamous males had significantly higher reproductive success and were significantly less likely to produce no young than monogamous males. Selection should strongly favour behaviour that increases the likelihood of attracting a second female (Dickinson et al. 1987). The female selects the territory in which she wishes to breed and the male that is defending it. In Wisconsin, no female undertook a pairing with another male while her first mate successfully defended his territory. Within-season mate changes occurred only when the first male disappeared or was displaced (Lanyon 1956a). One nest contained 10 eggs suggesting intraspecific parasitism; it was subsequently abandoned (Davis and Lanyon 2020).

The Western Meadowlark forages on the ground in open areas, typically on arthropods but also on seeds. When feeding on sprouting grain, it occasionally eats the kernel but usually crushes it in the bill to obtain the milk and then discards it (Davis and Lanyon 2020). During a late spring snowstorm in Wyoming, it scavenged dead birds along a road, and attacked and killed others. It consumed 35 Horned Lark, 4 Western Meadowlark, 2 longspur, 2 robin, and 2 Dark-eyed Junco carcasses. It preyed upon live Horned Larks and juncos. It approached them from behind, seized the back of the skull in its beak, pinned them down, and pecked them until they were dead. In all predation events, it ate only the eyes and brain of the other bird. When muscles or internal organs were exposed in carcasses, it also ate them. This suggests that it is an effective predator during severe weather. It is possible that it is predatory at other times (Porter and Behl 2016). Scavenging and predation of other birds has been reported during severe winter snowstorms for both species of meadowlarks (Hubbard and Hubbard 1969; Krutzch 1950; Tyler and Choate 1990; Waters 1970).

Both adults feed the nestlings and assistance by the male is important in ensuring that nestlings do not starve. In Manitoba, 22 of 34 males (64.7%) were observed carrying food during the nestling period. Each fed nestlings of the primary female and 6 also fed the nestlings of the secondary female, but only after the primary female's young fledged or the nest failed. Eleven of 20 broods (55.0%) experienced some nestling starvation. These were always nestlings that hatched a day after the others. In each case when primary and secondary females were feeding their nestlings at the same time, the secondary female lost over half her brood to starvation. Larger nestlings were preferentially fed over younger, smaller nestlings so those that did fledge were in good condition. Two secondary females that were feeding their nestlings when the primary female lost her nest successfully reared all their brood with the assistance of the male. Primary females that are forced to share a territory may experience competition for food for their nestlings, reduced male vigilance for predators, and the possibility of losing primary status if their nest fails (Dickinson et al. 1987). Nestlings are fed invertebrates almost exclusively, predominantly caterpillars, beetles, and grasshoppers, plus ants, cutworms, and spiders. Some wheat has been reported in nestlings' stomachs and a few contained weed seeds (Bent 1958; Davis and Lanyon 2020). In Washington, food items collected from the esophagus of nestlings included 50 short-horned grasshoppers, 42 beetles, 36 spiders, 32 long-horned grasshoppers, 22 hymenopterans, 16 stink bugs, 15 flies, 4 crickets, 4 snails, 3 true bugs, 2 mayflies, 2 mosquitoes, 2 skippers (butterflies), 2 scorpions, and 1 each of assassin bug, shield bug, robber fly, and predaceous diving beetle (Orians and Horn 1969). In Saskatchewan, an adult fed a 2.5-cm-long frog to one of its nestlings (Ranford 1972).

The adult diet consists mostly of insects, with orthopterans, beetles, and caterpillars the most abundant prey. Ninety-one stomachs collected in California contained 70% animal matter and 30% vegetation. Beetles constituted 27% of the diet, particularly ground beetles. The remainder of the animal food consisted of 15% caterpillars, 6% wasps and ants, 12% grasshoppers (42% of the August diet), 4% bugs, and lesser amounts of crickets, crane flies, spiders, isopods, and snails. The vegetable food was mostly grain, including oats, wheat, barley, and corn. Two percent of the diet consisted of weed seeds and 1 bird had eaten fruit. Another California study examined nearly 2,000 stomachs which contained 63.3% animal food and 36.7% vegetation. The animal food consisted of 21.3% beetles (mostly ground beetles and click beetle larvae), 20.3% grasshoppers and crickets, 12.2% caterpillars, 5.6% hymenopterans (mostly ants), 1.7% bugs (mostly stink bugs), 0.1% flies, 0.2% spiders, and 1.9% miscellaneous insects. The Western Meadowlark often consumed cricket and locust eggs. The vegetation consisted of 30.8% grain, 5.3% weed seeds, and 0.6% miscellaneous plant material (Bent 1958). In Saskatchewan, the most common prey in 185 stomachs included ants, beetles, grasshoppers, and caterpillars; 9 orders of insects were documented in the diet. These were mostly beetles early in the breeding season, hymenopterans in June, and orthopterans from July to September. Thirteen percent of stomachs contained seeds, with 25% occurrence in spring and less than 1% in summer. In December, Wisconsin birds ate mostly corn and oats. One bird had eaten weevils, true bugs, and caterpillars (Davis and Lanyon 2020). Wiens and Rotenberry (1979) studied the diet of meadowlarks in shrubsteppe vegetation in Oklahoma, Texas, South Dakota, and Washington. In some states, the diet of the 2 meadowlarks was combined in the results, but they were separated in the west where only the Western Meadowlark occurred. The meadowlarks were the most highly carnivorous of the species studied. Over 3 years, the diet consisted of 18-45% beetles, 15-42% orthopterans, and 15-55% caterpillars. The diet over the years and sites ranged from 95.7-100% animal matter and 0-4.3% vegetable matter. The most important beetles in the diet included weevils and ground, scarab, leaf, and darkling beetles. It also consumed solder, long-horned, click, and clown beetles. Crickets were the most important orthopterans but it also ate long-horned and short-horned grasshoppers. Other prey items included hymenopterans (bees, ants, sweat bees, ichneumonid wasps, and thread-waisted wasps), odonates, millipedes, true bugs (leaf-footed, seed, squash, stink, ambush, and jewel bugs), soft-winged bugs (leafhoppers, cicadas, and scale insects), caterpillars, flies, snakeflies, spiders and sun jumping spiders, and snails. Seeds consumed included those of goosefoots, mustards, grasses, and legumes. The functional groups of prey were similar among all sites, but there was considerable variation in the orders of prey consumed among sites and years. Variations among sites were greater than those among years at a given site. It had a large niche breadth because it exploited both large and small prey items, consuming prey 1-32 mm in length with a peak at 4-16 mm. The mean prey size by location and year ranged from 7.54-14.13 mm. The diet overlap of the Western Meadowlark was 11-86% with the Horned Lark over 3 years and 67-83% with the Grasshopper Sparrow. At 1 site, the mean prey size consumed by the meadowlark and Horned Lark was significantly different. The authors concluded that food was not a limiting resource and that the Western Meadowlark exploited these resources in an opportunistic manner resulting in considerable individual, between-year, and between-location variation in diet composition and interspecific overlap. In the same Washington shrubsteppe habitat, Rotenberry (1980) compared the diets of the Horned Lark, Sagebrush Sparrow, and Western Meadowlark. All were highly insectivorous during the breeding season. The most

common prey of the Western Meadowlark early in the season was beetles, particularly weevils and larvae. Ants, wasps, caterpillars, small spiders, true bugs, and grasshopper nymphs occurred consistently in the diet, but contributed less to the diet combined than beetles. There was an abrupt shift in June and August when grasshoppers became much more abundant in the diet, often constituting more than 50% of the food. The average length of prey consumed was 7.66-8.23 mm in May in 2 years, 14.62 mm in June, and 12.51 mm in August. Each individual bird was likely to have eaten about 50% of the total taxa reported for the species, and individual dietary diversity was nearly 80% of that eaten by the entire population. There was a great deal of similarity in the diets of the 3 species and a substantial overlap in the size of prey consumed. In spring, the meadowlark ate a higher proportion of ground and darkling beetles than the other species, with a dietary overlap of 51%. When food items were categorized into groups of goosefoot seeds, orthopterans, grass seeds, scarab beetles, mustard seeds, caterpillars, and weevils, most individuals regardless of species were eating the same things at any given time. There was no apparent niche separation on the basis of food type. From June to August, this meadowlark ate more large items than the other 2 species, which ate more and smaller seeds. When only invertebrates were considered, the meadowlark consumed significantly larger prey than the other 2 species during this period. Animal food of the Western Meadowlark comprised 100% of the May diet, 97.3% of the June diet, and 95.2% of the August diet. Animal prey included spiders, beetles (weevils and darkling, scarab, and ground beetles), ants and wasps, caterpillars, robber flies, neuropterans, true bugs, orthopterans, and leafhoppers. Vegetable food consisted of grass seeds and miscellaneous forb seeds. Food was not limiting and all species were opportunistic foragers. In Nebraska, Kaspari and Joern (1993) compared the diets of the Western Meadowlark and Lark and Grasshopper sparrows. The meadowlark was largely carnivorous, consuming no more than 5% seeds in its diet. The diets of the Lark and Grasshopper sparrows consisted of 61% and 33% seeds, respectively. The most abundant items in the meadowlark's diet included 42% short-horned grasshoppers, 22% adult beetles, and 15% caterpillars. It consumed lesser amounts of long-horned grasshoppers, spiders, hymenopterans, true bugs, flies, beetle larvae, leafhoppers, and froghoppers. It preferred larger prey and exclusively consumed the largest sizes of 5 taxa and beetle larvae 5-14.9 mm in length. It uniformly avoided prey in all taxa groups that were shorter than 5 mm and 5-15.9 mm (except beetle larvae), preferred prey 15-35 mm long, and exhibited an increased preference for prey 35-45 mm in length over the other 2 species. It consumed 97% of the arthropod species that were collected in sweep samples. It selected short-horned grasshoppers, more so than the more abundant leafhoppers and froghoppers. It avoided small prey even though they were much more abundant. Small prey may be more difficult to find but, more importantly, have a higher proportion of chitin per unit of weight. Consequently, they may fill up the gut with less nutritional food. These authors concluded that their results did not support the conclusions of Wiens and Rotenberry (1980) that the Western Meadowlark was a dietary opportunist.

In Manitoba and Colorado, the Western Meadowlark punctured eggs in other species' nests and attacked nestlings. It does not appear to eat either the egg contents or young and may depredate nests to minimize competition (Creighton and Porter 1974; Schaeff and Picman 1988).

The Western Meadowlark is a fairly common host of the Brown-headed Cowbird, particularly in the Great Plains where this parasite is most abundant. In Illinois, Peer et al. (2000) artificially

parasitized nests with eggs painted similar to those of a cowbird and with nonmimetic eggs. It regularly rejected both types of eggs within 24 hours of parasitism: 77.8% of mimetic eggs and 100% of nonmimetic eggs. A real cowbird egg was accepted at the only naturally parasitized nest. Spots on the real cowbird egg were larger and resembled meadowlark eggs more closely than the artificial eggs. In Saskatchewan, parasitism rates were negatively correlated with grassland size but unrelated to distance to perches for cowbirds and amount of concealment at the nest (Dechant et al. 2002j). Parasitism significantly affected meadowlark clutch size and fledging success in Saskatchewan. Clutch size of parasitized nests averaged 4.0 eggs compared with 5.1 eggs in unparasitized nests. Successful parasitized nests fledged an average of 2.4 young compared with 3.7 for unparasitized nests (Davis 2003). Fledging success was also lower for parasitized nests in Manitoba: 0.6 young per parasitized nest and 1.1 per unparasitized nest (Davis and Lanyon 2020). The cowbird may adversely affect nests that are not parasitized by puncturing the eggs. This may prompt the female to renest, thereby offering another opportunity to parasitize (Granfors et al. 2001). No cases of parasitism have been documented in Ontario. Parasitism rates reported elsewhere are variable and may vary significantly annually at a given location. In Saskatchewan, 26 of 103 nests (25.2%) were parasitized over a 4-year period. Rates were 42% and 45% in 2 years and 0% in the other 2 years (Davis 2003). Other reported parasitism rates in Saskatchewan include 2 of 29 nests (6.9%) and 11 of 24 nests (45.8%; Dechant et al. 2002j). Other parasitism rates include 2 of 139 nests (1.4%) in British Columbia (Campbell et al. 2001); 4 of 26 nests (15.4%) in Alberta (Ludlow et al. 2014); 0 of 17 nests in Saskatchewan (Gaudet et al. 2020); 28 of 65 nests (43.1%) in Manitoba; 0 of 45 nests in Washington (Vander Haegen et al. 2015); 5 of 26 nests (19.2%), 5 of 39 nests (12.8%), 47% of nests, and 4 of 26 nests (15.4%) in North Dakota; 26% of nests and 32 of 118 nests (27.1%) in Montana; 2 of 29 nests (6.9%) in Kansas; 5 of 31 nests (16.1%) in Nebraska; and 14 of 76 nests (18.4%) in Minnesota (Davis and Lanyon 2020; Jones et al. 2010).

Hybridization of the 2 meadowlarks rarely occurs, and only in the extreme eastern portion of the Western Meadowlark's range. Hybridization has been documented in Ontario and Quebec (Bannon in Gauthier and Aubry 1996; Szijj 1966). Over 4 years, Szijj (1966) found 9 nests belonging to mismatched pairs in southwestern Ontario. Most Western Meadowlark populations in Ontario consist of isolated groups of 2 or 3 pairs, or even solitary pairs, surrounded by breeding Eastern Meadowlarks. Mixed pairs consisted of a male Eastern Meadowlark and 1 or 2 Western Meadowlark females. Females typically select a territory where the male is singing conspecific songs. All copulations occur within the territory, so these 2 factors usually inhibit hybridization. Hybridization has not been documented where both species are common in the zone of overlap. Where Western Meadowlarks are rare, females may not be able to find a conspecific mate. In Ontario, only 46.6% of eggs in nests of mismatched pairs hatched. Survivorship of fledglings was also poor. Only 2 of 5 young (40.0%) taken from nests were raised successfully compared with 5 of 7 pure young (71.4%). In 3 of the 9 nests, young were found dead in or around the nest. The overall breeding success of mismatched pairs was no higher than 25%. Fledglings that survive initially do not appear to fully develop. One young was considerably smaller than normal, failed to acquire adult plumage, and subsequently died for no apparent reason. Another was larger than normal and gained full adult plumage, but its gonads failed to develop despite receiving hormone injections. Hybridization is unlikely to affect the gene pool of either meadowlark species because it is a rare occurrence and the

resulting young are unlikely to survive or develop physically enough to mate with other birds (Lanyon 1956a; Szijj 1966).

The most significant limiting factor for the Western Meadowlark is habitat loss and degradation. Habitat loss is due predominantly to conversion of hayfields and pastures into row crops. Losses also occur due to natural succession of abandoned fields, tree planting, and conversion of agricultural land into urban areas or other land uses. These types of losses occur rangewide and are not confined to Ontario. In the core of its range, extensive habitat degradation has occurred by converting native grasslands to planted grasslands. Nonnative grasslands are inferior habitat and support lower densities than prairies. Nonnative grasslands also promote the growth of nonnative forb species, such as sweet clover, that may greatly reduce habitat suitability. In the east, conversion of hayfields dominated by grasses and clovers in the genus *Trifolium* to those planted to alfalfa has been detrimental. Alfalfa fields grow much denser than it prefers and do not provide the grasses that it requires to construct its nest. In Ontario, there is much less pastureland available than when the Western Meadowlark was more common. The remaining pastures are grazed at a much higher intensity than previously and the resulting short-cropped grass does not provide suitable habitat (Campbell et al. 2001; Falls 2000; Greer et al. 2016; Swanson 1996; Walk et al 2010).

Mowing may be detrimental or beneficial for the Western Meadowlark depending on the timing of mowing and the original density of grasses. Mowing of hayfields during the breeding season typically results in the loss of all nests and fledglings. In Iowa, densities of meadowlarks were the same before and after mowing an alfalfa field. Results were inconclusive because territories were large and extended into unmowed areas. In dense grasses in CRP lands, spot mowing creates patches of shorter grasses that improve habitat. In North Dakota native grasslands, density was highest in hayfields mowed the previous year compared with those grazed. Emergency mowing of CRP lands in the Midwest due to drought increased coverage by herbaceous species and the proportion of grasses in the cover the following year. This resulted in an increase in its population. In Saskatchewan, it occurred consistently in hayfields that were mowed annually and was occasional in periodically mowed fields, but was most abundant in idle native grasslands. Mowing or spot mowing after the breeding season may be an important management practice in dense or tall grasslands. Mowing during the breeding season and in short, sparse grasslands may be detrimental (Davis and Lanyon 2020; Dechant et al. 2002j; Frawley and Best 1990; Patterson and Best 1996). Wolcott et al. (2023) recommended that grassland management be deferred until August to protect both nests and fledglings.

Prescribed burning is a regular management practice in western grasslands. Without periodic burning, shrub density eventually reduces habitat quality. The general response of the Western Meadowlark is a decline in numbers immediately following fire, an increase for a few years postburn due to recovery of grasses and herbaceous species and a lack of shrubs, and a subsequent decline when shrubs reinvade. In North Dakota, grass cover increased after fire but its density decreased as did coverage by shrubs. It was absent in unburned areas and responded positively to the extent and frequency of fire. It reached its highest abundance in areas that were burned 4 times within 15 years, with the last fire occurring 2 years previously. It was most common 2-5 years postfire and declined starting about 5 years postfire (Madden et al. 1999). In Saskatchewan, Pylypec (1991) studied the

effects of an October fire. It was adversely affected by fire the first 2 years following the burn, but densities were similar in burned and unburned areas 3 years after fire. Its recovery was related to the recovery of the grassland community. In Texas, there was no difference in its abundance on burned and unburned plots after a 3,600-km^2 wild fire (Roberts et al. 2012). Earnst et al. (2009) reported its response to a wild fire in shrubsteppe habitat in Washington. Its population was declining prior to the fire. After the fire, it stabilized but at a lower population level. There was a substantial loss of vegetation after the fire and shrubs showed little sign of recovery 4 years later. There are some differences between prescribed and wild fires that may result in different habitat regimes. Prescribed burns tend to be of uniform low or moderate intensity and usually result in an even burn over an area. Wild fires tend to have varying intensities in different areas and isolated patches may escape without being burned. In North Dakota, it was absent from unburned mixed-grass sites but present in areas subject to repeated burning at 3-year intervals. It was absent in prairies that had not been burned for more than 80 years. Meadowlark density peaked 1-3 years postburn. In South Dakota, its use of native pastures burned in spring increased in June and July. Its abundance in burned areas was significantly higher in July than in June. In July it was more abundant in burned than unburned areas. In Idaho shrubsteppe, densities were higher 1-3 years postburn than prior to the burn; densities levelled off 4 years postburn. In Montana, it was more abundant in burned than unburned shrubsteppe. Occupied areas within burns contained significantly less grass and herbaceous cover than random areas within the burn (Dechant et al. 2002j).

The Western Meadowlark responds positively to light to moderate grazing and negatively to heavy grazing. In some cases, it exhibits no response to grazing. Harrison et al. (2010) studied its response to grazing in short-grass habitat in British Columbia. Some sites were ungrazed; others were lightly, moderately, or heavily grazed. Vegetation characteristics were significantly different in grazed and ungrazed plots, but vegetation was similar in plots with different intensities of grazing. Grazed plots had 46% less coverage by native grasses and 400% higher coverage by Kentucky bluegrass. There was a weak indication that it was more abundant where there was less bare ground and where vegetation was taller. It appeared to find suitable nesting patches even in grazed areas. In Nebraska, grazing had no effect on it (Kim et al. 2008). In 1 Saskatchewan study, it was 3 times more abundant in ungrazed than grazed grassland, although it was abundant in both habitats. In another Saskatchewan study, it was equally abundant in grazed and ungrazed areas. In Alberta, it was equally common in different grazing systems but more abundant in idle mixed-grass prairies than continuously grazed prairies. In short-grass prairies in Colorado, it nested in lightly to moderately summer- or winter-grazed pastures and heavily grazed winter pastures but avoided heavily grazed summer pastures. In Oklahoma, it nested more frequently in moderately grazed tallgrass prairies than in undisturbed prairies. In Wisconsin, it was equally abundant in rotationally grazed pastures, continually grazed pastures, and ungrazed pastures. In short-grass prairies in Arizona, it was absent in pastures heavily grazed by sheep and common in moderately grazed pastures. In North Dakota, its density was higher in grazed native prairies than in DNC planted to alfalfa and wheat grass. It also occurred in formerly grazed fields that had been idle for a year. In South Dakota, a 20-year drought and a year of grazing on restored fields caused a decrease in plant height and vertical and horizontal density. This resulted in an increase in this meadowlark (Dechant et al. 2002j).

In extensive grasslands in the core of its range, habitat fragmentation by woody vegetation may adversely affect the Western Meadowlark. In Minnesota tallgrass prairies, nest depredation and parasitism decreased with distance from a woody edge, and predation rates were lower on large (130-486 ha) than small (16-32 ha) grasslands. On large patches, the probability of finding nests was highest near forest edges but nest productivity was highest distant from edge (Dechant et al. 2002j). Zuckerberg et al. (2018) concluded that large patches appeared to moderate the effects of weather on this meadowlark. The positive effects of precipitation in the preceding year were strongest on small patches and had little effect on large patches. Warm temperatures reduced nesting success in small patches and increased it in large patches.

The Western Meadowlark population may be affected by drought and weather conditions, particularly in the core of its range. It appears to respond negatively to extreme drought or very wet conditions. In Wisconsin, its abundance was strongly correlated with the amount of spring precipitation but unrelated to summer precipitation (Lanyon 1956a). In Nebraska, it experienced the most erratic patterns of any species in response to drought severity levels. Its abundance declined significantly as conditions changed from mild drought to very wet conditions (Kim et al. 2008). Within nesting seasons, Ludlow et al. (2014) found that weather had no effects on nest survival. Gorzo et al. (2016) analyzed 45 years of BBS data for the United States prairie and badlands area to determine effects of extreme weather events. Its abundance did not respond to significant weather events related to temperature or precipitation. Single-year extreme weather events did not result in abundance declines in the following year. Nests were abandoned in mid-June in 1 year, but this did not result in lower abundance the next year. In short-grass prairies in Colorado, nest survival was lower after very hot days, after dry days, and on stormy days during both the incubation and nestling phases. Survival rates were lower during warmer and drier breeding seasons. They modelled the projected effects of climate change assuming a 2-3°C increase in daily maximum temperature and 1-2 additional dry days experienced by each nest. This suggested a decline of 5% in daily nest survival in the most conservative scenario and 8-10% in the least conservative. Increasing dryness had a greater effect than increasing temperatures. The combined effects of increasing temperatures and dryness could result in a 50% decline in overall nest success. In North Dakota, abundance of the Western Meadowlark was positively correlated with the number of ponds present in May in the current and previous years combined, but not by the number of ponds in the current year on its own or by drought indices (Niemuth et al. 2008). In the United States, higher amounts of precipitation in the preceding year were associated with higher nesting success, but wetter conditions during the breeding season reduced success. Extremely hot or cold conditions early in the breeding season were associated with lower nest success rates (Zuckerberg et al. 2018).

Agricultural chemicals may have adverse effects on the Western Meadowlark. It may die from eating poisoned grain designed to kill rodents (Bent 1958). In Oklahoma, several died after eating grain treated with insecticides. These were known to bioaccumulate and be toxic to vertebrates (Griffin 1959). The effects of grasshopper control methods (malathion, carbyl in oil, carbyl bait, and another bait) were evaluated in Colorado, Idaho, North Dakota, Utah, and Wyoming. Its density declined 10 and 21 days post treatment due to a reduction in insect prey. In Colorado and New Mexico, it suffered mortality where toxaphene was applied. No effects on brain levels of

acetocholinesterase were detected due to carbyl. Fenitrothion has been reported causing declines and diazinon caused mortality and significant declines in Wyoming (Dechant et al. 2002j).

Shaffer and Buhl (2015) studied the effects of 3 wind-energy facilities on the Western Meadowlark in North and South Dakota. Immediate displacement occurred in 1 year at 1 site overall and within 100 m of wind turbines. Long-term displacement (2-5 years after installation) occurred at the same site but not the other two. Delayed displacement may have been due to site fidelity. Sustained displacement mostly occurred within 100 m of turbines. The inconsistent response across study areas probably resulted from habitat differences. The site where the response occurred may have been a cumulative effect of conversion of adjacent grasslands to croplands. There were few other disturbances at the other 2 wind farms.

Ludlow et al. (2015) studied the effects of oil and gas development facilities in extensive tracts of mixed-grass prairie in Alberta on the Western Meadowlark. The proportion of nests within 100 m of a well was significantly higher than expected. Nest density was lower than expected within 100 m of a gravel road. Road avoidance may be due to presence of unsuitable habitat, increased predation risk, or disturbance by vehicles. Wells may provide singing perches for territorial males and therefore attract birds. In Alberta, it was less abundant within 805 m of gas wells. Noise did not appear to be a factor. Results were similar at quiet gas wells and noisy oil wells (Daniel and Koper 2019).

The Western Meadowlark may be affected by human disturbance. It is sensitive to the presence of humans in its territory. Females flushed during laying or early incubation often abandon the nest (Davis and Lanyon 2020). In Colorado, it was significantly more abundant along control transects than along recreational trails in mixed-grass prairies (Dechant et al. 2002j). During spring snowstorms, it may be attracted to bare areas along roadsides. These birds may be lethargic due to food scarcity. In Wyoming, hundreds were killed by vehicles during such an event (Porter and Bell 2016).

Nixon et al. (2016) projected the response of the Western Meadowlark to climate change in Alberta. They projected a 29% expansion in the area of suitable climate: 150% by 2050 and 200% by 2080, and that all existing habitat would remain climatically suitable. They predicted a 20% increase in the amount of suitable habitat by 2050 and 25% by 2080. The area of suitability shifted northward with projected climate change.

Status

Prior to European settlement, the range of the Western Meadowlark extended eastward only to the edge of forest coverage in Missouri, Illinois, and Wisconsin. After the clear-cutting of forests and their conversion to agricultural lands, it extended its range northeast. It was almost unknown in Michigan in the 1930s but about 20 years later it occurred in all counties. In Wisconsin, it was originally confined to isolated patches of prairies surrounded by Eastern Meadowlarks, but the Western Meadowlark is now widespread in that state. It now occurs in Indiana and reached Ohio in 1930. No significant eastward expansion occurred in the south in Missouri, Kansas, Oklahoma, or Texas (Davis and Lanyon 2020; Lanyon 1956b; Swanson 1996).

The Western Meadowlark extended its range into Ontario from the west with the first specimens collected at Ottawa in 1900, Thunder Bay in 1917, and Sault Ste. Marie in 1921. Breeding was first confirmed at Emo in Rainy River District in 1929. At that time, it was fairly common in the farmland between Fort Francis and Rainy River. Widely scattered populations occurred around the Lakehead by 1934 and a nest was found there that year. By 1940, it was a common resident in that area in agricultural lands. The first record south of Lake Nipissing was at Franks Bay in Parry Sound District in 1932 and one was present in Elgin County in 1935. From then until 1960, it occurred in increasing frequency over a wider area of southern Ontario from Lake Huron east to at least Peterborough and Northumberland counties. It was documented in the Ottawa area in 1954 and 1955. By then, it was a regular breeder east of Lake Superior and on the Clay Belt (Baillie 1939, 1960, 1967; de Vos 1964). It was first seen in the Hamilton area in 1940, and bred intermittently in old fields south of the city from about 1945-60. A nest was found there in 1947. From 1953 onwards for about 4 decades, one to several occurred on territory annually. A colony of 5 occurred in prairie-like pasture near Hagersville (Curry 2006). The first record for Niagara Region was in 1953 at Port Colborne and there were numerous records there until 1966. A decline was apparent after that, with only 5 observations 1966-76 and only 2 in the following 30 years. A nest was found in Wainfleet Bog in 1966 (Black and Roy 2010). From 1958 to 1962, 33 nesting sites were documented in southern Ontario ranging from Essex County to Oshawa. In many years, what was reported as a single singing male turned out to be a small colony of 2-8 individuals surrounded by Eastern Meadowlarks (Falls 2000). The Western Meadowlark first reached Kingston in 1969 with an invasion occurring for several years before it began to decline after 1974. By the late 1970s, it was difficult to find more than a half dozen birds in the southwest (Austen et al. 1994; Falls 2000; Weir 2008). By the time of the first atlas, the population had declined considerably. The first atlas indicated that the Western Meadowlark occurred in the Thunder Bay and Rainy River areas and in scattered locations in southern Ontario, including Manitoulin Island and southwestern Ontario east to the Peterborough area. Highest concentrations in the south were in Bruce County. It was most abundant in the Rainy River area where it was more common than the Eastern Meadowlark. It was reported from 84 squares with 69 of them in the south. It was doubtful that it nested in all these squares and it was concluded that the distribution map overestimated its abundance. It was estimated that fewer than 100 pairs nested in the southern portion of the province, but that the northwestern population might be higher (Eagles in Cadman et al. 1987). James (1991) considered the Western Meadowlark a common summer resident in western Rainy River District, rare in the Thunder Bay area, and rare to locally uncommon in the south in agricultural land, mostly west of Toronto.

Falls (2000) noted further declines in the Western Meadowlark before the second atlas was initiated. BBS data for 1966-96 indicated that it had declined in Ontario at a rate of 5.7% per year in Ontario. In the last 2 years of this period, none were reported. The breeding population in the northwest was still extant, but it appeared to have declined over the 15 years since the atlas. It also declined in the Great Lakes states suggesting that sources for Ontario birds are dwindling.

The second atlas indicated no change in the range of the Western Meadowlark, but its probability of occurrence declined significantly province-wide and in all regions where it occurred. It was observed in only 34 squares in the entire province, with almost all losses occurring in the southwest. Most squares in the southwest were occupied by a single pair and often only for 1 or 2

years. There were only 2 squares in the south that were occupied during both atlases. The population in the Rainy River area was still present but it was less common than during the first atlas (Leckie in Cadman et al. 2007). In the Hamilton area, the decline in the Western Meadowlark was obvious after the mid-1980s and there were only 2 records in the decade prior to 2006 (Curry 2006).

BBS data indicate that the Western Meadowlark decreased at annual rates of 1.5% in Canada and 3.61% in Ontario 1970-2021. Trends for 2011-21 were annual increases of 1.28% in Canada and 1.03% in Ontario. All results were highly reliable except that the short-term trend for Ontario was of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings are incapable of fight when they leave the nest and spend their first week crawling and hopping among the vegetation. During their second week they make short flights and are capable of sustained flight in the third week. They remain with their parents and are dependent upon them for the first 2 weeks out of the nest (Bent 1958; Davis and Lanyon 2020; Giovanni et al. 2015). In Nebraska, Giovanni et al. (2015) radiotracked 28 fledglings from 12 nests on a 500-ha meadow dominated by smooth brome, redtop, timothy, wheat grass, quack grass, Kentucky bluegrass, and reed canary grass with some native grasses, sedges, spikerushes, and clovers. As young aged, they moved greater distances from their nest and between sequential sites. They began dispersing further than 0.5 km from nest sites during their fourth week postfledging. They selected sites with shallower litter, taller vegetation, and less cover by grasses and sedges than occurred at random sites. The amount of bare ground and cover by forbs appeared to have no influence on habitat selection. The probability of a habitat being selected by a 30-day-old fledgling decreased with litter depth and increased with vegetation height. Seventy-day-old fledglings selected areas with increasing litter depth and lower vegetation height. Habitat selection varied with ambient temperature. At 39°C, they selected areas with increased litter depth, lower vegetation, and lower coverage by grasses and sedges. At 19°C, they selected areas with taller vegetation, decreased litter depth, and lower coverage by grasses and sedges. Selecting areas with taller vegetation and shallower litter may have allowed fledglings to maximize thermoregulation and minimize caloric expenditure on movement respectively. Twenty-two of 23 mortalities (95.7%) occurred during the first week postfledging. Survival increased with age and ambient temperature and decreased with litter depth. The probability of habitat use was 22% when litter depth was 0 cm and near 0% at 12 cm; 15% at 0-cm vegetation height, 20% at 40-cm vegetation height, 30% at 60 cm, 40% at 95 cm, and 55% at 100 cm; and 60% at 0% cover by grasses and sedges, 40% at 20% coverage, 30% at 40% coverage, 20% at 60% coverage, and 10% at 80% coverage.

Fledglings have roosted at night in low shrubs with other juveniles (Bent 1958).

In Saskatchewan, juveniles consumed 8 orders of insects and had a diet similar to that of adults, although they ate more grasshoppers in July and August than adults. Beetles and hymenopterans were also important prey (Davis and Lanyon 2020).

Once young are capable of strong flight, they amalgamate into flocks and are joined by adults after the last broods fledge. Birds remain in flocks until next spring when breeding is initiated again. Where they coexist, flocks may contain both Western and Eastern meadowlarks (Bent 1958; Campbell et al. 2001; Davis and Lanyon 2020).

MIGRATION

The Western Meadowlark is a diurnal migrant that may travel in loose flocks of 15 or more birds (Davis and Lanyon 2020). Three recoveries have been made of birds banded in Ontario. One banded in June in Blenheim was recovered in March in North Carolina (a distance of 783 km), 1 banded in Nilestown in June was recovered in January in South Carolina (1,066 km), and 1 banded in Sandhill in June was recovered in December in Mississippi (1,398 km). The first 2 records are noteworthy because these birds wintered outside the known wintering range and within the wintering range of the Eastern Meadowlark (Brewer et al. 2018).

Migrant Western Meadowlarks return to their breeding grounds in March and April and leave in mid-October, with some staying into November. Females arrive in spring 1-4 weeks after males and yearlings presumably arrive even later (Dancey 1990; Davis and Lanyon 2020). In Ontario, spring migrants have been observed from mid-March until the first week of June. Most autumn records are in October, but birds may tarry until early January (Curry 2006; Lancaster et al. 2004; Tozer 2012; Weir 2008).

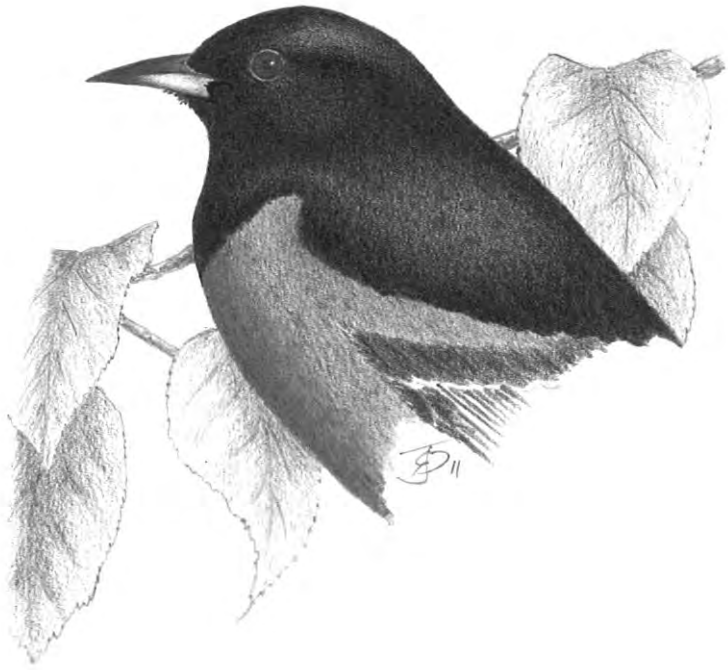
In Manitoba, Murphy-Klassen et al. (2005) found no change in the Western Meadowlark's spring arrival dates in response to climate change over the period 1939-2001.

The Western Meadowlark uses habitat during migration that is similar to its breeding habitat. It occurs predominantly in grasslands but may visit agricultural fields (Davis and Lanyon 2020).

James (1991) considered the Western Meadowlark a rare migrant in Ontario. It occasionally wanders north to Sandy Lake and Moosonee.

Orchard Oriole

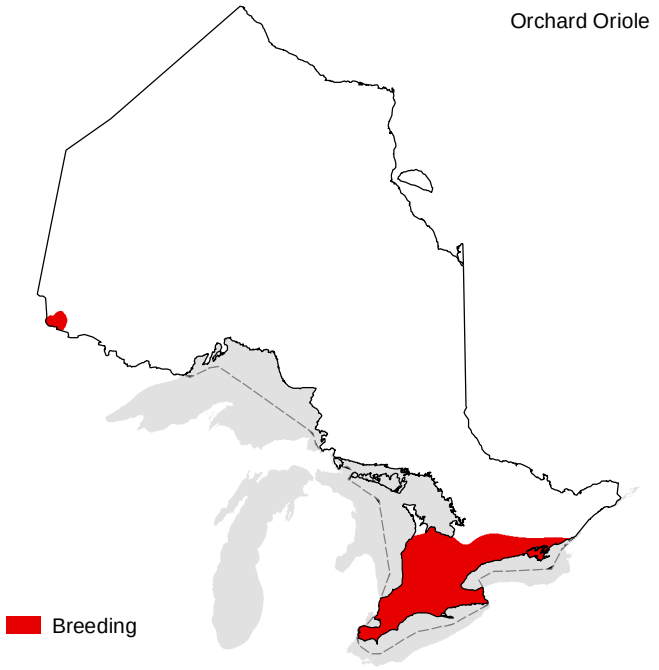
Icterus spurius



BREEDING SEASON

Habitat Requirements

Ontario Orchard Oriole nests were in rural areas in orchards, shrubby fields, and rural gardens (42.9% of nests); in open parkland areas such as campgrounds, picnic areas, and near buildings (34.3% of nests); in urban gardens (20.0%); and along woodland edges (2.9%). Breeding habitats were characteristically open with little or no understorey (Peck and James 1987). Nearly every orchard along the Lake Erie shoreline in Elgin County supported a pair in the early 1950s (Lancaster et al. 2004). It often breeds in orchards or farmyards, suburban areas, campgrounds, nurseries, hedgerows, roadsides, open second-growth woodlands, lightly wooded river shores, and open fields with scattered trees (Austen et al. 1994). In Peel Region, a pair nested in a damp depression regenerating



with 3-m tall trembling aspens with an understory of red-osier dogwood. The patch was 0.28 ha in a 4.8-ha meadow (personal observation).

The Orchard Oriole avoids large forests and grasslands without scattered shrubs or trees or small patches of trees. It exhibits a strong preference for riparian zones bordered by narrow strips of trees, floodplains, marshes, and shorelines of large rivers and lakes. It often nests in shade trees and open shrublands and thrives in habitats with low-density human intrusion such as farms and parklands. It frequently nests in orchards. Trees along roads and scattered shade trees around dwellings are favoured habitats. Where orchards are uncommon, it may nest in nurseries and other habitats with an abundance of trees and shrubs within open habitats (Bent 1958; Scharf and Kren 2022). In Manitoba, it nested in a narrow 2-km long sand dune ridge separating Delta Marsh and Lake Manitoba. The area was treed with peach-leaved willow, Manitoba maple, cottonwood, and green ash with a shrub layer comprised of sandbar willow, red elderberry, and red-osier dogwood (Sealy 1980a). In Illinois in a mosaic of old fields, camp sites, and woodlots, it nested in isolated trees in second-growth fields and along hedgerows and woodland borders (Enstrom 1993). Graber and Graber (1963) concluded that hedgerows and edge shrubs were probably the best habitat in Illinois, but densities were highest in orchards. It occurred in pastures, fallow fields, residential areas, and forests, but these were not preferred habitats. Fallow fields, mixed hayfields, clover fields, and wheat fields were visited for foraging but were not used for breeding. In Wisconsin, it was rare overall in pine and oak barrens but uncommon in oak savannahs (Mossman et al. 1991). McCabe (1948) reported it nesting in a university arboretum in Wisconsin. It was widespread in Louisiana but seldom found in forests and swamps. It was most abundant along ditches, bayous, and canals; in open marshes; and on grassy and shrubby islands along the coast (Kopman 1915). In the same state, Dennis (1948) reported very high nesting densities in a wildlife sanctuary where there were 10 buildings, lawns, 78 shade trees, and numerous shrubs and ornamental plantings within an area of 2.8 ha. There appeared to be similar densities nesting in willow shrubs along the Mississippi River and larger backwaters. Low densities of nests occurred in extensive common reed marshes as far as 8 km from the nearest trees. All nests were on the outer edge of the common reeds overlooking a body of water. It also appeared to nest in dense mangroves and wax myrtle on an island 16 km offshore. In Arkansas, a colony nested in a deciduous woodlot dissected by streams (Thomas 1946b). In Kansas, it nested in forests dominated by hackberry, green ash, black walnut, white elm, and oaks bordering low-lying streams (Verheijen et al. 2017). Most trees used for nesting in the Great Plains grew in linear stands along streams (Schaefer 1976). Zimmerman (1989) also

reported this for Kansas with birds also nesting in isolated trees beside ponds. In South Dakota, it nested in strips of green ash woodland that were mostly 30 m or less in width. Canopy closure and shrub density within the wooded areas had no effect on its density (Rumble and Gobeille 1989). In the same state, it nested both in upland woodlots 3 ha or smaller and in large contiguous riparian woodlands (Gentry et al. 2006). In South Dakota, it nested in shelterbelts with 3 common vegetative features: a tree layer, shrub rows at the edge, and an interior grass layer. It nested in willow shrubs within cattail marshes in Nebraska. Typical habitat there was eastern cottonwood, common hackberry, and ashes where it nested colonially. It nested singly in marginal habitat in willows and junipers. It was strongly associated with riparian woodlands and islands in rivers (Scharf and Kren 2022)

In North Dakota, the Orchard Oriole preferred areas with 7-30% tree cover at the 200-m and 1,200-m scales (Cunningham and Johnson 2019).

Some studies identified microhabitat preferences of the Orchard Oriole or compared its usage of different habitats. In Nebraska, 41% of nests were within 15 m of water and 68% were within 15 m of a road (Scharf and Kren 2022). In Maryland and Delaware, there were no significant differences in its probability of detection in riparian forests 50, 100, 200, or 300 m wide, but it was significantly less likely to be detected in forests 800 m wide (Keller et al. 1993). In Mississippi, it was equally abundant in mature and recently clear-cut forests but absent in 4-year-old regenerating stands with hardwood saplings evenly distributed throughout them (Hurst and Bourland 1996). In the same state, Conover et al. (2009) compared its abundance in fields with no, narrow (7.3-8.5 m), or wide (38.8-44.3 m) borders around them. The borders were native grasses and forbs between agricultural lands and wooded hedgerows. It was absent in fields with no and wide borders and occurred in low density in fields with narrow borders.

Scharf and Kren (2022) compared the habitat requirements of Orchard and Baltimore orioles. The Orchard Oriole preferred smaller-diameter shorter trees that were more densely spaced than the Baltimore Oriole. They were also separated by the distance of the nest to the tree perimeter (2.14 m for the Orchard Oriole and 4.04 m for the Baltimore Oriole), more trees 7.6-15.2 cm diameter at breast height within a 0.04-ha circle around Orchard Oriole nests, and more tree species within this area for the Orchard Oriole. The niche overlap of the 2 species is further ameliorated by later nesting of the Orchard Oriole and it also feeds lower in trees than the Baltimore Oriole.

All Ontario nests were elevated in trees, shrubs, and vines. Deciduous species (77.1% of nests in 12 species) were preferred to coniferous species (22.9% of nests in 3 species). The most frequently used trees were apple (9 nests), maples (4 nests), spruces (4 nests), and pear (3 nests). Nests were usually suspended in forks near ends of horizontal branches and positioned randomly from near the top to the lower portions of trees. They were sometimes well concealed in foliage. There was a pronounced tendency for nests to be built in the same vicinity in successive years. A pair used the same tree for 3 successive years and another nest was built 5 m from the previous year's nest. Nests were 1.8-20 m above ground, with most 3.7-6 m up (Peck and James 1987, 1998b). Lancaster et al. (2004) reported 4 nests in Elgin County: 2 in red pine and 2 in white spruce.

Nests are typically in trees and shrubs, with a strong preference for nesting in deciduous species. The Orchard Oriole occasionally nests in tall conifers planted around buildings. Species it has nested

in include Manitoba maple, green and other ashes, cottonwood, sandbar and other willows, hawthorn, crabapple, spruces, red cedar, elm, white pine, ornamental shrubs, elderberries, apple, pear, oaks, hickories, sycamore, peach, and privet. Most nests are woven around outer forks of branches. Nests tend to be well concealed yet be situated where they receive the greatest amount of sunshine. In Florida, it often nests among Spanish moss where the nest is attached to the moss rather than to twigs. In Louisiana, it nests in common reed marshes. Nests were woven around several stems of common reed in these cases. Nests have been reported in cattail marshes with scattered willows in Nebraska. A nest in a pine was lodged among needles near the top of the tree. Nests have been reported 0.8-20 m from the ground. In Manitoba, mean nest height was 8.8 m in trees that averaged 11.7 m in height. In Nebraska, mean nest height was 3.6 m in willows and 7.9 m in cottonwoods. All Louisiana nests in common reed were 2.1 m above water (Bent 1958; Dennis 1948; Leighton et al. 2002; McCabe 1948; Scharf and Kren 2022; Sealy 1980a). Nest orientation is random. There is no evidence of nest reuse, but 1 pair used an old Baltimore Oriole nest. Although nests do not appear to be reused, the same tree is frequently used for nesting in multiple years (Bent 1958; Dennis 1948; Schaefer 1976; Scharf and Kren 2022).

Other species may influence where the Orchard Oriole nests. It preferentially nests near nests of Eastern and Western kingbirds. In Kansas, Orchard Oriole nests were as close as 0.9 m to an Eastern Kingbird nest and in Louisiana, as many as 4 Orchard Orioles nested in a tree that supported an Eastern Kingbird nest. The aggressive nature of kingbirds in defending their nests may deter predators and benefit nesting orioles. In Wisconsin, 1 oriole nest may have been abandoned because of persistent harassment by a pair of Eastern Kingbirds (Bent 1958; Dennis 1948; McCabe 1948; Scharf and Kren 2022). In Louisiana, Boat-tailed Grackles and Orchard Orioles nested in the same trees. The grackles occupied the uppermost parts of the trees. After the grackles finished nesting, the orioles spread into areas formerly occupied by grackles and built a large proportion of their nests in the central and upper portions of trees (Dennis 1948).

The Orchard Oriole exhibits some territoriality, but is often semicolonial in prime habitat. Some authors never observed any signs of aggression, others stated that a small area is defended around the nest, and others noted intense aggression. Little aggression occurs among birds. Aggression may occur at rich food resources such as a feeder or other sites suggesting that there may be some defence of foraging areas regardless of how close nests are together. In optimum habitat, 4-8 nests may occur in a single tree and 20 nests were reported in an oak tree. Nests are occasionally as close together as 1.2 m. In most cases, nests are more scattered and single isolated pairs are common. In Manitoba, distances between nests ranged from 95 to 610 m. No information is available on home range size (Dennis 1948; Enstrom 1993; Kopman 1915; Scharf and Kren 2022; Sealy 1980a; Thomas 1946b).

Natal philopatry rates are low. In Arkansas, 8 of 127 juveniles (6.2%) returned and 1 returned in 3 consecutive years. Three returned as yearlings but 2 did not return until they were in mature plumage (Thomas 1946b). In Manitoba, 0 of 13 young returned (Sealy 1980a). Scharf and Kren (2022) reported that 22 of 682 young (3.2%) were recaptured in Nebraska.

Adult site fidelity is fairly low. Outside areas where it is very abundant, individual sites may support birds for 2-3 years and then they disappear. In Arkansas, 9 of 26 mature males (34.6%)

returned. One was present in 6 consecutive years, 1 in 4 of 6 years, 1 for 3 consecutive years, 2 for 2 of 3 years, and 4 for 2 consecutive years. Zero of 14 yearling males were recovered, suggesting that they moved to a different nesting area or suffered mortality. Mature males may force yearling males to nest in suboptimal habitat and they may move to better habitat the following year once they attain adult plumage (Thomas 1946b). In Manitoba, 0 of 8 females returned. In 1 year, all 4 nests that were attended by adult males had nested successfully the year before, 2 as adults and 2 as subadults (Sealy 1980a). In Maryland, 25 of 71 birds (35.2%) returned (Dowling and Omland 2009). In Kansas, 1 of 42 males (2.4%) and 1 of 55 females (1.8%) returned (Verheijen et al. 2017). In Nebraska, 1 yearling returned to breed 1 km from where it was banded and bred there each year for 9 years. At 2 sites over 13 years, 123 of 975 birds (12.6%) returned (Scharf and Kren 2022).

Limiting Factors

Eggs have been reported in Ontario nests from the last week of May until mid-July, with most present in the first 3 weeks of June (Peck and James 1998b). In Louisiana, mating began about 1 week after the females arrived and nest building began after another 2 weeks. It is likely that these intervals are shortened at higher latitudes. Nests take 3-7 days to complete. After 1 nest was blown down by the wind, a replacement nest was finished within a week. Eggs are laid at the rate of 1 a day, often starting 3-7 days after the nest is finished. No information is available on when incubation is initiated, but hatching asynchrony suggests that this may occur as early as the laying of the first or second egg. The incubation period is 12-15 days (mean 13.9 days in Louisiana). The first-laid egg hatches first and the others follow in sequence about a day apart. The nestling period is 10-14 days (mean 12.5 days in Louisiana). Nestlings leave the nest in order of age over a 1-3-day period, but all may leave the nest at once if they are disturbed (Bent 1958; Dennis 1948; Scharf and Kren 2022; Sealy 1980a).

Until recently, it was believed that the Orchard Oriole raised a single brood. This is still true in much of its range where it usually leaves the breeding grounds shortly after the fledglings become proficient fliers. Ligi and Omland (2008) documented the first cases of double brooding in 2004 in Maryland. Eight of 24 pairs (33.3%) had a second brood. Sixteen of the first nests were successful and half these females attempted a second brood. Seven of the 8 (87.5%) successfully reared a second brood. Most double-brooded females initiated construction of their second nest within 5 days of fledging their first brood. One pair remained mated the following year and raised 2 broods in each of the years. Double broods have also been confirmed in Georgia (Scharf and Kren 2022). Ontario egg dates indicate that only a single brood is raised (Peck and James 1998b) and only single broods occurred in Manitoba (Sealy 1980a). Rohwer et al. (2009, 2012) presented evidence that some birds raised a second brood in Mexico after breeding in Canada or the United States. Stable isotope analyses supported this theory. Several females that initiated nesting in Mexico had regressed brood patches indicating that they had bred earlier. There was no evidence of recently fledged young suggesting that they had not bred there. Rohwer and Wood (2013) later determined that Mexican birds had bred unsuccessfully prior to initiating a replacement clutch, refuting the post-migration-breeding hypothesis. The Orchard Oriole may renest if the first nest is lost. In Manitoba, 3 of 4 unsuccessful females renested but only one was successful in rearing a brood. Replacement nests were 10-520 m from the original nest. One renested in the same species of tree and the other 2 switched tree species (Sealy 1980a). Clutches of 1-5 eggs have been reported in Ontario, with 4-egg

clutches most common (mean 4.54 eggs; Peck and James 1998b). Elsewhere, clutches of 2-7 eggs have been reported, with most containing 4 or 5 eggs. Mean clutch sizes were 3.6 in Manitoba, 4.1 in Kansas and Nebraska, and 3.80 in Louisiana (Bent 1958; Dennis 1948; Scharf and Kren 2022; Sealy 1980a).

Both sexes are capable of breeding when they are 1 year old (Kopman 1915; Scharf and Kren 2022), and it is probable that most females do so. Yearling males maintain a distinctive subadult plumage which is a significant disadvantage. Adult males are more intensively aggressive toward yearling- than adult-plumaged males. Females select mates rather than territories and move frequently among displaying males before choosing one as a mate. Females display significantly more to adult than subadult males. In Illinois over 2 years, 97% and 100% of adult males and 18% and 11% of subadult males were mated (Enstrom 1993). In Manitoba, 55% of nesting males were adults and 45% were yearlings. There was no different in the nesting success of the 2 age classes (Sealy 1980a).

The mating system consists of season-long monogamy (Enstrom 1993; Scharf and Kren 2022; Sealy 1980a). The pair bond is usually maintained through the season even if renesting or double brooding occurs. In Maryland, mate switching occurred in 1 of 8 cases (12.5%) of double broods. A male paired with a second female for his second nest (Ligi and Omland 2007; Sealy 1980a). It was thought that pair bonds are not maintained between years (Enstrom 1993), but some cases of mate fidelity in subsequent years have been documented. In Maryland, both members of a pair returned in only 2 cases. One of the 2 returning pairs remated and the members of the other pair changed mates. Because of the low site fidelity of adults, there may be limited opportunities for pairs to remate (Dowling and Omland 2009). In Maryland, 1 of 24 pairs (4.2%) returned and reunited, raising 2 broods in each year (Ligi and Omland 2007).

The Orchard Oriole regularly feeds on nectar of flowering trumpet creepers and other flowers and visits hummingbird feeders for sugar water. It has taken grain from gardens and eaten stamens of fruit blossoms. It gleans arthropods from twigs and leaves, pecks ripe fruit with its bill, holds grapes with its foot against a perch while pecking them, forages for grasshoppers in forbs 0.5-2 m tall in open areas, seldom forages on the ground, aerially chases dragonflies and moths, forages for seeds in lawns, gleans arthropods from sweet clover and alfalfa when they are in bloom, and feeds on insects in agricultural fields. During late autumn in northern Ontario, one fed on the ground in dead grasses, in patches of fireweed, in mountain-ash and white birch, and in red elderberry. It selects only ripe fruit for consumption and exhibits a significant preference for mature flowers with the highest nectar content (Bent 1958; Dennis 1948; Graber and Graber 1963; Leck 1974; Lohrer 1977; Scharf and Kren 1997, 2022; Thomas 1946b; Wormington and Lamond 1987). Both sexes forage away from the area that is defended around the nest (Enstrom 1993). When adult males are foraging, they chase away subadult males, and male-female chases may occur. These usually take place in mid-May early in the breeding season. It is uncertain if this behaviour represents defence of foraging territories or is related to defence of territories while selecting nest sites (Scharf and Kren 2022).

Nestlings are fed mostly insects and possibly spiders. In Louisiana, adults chased dragonflies and moths and carried them and other types of insects to their young. Dennis (1948) also found

fragments of oyster shells, crustaceans, and snails in nests. Bent (1958) stated that young were fed mostly katydids.

Early in spring, the Orchard Oriole frequently feeds on nectar and insects. During the breeding season, its diet consists predominantly of insects and spiders but it consumes mostly ripe fruit later in the season, usually after the young fledge. During spring arrival following transgulf migration, hundreds have been observed feeding in black locusts, presumably obtaining nectar. In Kansas, it fed on flower buds of Kentucky coffee-trees and has eaten mulberries in April in Alabama. It often visits hummingbird feeders in spring and early summer until the weather becomes hot. Eleven stomachs collected in Maryland contained 91% animal material and 9% vegetation. The animal matter consisted of 27% mayflies, 14% beetles, 13% grasshoppers and crickets, 13% spiders, 12% caterpillars, 5% bugs, 4% ants, 2% parasitic wasps, and 1% flies. The vegetation consumed was entirely mulberry fruit. In a Texas orchard infested with cankerworms, 80% of the diet consisted of cankerworms. Other caterpillars constituted 17% of the diet. In Texas cotton fields, cotton boll weevils comprised a third of the diet. In samples collected in the 1890s, the Orchard Oriole was documented eating small beetles, aphids, flies, hairless caterpillars, bugs, and a variety of larvae. In Louisiana, it ate bur clover in lawns and highly preferred mulberries (Bent 1958; Dennis 1948; Fitch 1958; Holt 1918; Scharf and Kren 2022). In Nebraska, 116 Orchard Orioles had eaten 30.3% orthopterans, 20.2% spiders, 19.3% beetles, 9.9% fruit pulp, 4.8% lepidopterans, 4.6% true bugs, 2.5% aphids, 2.1% book lice, 1.7% mites, 1.7% flies, 1.5% hymenopterans, 1.2% odonates, and 0.4% soft-winged bugs. The diet consisted of 90.1% arthropods and 9.9% fruit. All spiders that it consumed were less than 4 mm in length and many of the beetles were weevils less than 2.5 mm long. All the true bugs were plant bugs. Some of the hymenopterans were cuckoo wasps. The mites that it consumed were northern fowl mites. It was uncertain if they were ingested incidentally or in an attempt to eliminate them from the nest. Fruit consumed included those of mulberries, chokecherries, and bittersweet nightshade. It shifted from consuming mostly arthropods to fruit in the third week of July, but the timing of this depended upon weather conditions, when fruit ripened, and nestling development. The foraging niche became broader during the brooding period, probably due to the increasing food demands of the nestlings (Scharf and Kren 1997).

The Orchard Oriole is a common host of the Brown-headed Cowbird. It mostly accepts parasitic eggs, but occasionally abandons parasitized nests. In 1 study, parasitized nests fledged 1.5 orioles compared with 3.0 in unparasitized nests. In Ontario, 10 of 32 nests (31.3%) were parasitized. Parasitism rates in other areas include 7 of 7 nests, 6 of 13 nests (46.2%), and 8 of 15 nests (53.3%) in Kansas; 20 of 71 nests (28.2%) in Louisiana; 1 of 6 nests in Manitoba (16.7%); 8 of 13 nests (61.5%) in Nebraska; 1 of 15 nests (6.7%) in Kansas, Nebraska, and Missouri; and 6 of 83 nests (7.2%) reported to the Western Foundation of Vertebrate Zoology. Parasitism by the Brown-headed Cowbird may be a significant limiting factor (Peck and James 1998b; Rivers et al. 2010; Scharf and Kren 2022; Sealy 1980a).

Although the range of the Orchard Oriole is expanding and its population is increasing, it is declining in some local areas due to habitat loss. Natural succession that results in closing of forest gaps and reforestation to coniferous plantations degrade habitat and result in some direct habitat loss. Largest declines appear to be related to the decrease in area covered by orchards, a preferred

habitat. Many early farms had small orchards that provided optimum habitat. These have mostly been removed and replaced with larger, more commercial orchards that are manicured and routinely sprayed with pesticides that reduce food supplies. Loss of orchards and small woodlots has been identified as a significant limiting factor rangewide and specifically in Niagara Region and Norfolk and Haldimand counties in Ontario, and in Illinois. In Illinois, it was common in residential areas 1907-09, but considerably less abundant in this habitat 1957-59. Over time, residential lots became smaller, were less treed, and were more highly manicured. It is even less common in residential areas now as these trends continue (Austen et al. 1994; Graber and Graber 1963; Scharf and Kren 2022).

There are a number of miscellaneous factors that affect the Orchard Oriole. Grazing that destroys shrub habitat has a negative effect. A snowstorm in Nebraska resulted in high egg mortality and probably some starvation. It frequently nests along roads and is struck by vehicles (Scharf and Kren 2022). In Saskatchewan, mortality occurred due to spraying for grasshopper control (Leighton et al. 2002).

Price (2004) predicted that the breeding range of the Orchard Oriole would increase in Ontario if the average summer temperature increased by 2°C.

Status

The first Ontario record of the Orchard Oriole was an immature male in 1865 in Hamilton. It was not observed again in that area again until 1883 when it was found breeding at several locations. At that time, it bred in considerable numbers in the London area and further west along the north shore of Lake Erie near Dunnville (McIlwraith 1894). More recently in the Hamilton area, breeding occurred at Van Wagner's Beach 1937-39 and others were seen in the general area after which it was not observed again until 1954. Nesting has been regular since 1967, with it becoming more common in the 1990s (Curry 2006). In 1891 in Elgin County, it was a very rare breeder until a few years before that time when it became quite common. Nests were found in the St. Thomas area in 1887. By 1954, it was quite common along the Lake Erie shoreline but less common inland. In 2000, it was a rare breeder that was also cyclical, nesting in an area for a couple of years, then disappearing. Most nesting in that county occurs within 2 km of Lake Erie (Lancaster et al. 2004). In Toronto, Fleming (1907) considered it a very rare breeder where nesting was confirmed in 1900. In Niagara Region, it bred at Vineland from 1923 to 1945 then deserted the area (Curry 2006; Sheppard et al. 1936). In the Kingston area, it was first recorded in the summers of 1922-25, with no more records until 1961. After 1971, it was documented in 36 of 37 spring seasons (Weir 2008). It was first recorded in northern Simcoe County at Waubauschene in 1976 (Mills 1981). Baillie and Harrington (1937) reported that it was fairly common in some places along Lake Erie but rare elsewhere. It was confined to the south, breeding north to Lambton and Middlesex counties and east to at least Durham Region. The most northerly records were from Huron County, but these may have been nonbreeders. It has slowly continued to expand its range eastward along Lake Ontario and northward away from the Great Lakes (Austen et al. 1994). During the first atlas, the breeding range included the shorelines of extreme southern Lake Huron, Lake Erie, and Lake Ontario eastward to Kingston. Records were obtained north to Lindsay and northern Grey County. The highest concentrations of records were along the shoreline of Lake Erie with inland extensions in Elgin, Norfolk, Haldimand, and Brant

counties, and in the Hamilton and Toronto areas (Flood in Cadman et al. 1987). James (1991) considered the Orchard Oriole an uncommon summer resident in the Carolinian Forest Region and rare north to Georgian Bay and Kingston.

The second atlas revealed that the distribution of the Orchard Oriole was essentially the same as during the first atlas, but 2 breeding records were obtained from the Lake of the Woods area. Its probability of occurrence increased significantly province-wide since the first atlas. Increases were most dramatic in the Carolinian Forest Region but significant increases also occurred in the Great Lakes–St. Lawrence Forest Region south of the Shield. It continued to be most abundant along the north shore of Lake Erie, with greatest concentrations in the extreme southwest and in the Long Point area. Lower abundance occurred along the Lake Ontario shoreline east to Prince Edward County and along the Lake Huron shoreline north to the base of the Bruce Peninsula. Outside the Carolinian Forest Region, many records were of isolated unmated males. It may be quite frequent in some years and absent in others (Woodliffe in Cadman et al. 2007).

Since about the 1980s, the Orchard Oriole has extended its range to the north, south, and west. Its population has increased within the past 40-50 years (Scharf and Kren 2022). In Ontario, it increased at an annual rate of 5.1% 1983-2013, the 12th largest increase of any species in the province (Cadman et al. 2016). Breeding Bird Survey data indicate that it increased at annual rates of 2.84% in Canada and 1.81% in Ontario 1970-2021. Trends for 2011-21 were an annual decrease of 0.434% in Canada and an annual increase of 4.05% in Ontario. The long-term trend for Canada and the short-term trend for Ontario were highly reliable; the other trends were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Brood division occurs, with each adult caring for half the brood, even though all brood members are occasionally together. Presumably the male cares for all the first brood if the female initiates a second brood. In Manitoba, fledglings spent their first week out of the nest in dense cover within 20-30 m of the nest. The family unit then moved away from the nest. Once fledglings are proficient fliers, they gather in flocks of 5-12, travelling with adults. Yearlings and older males frequently initiate migration as early as mid- to late July. Flocks of females and fledglings of both sexes remain to forage together for another 4-6 weeks before migrating. In some cases, both yearling and older males may stay longer into August and adults continue to split parental duties for half the fledglings. In Arkansas, young that fledged in mid-June stayed until mid-or late July. Those that fledged in July left as soon as they could fly strongly. In Manitoba, family groups moved off the territories, but remained together until autumn migration (Bent 1948; Kopman 1915; Scharf and Kren 2022; Sealy 1980a; Thomas 1946b).

Habitat used during the postfledging period is similar to the breeding habitat. In Arkansas, juveniles foraged on blackberries in openings in wooded areas. Flocks feed on wild cherries, wild grapes, and other wild fruits, and sometimes visit orchards (Bent 1958; Thomas 1946b). In Missouri, Porneluzi et al. (2014) reported Orchard Orioles in clear-cuts in oak-hickory-pine forests during the postfledging period. They captured a total of 6: 4 2 years after clear-cutting, 2 3 years after harvesting, and 0 4-14 years after harvest.

MIGRATION

The Orchard Oriole is a complete migrant in North America, with the entire population moving south of the United States to winter. Migration is nocturnal (Bent 1958; Ligi and Omland 2007; Scharf and Kren 2022).

In Louisiana, adult males arrived first in spring, yearling males arrived a few days later, and females arrived another week later. In Manitoba, both age classes of males arrived at the same time (Dennis 1948; Enstrom 1993; Scharf and Kren 2022; Sealy 1980a). In Ontario, most Orchard Orioles arrive in early to mid-May, with the earliest migrants in mid- to late April (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

The Orchard Oriole is one of the earliest passerine species to migrate in autumn. It leaves the breeding territories in late July to early August and some birds arrive in the wintering areas as early as mid-July (Scharf and Kren 2022). Wormington and Lamond (1987) reported a vagrant at Terrace Bay Township in northern Ontario on 25 September, well north of its breeding range. In the Hamilton area, it is seldom seen after the young fledge. Families leave the breeding areas in late June, but it has been observed in autumn from late August to mid-November (Curry 2006). In most of southern Ontario, it disappears suddenly in early to mid-August (Black and Roy 2010; Lancaster et al. 2004; Weir 2008).

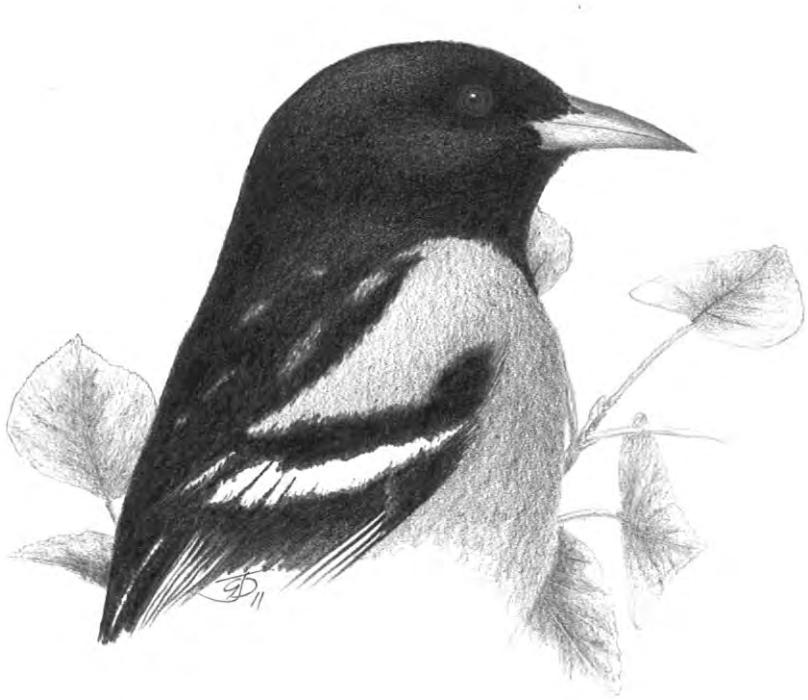
During migration, the Orchard Oriole occurs in wooded margins and parks, gardens, ranches, and farmlands where flowering trees and plants provide nectar (Scharf and Kren 2022). It is often conspicuous in cold springs because it visits hummingbird feeders at rural residences (Lancaster et al. 2004). It is also attracted to grape jelly at feeders (Scharf and Kren 2022).

Some fatalities occur during migration as a result of striking buildings and communication towers (Scharf and Kren 2022).

James (1991) considered the Orchard Oriole an uncommon migrant in Ontario.

Baltimore Oriole

Icterus galbula



BREEDING SEASON

Habitat Requirements

In Ontario, the Baltimore Oriole nested in wooded areas that were usually deciduous but occasionally mixed or coniferous with a few deciduous species present (30.2% of nests); in rural and residential gardens (19.8%); at shorelines of rivers, lakes, marshes, and swamps (17.3%); along roadsides (14.8%); in fields with shade trees and overgrown hedgerows (9.4%); in parks, schoolyards, and playing fields (4.1%); in orchards (3.5%); and tamarack bogs (0.9%; Peck and James 1987).

In Parry Sound and Muskoka districts, the Baltimore Oriole occurred mostly in rural and residential areas (Mills 1981).

The Baltimore Oriole occurred in a variety of habitats in Durham Region. These included young forest with an open canopy, a black spruce bog surrounded by a red maple–poplar swamp, a wet

open forest, a sugar maple stand with numerous openings, a mature maple-oak stand with sparse canopy on rocky ridges, a mature beech–sugar maple woodlot, and a beech woodlot (Speirs and Orenstein 1975).

In the Carolinian Forest Region, it was more common in the Hamilton area in ornamental trees in parks than in the country (McIlwraith 1894). In the same area, it was formerly an abundant nester in elms along roads, but has since adapted to nesting in cottonwoods and ashes (Curry 2006). In Niagara Region, it was a common resident, nesting in tall elms and maples in older residential areas of Niagara Falls, St. Catharines, and Welland, as well as in towns and villages and along roads (Sheppard et al. 1936). It occurred in both urban and rural settings in Elgin County (Lancaster et al. 2004). At Point Pelee, it inhabited open forests dominated by ash (Dodds and Otis 2009).

In Ontario south of the Canadian Shield, the Baltimore Oriole was positively correlated with the amount of forest cover 100 m or further from edge and negatively correlated with woodlot size, amount of forest cover within 2 km, and amount of regional forest cover. All relationships were nonsignificant (Austen et al. 2001).

The Baltimore Oriole prefers fairly open habitat with tall trees, especially deciduous species. Historically, it was probably confined to woodland edges, open riparian areas, savannahs, burns, and natural forest openings. It is now well adapted to nesting in human-altered landscapes. These include urban parks; shade trees in residential areas; tall trees along roadsides, hedgerows, and in regenerating old fields; isolated tall trees; university campuses; edges of fragmented woodlands; narrow strips of trees along watercourses and water bodies; grasslands with scattered trees; forested ridges between lake and marsh habitat in Manitoba; shelterbelts; open farmlands; orchards; pastures with some tree cover; oak savannahs; upland and swamp deciduous forests; regenerating strip mines; clear-cuts and burns; and pine and oak barrens. It may also nest in mixed forests and rarely in coniferous forests and plantations (Bielefeldt and Rosenfield 1994; Brush 1987; Campbell et al. 2001; Faanes 1987; Golet et al. 2001; Graf and Greeley 1976; Hurst and Bourland 1996; Keller et al. 2003; Leighton et al. 2002; Ligi and Omland 2007; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991; Packard 1948; Perreault and Aubry in Gauthier and Aubry 1996; Pleasants 1979; Rising and Flood 2020; Rumble and Gobeille 1988; Sealy 1980b; Suthers 1988; Zimmerman 1989). Substrates beneath nests may include herbaceous or shrub cover, lawns, uncut grass, forest understorey, grazed pastures, road shoulders, gravel and paved roads, and cultivated fields (Graf and Greeley 1976). In the Great Plains, it prefers small or narrow strips of green ash woodlands. It prefers

trembling aspen stands further west and in the aspen parklands. It may also inhabit balsam poplar stands (Campbell et al. 2001; Faanes 1987; Faanes and Andrew 1983; Grant and Berkey 1999; Johns 1993; Rumble and Gobeille 1998).

The Baltimore Oriole tends to avoid heavily forested landscapes. In Pennsylvania, Keller and Yahner (2007) detected it more frequently in fragmented than unfragmented landscapes. In the mid-Atlantic states, its abundance was negatively correlated with the amount of forest cover within 2 km (Robbins et al. 1989). In North Dakota in 400-m landscapes with 30% or less forest cover, its probability of occurrence increased from 5% with 0-30% tree cover within 100 m to 15% at 70% tree coverage. In wooded landscapes, its probability of occurrence was 0-5% with 0-70% tree cover within 100 m. It preferred landscapes that were 48-75% forested; no areas were more than 75% forested (Cunningham and Johnson 2016, 2019). Erskine (1977) considered the Baltimore Oriole characteristic of the prairie-forest ecotone.

Several studies examined microhabitat requirements of the Baltimore Oriole. In regenerating old fields in New Jersey, Suthers (1988) detected it in 20-year-old fields but not in those 10 or 40 years old. Fields 10 years old did not support large enough trees for nesting and 40-year-old fields were completely overgrown with trees. In Illinois, Karr (1968) found it on reclaimed strip mines only in late shrub habitat where the oldest trees were 37 years old. It was absent in areas of bare soils and in early shrub habitat where the oldest trees were 10 years old. It was present in bottomland deciduous forests but not in upland maple-oak forests. In California, Nevada, Utah, and Oklahoma, tree density at nesting areas was 5-116 trees per ha (Pleasants 1979). In Michigan in large contiguous riparian forests that sloped up from a river to upland habitat, it was most abundant near the river and its density tended to decrease toward the upland (Inman et al. 2002). In northeastern hardwoods, it was more abundant in disturbed and successional forests than in mature undisturbed forests (Noon et al. 1979). In Iowa, it was specialized in its selection of nest trees, with all nests in deciduous trees. Stauffer and Best (1980) considered it tolerant of a wide range of habitat and observed it in herbaceous areas, savannahs, scrub, wooded edges, and floodplain and upland forests. It was positively correlated with tree size and negatively correlated with the vertical patchiness of vegetation, slope, and forbs. In Maryland suburbs, it occurred in 45.0% of plots. It was well adapted to suburban areas. Its habitat typically contained deciduous shrub coverage and coniferous and deciduous trees. Its abundance was positively correlated with deciduous shrub volume 0-1.5 m from the ground, coniferous tree volume 7.9-9.1 m from the ground, and deciduous tree volume 1.8-3.0 m and 6.4-7.6 m from the ground. It was negatively correlated with children, dogs, mowed lawns, and building density, suggesting that it preferred quieter, older, and more established neighbourhoods (Thomas et al. 1977).

Most researchers consider the Baltimore Oriole a forest edge or obligate forest edge species (Austen et al. 1994; Freemark and Collins 1992; Golet et al. 2001; Grant and Berkey 1999: Keller and Yahner 2007; Keller et al. 2004; Suthers 1988). Faanes (1987) considered it a forest-interior species nesting in wooded draws in North Dakota. Most of these were narrow strips of forest, so it is unlikely that orioles nested very far from edges.

Freemark and Collins (1992), Golet et al. (2001), Grant and Berkey (1999), Keller and Yahner (2007), and Stauffer and Best (1980) concluded that the Baltimore Oriole was not area sensitive.

Johns (1993) considered it area sensitive in Saskatchewan trembling aspen stands. He examined stands 0.04-36.7 ha in size and found it in stands 1.2 ha and larger.

All Ontario nests were elevated in trees and shrubs, and all but 2 were living. Deciduous trees and shrubs (19 species, 94.3% of nests) were preferred to conifers (6 species, 5.7% of nests). The most frequently used species for nesting were elms (122 nests), maples (71 nests), poplars (56 nests), willows (33 nests), birches (28 nests), and oaks (14 nests). Most nests were suspended at ends of branches with only a few at the centre of the tree (4 nests were near the trunk). They almost invariably hung from branches where they were attached by their rims. One nest was not suspended and 2 were in the crotch of limbs. Old nests were sometimes reused in the following year. Nests were 1.2-30.5 m from the ground, with most 5.5-10.7 m up (Peck and James 1987). In Muskoka and Parry Sound districts, white birch and poplars were favoured nest trees, but 1 nest was in a pine. Nests were 5.5-17.7 m from the ground (Mills 1981). In the Kingston area, nests were in elms, poplars, birches, and tall lilacs (Weir 2008). In Elgin County, nests were in a willow tree and a white spruce (Lancaster et al. 2004). In Oxford County, Dance (2008) reported a nest in a black alder.

Throughout its range, the Baltimore Oriole nests in trees and tall shrubs, highly selecting for deciduous species. Elms are highly preferred for nesting, often used significantly more than their relative abundance. Nest trees are selected based on their height and size, with the habitat beneath the nest of no importance. Since the demise of most elm trees due to Dutch elm disease, it has adapted to nesting in other tall trees such as sycamores and cottonwoods. Nests have been reported in sugar and red maples, white and black oaks, apple, pear, shagbark hickory, weeping and black willows, trembling aspen, balsam and black poplars, locusts, Norway spruce, hemlock, horse chestnut, and birches. Most are near the tip of a branch distant from the trunk, attached to slender twigs. Nesting high in trees at tips of branches may be an adaptation to deter predation by squirrels. Less frequently, nests may be close to the trunk and supported in forks of larger branches. One nest was in a limb that had broken off but was still attached to the tree by Virginia creeper. The nest subsequently fell and the replacement nest was built in the remains of the Virginia creeper. It usually builds a new nest for each nesting attempt but occasionally refurbishes an old nest. Old nests from the previous year may be torn apart and the material incorporated into the new nest. Replacement nests and those built in subsequent years are often very close to earlier nests. In some areas, nests are oriented randomly but in others they are on the leeward side of trees. Nests have been reported 2-22 m above ground, with average nest heights ranging from 7.6 to 13.0 m. In Massachusetts, nests in white elm averaged 10.6 m from the ground. Those in sugar maples averaged 13.0 m from the ground (Campbell et al. 2001; Graf and Greeley 1976; Leighton et al. 2002; Mousley 1916a; Pleasants 1979; Rising and Flood 2020; Schaefer 1976; Stauffer and Best 1980; Tyler in Bent 1958). Schaefer (1976) examined 516 nests in winter near Campbellville and Pickering in Ontario, and in Quebec and the Great Plains region. At Campbellville, nests averaged 8.9 m from the ground, were 3.0 m from the top of the tree, 0.6 m from the perimeter of the tree, 2.3 m from the trunk, and on branches 1.6 cm in diameter. At Pickering, nests averaged 9.6 m from the ground, were 2.6 m from the top of the tree, 0.4 m from the perimeter of the tree, 0.7 m from the trunk, and on branches 1.7 cm in diameter. Pickering nests were oriented randomly but Campbellville birds tended to face their nests away from the east. Nests in Ontario and Quebec were in taller trees, closer to the perimeter of the trees, on thinner branches, and were less firmly attached than those in the Great Plains. Nest trees in

Ontario and Quebec were larger than those in the Great Plains. Nests in the latter region may experience greater wind stress and therefore be attached more firmly. Most nests were at least 1 m above the understorey and toward the periphery of the tree. In Ontario, most nests were in trembling aspen and maples. In Manitoba, Mackenzie et al. (1982) compared Baltimore Oriole nests with those of 2 other high-nesting species: Western Kingbird and Eastern Warbling-Vireo. The Western Kingbird nested exclusively in green ash and peach-leaved willow. Fifteen percent of Baltimore Oriole nests and 17.6% of warbling-vireo nests were in cottonwoods, which had a clumped distribution and represented only 0.9% of available trees. Nests sites of these 2 species were not significantly different from each other, with their habitat characterized by large trees with little or no understorey. Although the 2 species were very different in their nest construction and placement, these differences may not be sufficient to preclude competition for nest sites. Rising and Flood (2020) compared Baltimore and Orchard oriole nests in Nebraska. The Baltimore Oriole preferred larger, taller, and more openly spaced trees than the Orchard Oriole. Baltimore Oriole nests were in trees with larger crowns and closer to the tree trunk, but there was no difference in the height of nests above the ground for the 2 species.

Upon arrival, the male defends a large territory. Once nesting begins, the territory shrinks to a radius of approximately 5 m around the nest. Territories are defended against other males, and females also defend the territory against other females. Males frequently intrude into territories to seek extra-pair copulations. In Colorado, all intruding males were paired and both yearling and adult males trespassed into other male's territories. Those that were detected by the resident male were immediately chased out of the territory (Edinger 1988; Rising and Flood 2020; Sealy 1980b). As many as 3 nests have been reported in a single tree, but these are typically large trees where nests can be 7-10 m apart either horizontally or vertically. Usually 1 nest is well established before a second pair initiates a close nest, and these nests are usually attended by a yearling male. Average nearest-neighbour distances of nests vary considerably annually, with nests closer in years of higher nesting densities. Nearest-neighbour distances may range from 12.7 to 59.5 m (Graf and Greeley 1976; Pleasants 1979; Rising and Flood 2020; Sealy 1980b). Some feeding may occur on territories, but most foraging occurs 50-100 m from the territory. Feeding areas are not defended during the breeding season, and home ranges may overlap by 47.5% without any aggression. In narrow strips of treed habitat in extensive grasslands, nests sites may be limited but food in lands adjacent to the nesting habitat may be abundant. The amount of foraging that occurs in the nesting territory ranges from 16% to 81%, with lowest in-territory foraging rates occurring at higher densities. In extreme cases, this may lead to semicolonial nesting, but not for the usual reasons of highly clumped or unpredictable food supplies. In Nebraska, the average home range size of yearling males was 1.74 ha (range 0.41-1.86 ha). Older males had average home range sizes of 0.63 (range 0.15-1.68 ha; Pleasants 1979; Rising and Flood 2020; Sealy 1980b).

The Baltimore Oriole may defend food resources from other species, particularly in winter, but also during migration and the breeding season. Packard (1948) found a Baltimore Oriole and an Eastern Kingbird nesting in the same tree. There was a large web of tent caterpillars between the nests and both species fed from it and fed their young the caterpillars. Both species spent considerable time chasing the other from this food source. A male oriole that was feeding on caragana blossoms killed a Ruby-throated Hummingbird that ventured within 30 cm (Wright 1962).

In Costa Rice, orioles regularly defended 8-12 nectar-producing flower heads, each with approximately 50 flowers. Orioles aggressively hopped toward intruders and expelled them. Aggression was most common toward hummingbirds but was also directed toward wrens, tanagers, other oriole species, and Yellow Warblers (Schemske 1975).

The Baltimore Oriole often nests near the Eastern Kingbird (Packard 1948; Peck and James 1987; Tyler in Bent 1958). The kingbird is particularly aggressive in defending its nest from predators. Nesting near a kingbird may reduce the probability of an oriole's nest being depredated.

Natal philopatry rates are low. Zero of 51 nestlings returned in Massachusetts (Rising and Flood 2020). In Manitoba, 17 of 96 nestlings and 416 fledglings (3.3%) returned to nest in 1 year. In another year, 2 of 199 nestlings and 140 fledglings (0.6%) returned (Sealy 1980b).

Adult site fidelity rates are fairly low. In Maryland, 16 of 42 adults (38.1%) returned (Dowling and Omland 2009). In Kansas, 2 of 41 males (4.9%) and 2 of 64 females (3.1%) returned (Verheijen et al. 2017). Another Kansas study reported that 9 of 28 adult males (32.1%), 17 of 35 yearling males (48.6%), and 13 of 33 females (39.4%) returned (Rising and Flood 2020). In Manitoba, older males returned to the vicinity of their previous nest but most females paired with a different male than in the previous year (Sealy 1980b).

Limiting Factors

Eggs have been found in Ontario nests from mid-May until the third week of June, with most present in the first 2 weeks of June (Peck and James 1998b). In Algonquin Park, dependent fledglings have been seen from mid-July to late August (Tozer 2012).

Immediately upon arrival, older males and some yearlings start to defend a territory. When females arrive, they are vigorously courted as they forage within territories. Females may move among territories until they finally settle on one. Pairs form 1-7 days after the females arrive and most females begin nest building within 10 days of their arrival (range 1-14 days). In Colorado, the outer shell was woven in 4 or 5 days and another 4-6 days were required to add the lining. Other reports stated that it takes 4.5, less than 6, 5-8, or 15 days to build the nest. Most nests are built within a week. It is unknown if there is a delay between nest completion and the initiation of egg laying. Eggs are laid at the rate of 1 per day. Incubation begins with the laying of the penultimate or last egg. The incubation period at 1 Ontario nest was 14 days. Incubation periods of 11-14 days have been reported elsewhere (average 11 days). Hatching occurs over 2-3 days, but may take as long as 5 days during inclement weather. The nestling period is 11-14 days but mostly 12-13 days. Nestlings that leave the nest when they are less than 10 days old as a result of disturbance or other factors usually do not survive. One or 2 days before fledging, the young often cling to the outside of the nest and clamber in and out of it (Edinger 1988; Leighton et al. 2002; Peck and James 1998b; Rising and Flood 2020; Tyler in Bent 1958).

A single brood is raised in a season, but renesting may occur if the first nest fails. Clutches of 3-6 eggs were reported in Ontario, with most containing 4 or 5 eggs (mode 5 eggs, mean 4.54 eggs). Clutches of 3-7 eggs have been reported elsewhere, with 4- and 5-egg clutches most common (Ligi and Omland 2007; Peck and James 1998b; Rising and Flood 2020; Tyler in Bent 1958). In Manitoba, clutch size was 3-6, mostly 5 eggs. Mean clutch size over 3 years was 5.06-5.33 eggs (Sealy 1980b).

Mean clutch sizes reported elsewhere include 4.5 in Vermont, 4.7 in Massachusetts, 5.1 in Colorado, and 4.7 in Kansas (Rising and Flood 2020). In Kansas, Labedz (1984) reported a mean clutch size of 4.5 eggs. In 2 years, nests with yearling males had significantly smaller clutches (2.3 and 3.0 eggs) than those of older males (5.1 and 4.9 eggs). Nests with yearling males were initiated later than those with older males. More than half of young from nests with old males fledged before the first nestling from a nest with a yearling male fledged. In another Kansas study, nests attended by yearling males fledged significantly later than those attended by older males in only 1 of 2 years. In this population, there were no significant differences in clutch size and breeding success between male age classes (Flood 1984).

Both sexes are capable of breeding when they are 1 year old (Flood 1984; Rising and Flood 2020). All adult males and all females breed each year, but some yearling males fail to attract a mate. Over 2 years in a Kansas study, 58.2% and 71.0% of yearling males did not breed, suggesting that females were a limited resource. For yearling males that did breed, there were no significant differences in their territory quality, breeding success, or parental quality compared with older males. Yearling males have a plumage that is intermediate in colour between females and older males. This colouration is effective in reducing the amount of aggression elicited from older males and elicits less aggression from females than the plumage of the dullest females (Flood 1984). In Manitoba, 1 yearling male bred in a year during the beginning of a tent caterpillar invasion, 27 bred in the following year at the height of the outbreak, and 0 bred in the year following the outbreak (Sealy 1980b).

The mating system is typically monogamous. In Kansas, a mated male also mated with a neighbouring female whose mate had been removed, suggesting that the Baltimore Oriole may be an opportunistic polygynist (Flood 1985; Rising and Flood 2020). The pair bond typically lasts for a single breeding season. If a female loses her mate prior to egg laying, she may mate with another male. These are usually yearling males that were previously unmated (Flood 1985). In Maryland, both sexes of 4 pairs returned in a subsequent year. In 1 case, the pair reunited but in the other 3 cases, each bird mated with a different bird in the second year (Dowling and Omland 2009). Males frequently intrude into other territories, with older males seeking extra-pair copulations and yearlings possibly prospecting for territories in the following year. Intrusions occur most frequently when the resident female is building the nest, but may occur from prenesting to feeding of the nestlings. In some cases, the intruder chases the female from the nest and may force it to the ground and copulate with it. One female copulated with an intruding male after he displayed to her. In Colorado, intruding males had territories 110-280 m from the resident female's nest. Their females were also fertile when extra-pair copulations were attempted. Males attempt to avoid cuckoldry by guarding their females by following them, driving them away from neighbouring males, spending considerable time foraging or perching near the nest, and copulating with their mate very rapidly (Edinger 1988; Flood 1985; Rising and Flood 2020).

Upon spring arrival, the Baltimore Oriole often visits feeders to feed on sugar water, orange sections, and bananas. Blossoming apple trees are a strong attractant, where it gleans insects and possibly feeds on nectar. During the breeding season, it forages solitarily in trees and less frequently on the ground, in shrubs, or in alfalfa and sagebrush. In Manitoba, it usually foraged high in the

canopy but lower during windy weather. In Colorado, 80% of its foraging time was spent in cottonwoods and the remainder of the time was spent on the bark of these trees, in willows and currants, and on forbs. Sixty percent of foraging was at heights of 7-12 m, 30% below 7 m, and 10% above 12 m. Most foraging occurred on branches 0.3-1.0 cm in diameter. It hunts insects and spiders by gleaning or probing, usually in trees and shrubs and rarely on the ground. It picks insects from spider webs and tears open webs to prey upon tent caterpillars. It rarely captures flies, moths, and dragonflies in the air. It often feeds by gaping, thrusting the closed bill into a fruit then opening the bill, allowing the tongue to swallow the juice and perhaps some of the pulp. It sometimes opens rolled leaves to access the insects inside. It may pick peas from plants and fruits from trees, shrubs, and vines (Beal 1897a; Lancaster et al. 2004; Perreault and Aubry in Gauthier and Aubry 1996; Rising and Flood 2020; Sealy 1980b; Tyler in Bent 1958). In Illinois, there were no differences in foraging manoeuvres between forest and savannah habitats: 65-75% gleaning, 2-12% hanging, 1-20% flycatching, 4-7% hovering, 0-1% sallying, and 2-7% other techniques. The same foraging heights were preferred in the 2 habitats. The area 0-5 m from the ground was strongly avoided, heights of 6-10 and 11-15 m were strongly preferred, and areas above 16 m were used relative to their abundance. It foraged significantly more in black locust and hackberry than their availability. The preference for hackberry may have been because of the high density of leafroller caterpillars. It was not observed foraging in sugar maple or red elm. Sugar maple was a dominant species in the forest but did not provide suitable foraging conditions (Hartung and Brawn 2005). Pleasants (1979) concluded that the abundance of undergrowth in small forest patches was a good indicator of food abundance that potentially influenced nesting density.

Females that lose their mate are capable of rearing nestlings on their own. Nestlings are initially fed by regurgitation but all food is supplied fresh once they reach the age of 4 days (Flood 1984, 1985; Tyler in Bent 1958). Regurgitated food fed to nestlings includes soft parts of grasshoppers and dragonflies plus caterpillars and other insect larvae. Tent caterpillars are frequently fed to nestlings and they may be fed mulberries, cherries, and other fruits later in the season (Packard 1948; Rising and Flood 2020; Sealy 1980b; Tyler in Bent 1958). In Manitoba, Sealy (1980b) analyzed nestling diet in a year when tent caterpillars were extremely abundant and in the next year when they were scarce. In most years, nestlings were fed predominantly midges. Food fed to nestlings in the years when tent caterpillars were abundant and scarce, respectively, consisted of: mayflies, 0% and 14.9%; odonates, 0% and 0.6%; beetles, 0% and 0.6%; moths, 2.0% and 25.4%; geometer moth caterpillars, 8.7% and 1.6%; owlet moth caterpillars, 0% and 5.0%; tent caterpillars and pupae, 63.3% and 0%; midges, 26.5% and 41.4%; and red elderberry fruit, 0% and 0.6%.

In most years in Manitoba, adult Baltimore Orioles subsisted predominantly on midges. In a year when tent caterpillars were abundant, they preyed on most life stages of the tent caterpillar despite the presence of the usual midge population. The nesting density doubled in the second year of the outbreak. Productivity of individual pairs decreased during the second year of the outbreak (with fewer young fledged per nest) but productivity as a whole increased as a result of more pairs nesting (Sealy 1980b). Beal (1897a) analyzed the contents of 113 stomachs. The diet was comprised of 84% animal matter and 16% vegetable matter. Caterpillars were the most important food item, constituting 34% of the diet. They were consumed throughout the breeding season, with fewest eaten in July when some fruit was consumed. Other insects consumed included beetles (mostly

click beetles), bugs (aphids and book lice), ants, wasps, and grasshoppers plus some spiders. Ants were eaten mostly in spring, grasshoppers in July and August, and wasps and spiders were eaten in considerable numbers throughout the season. Vegetable matter included blackberries, cherries, wild fruits, a few peas, and some miscellaneous seeds. Many of the caterpillars it consumes are hairy. In addition to tent caterpillars, these include those of the fall webworm, mourning cloak butterfly, gypsy moth, and tussock moths. Other animal food items include parasitic wasps, snails, treehoppers, lace bugs, scale insects, shining leaf chafers, June beetles, metallic wood-boring beetles, long-horned beetles, leaf beetles, weevils, sawfly larvae, potato beetles, carpenter bees, and pine needleminer moths. It also ate sycamore and hollyhock seeds and aspen leaves, and drilled into grapes, apples, and pears (Tyler in Bent 1958). Prey items in Colorado included 58% leafroller moth caterpillars, 10% sphinx moths, 15% other lepidopterans, 5% ants, 5% aphids, 2% leaf beetles, 1% crickets and grasshoppers, and 4% miscellaneous. In Manitoba on 25 and 26 May, the diet consisted of 57% beetles, 8.5% midge larvae, 7% small midges, 7% small caterpillars, and 20% other insects and spiders. On 8 and 9 June, the diet consisted of 93% large midges. On 20 and 21 June, the diet consisted of 50% large midges, 12.5% medium-sized caterpillars, 6.5% small beetles, 6% spiders, 6% large caterpillars, and 19% other insects. On 1-3 July, the diet consisted of 42% midges; 77% of the food items on 13 and 14 July were midges. The study was repeated 2 years later with similar results except that 42% of the 12 June diet consisted of leafhoppers. It did some damage in Niagara Region to cultivated grapes, usually in late August (Rising and Flood 2020). There are 2 cases of it eating tartarian and Morrow's honeysuckle berries in Ontario. These berries contain rhondoxanthin and impart a reddish colour to the orioles' plumage (Derbyshire and Flinn 2007; Hudon et al. 2013).

The Baltimore Oriole is an ejector of Brown-headed Cowbird eggs, so the rate of parasitism is underestimated. Both sexes eject eggs, often within minutes of the parasitic event. In 2 separate experiments where nests were artificially parasitized with either real or plaster cowbird eggs, all parasitic eggs were ejected. Eggs are spiked with the bill and usually carried away where the contents are often eaten. Occasionally the parasitic egg is simply dropped to the ground below the nest. Orioles can distinguish between their own and cowbird eggs and have not been documented ejecting their own eggs. Cowbird eggs are unusually thick for their size and occasionally the oriole's bill deflects off the cowbird egg and damages one of its own eggs. In Manitoba, 0.38 eggs were broken or damaged for every cowbird egg ejected, so parasitism has a cost even if no cowbird eggs hatch (Rohwer et al. 1989; Rothstein 1977; Sealy and Neudorf 1995; T.S. Smith 1972). One Manitoba nest had a cowbird egg buried in the lining, the only known case of this occurring. The nest was new and contained no oriole eggs, so it is unknown if this was a response to parasitism or simply continuation of nest building. Egg burial may be more prevalent because it is necessary to dissect the nest to find buried eggs (Hobson and Sealy 1987b). Schaefer (1976) found no buried eggs in almost 300 nests from Ontario, Quebec, and the Great Plains. In Ontario, 10 of 181 nests (5.5%) were parasitized (Peck and James 1998b). In Manitoba, 3 of 136 nests (2.1%) were parasitized. At 1 nest, both orioles and cowbirds fledged, representing one of few records where a cowbird successfully fledged from a Baltimore Oriole nest (Hobson and Sealy 1987b). In the same area, 5 of 153 nests (3.3%) were parasitized (Sealy and Neudorf 1995). In 2 Kansas studies, 1 of 17 (5.9%) and 2 of 61 nests (3.3%) were parasitized. Four of 283 nests (1.4%) in the collection of the Western Foundation of

Vertebrate Zoology were parasitized. Oriole nestlings in parasitized nests may be malnourished (Rising and Flood 2020).

Forest fragmentation as a result of clearing for agriculture and urban areas was beneficial for the Baltimore Oriole (Perreault and Aubry in Gauthier and Aubry 1996; Rising and Flood 2020). Friesen et al. (1995) studied the effects of residential development in Waterloo Region. They examined small (3-4 ha), medium (8-15 ha), and large (20-50 ha) woodlots with no development, low development (1-3 houses), medium development (8-15 houses), and high development (25 or more houses) within 100 m. They concluded that the Baltimore Oriole tended to avoid high density housing. Older residential areas were once good habitat, but this habitat has deteriorated and new urban habitat is unsuitable. The large elms that once lined streets died and were removed in the 1960s and 1970s. Many other large trees have become hazardous and have been removed. Many municipalities conducted widespread planting of ash trees as shade trees and these are now dying and being removed. Lots in new subdivisions are too small to support a large tree.

The Baltimore Oriole responds positively to forest management or other factors that open up the forest canopy. In mixed sugar maple stands in southern Ontario, it was most abundant in stands that had experienced heavy diameter-limit cuts, with lesser numbers in stands that had been selectively harvested and those that had not been cut. It was significantly negatively correlated with the basal area of trees (Holmes et al. 2004). In deciduous forests in Pennsylvania, it was 2.7 times more abundant where 50% of 4-ha blocks had been clear-cut than it was in uncut blocks. It was absent where 75% of the block was cut (Yahner 1993). In New York, it was absent or occurred at very low abundance in clear-cuts in northern hardwoods 2-4 years after cutting, gradually increasing with stand age and reaching maximum abundance 55-120 years after cutting (Keller et al. 2003). In Pennsylvania and New Jersey over a 15-year period, hemlock declined from 56% of the total basal area to 46% due to the hemlock woolly adelgid, resulting in increased deciduous understorey. It increased over this period, probably in response to the more fragmented canopy (Toenies et al. 2018).

Inclement weather during the breeding season may delay breeding, reduce the Baltimore Oriole's abundance, or cause females to suspend nest building or abandon the nest. Nests initiated later in the season are more likely to fail or be abandoned (Rising and Flood 2020).

Declines in Baltimore Oriole populations have been documented as a result of gypsy moth control and spraying of DDT. It is occasionally killed by vehicles, but this is not a significant limiting factor (Rising and Flood 2020).

Price (2004) concluded that the breeding range of the Baltimore Oriole might contract in southern Ontario if the average summer temperature increased by 2°C. In southern Quebec, DesGranges and Morneau (2010) considered it very sensitive to climate change. It was associated with warm summers and the mean number of annual degree-days 10°C or more in May, June, and July. They concluded that it may be limited by the number of degree-days.

Status

The Baltimore Oriole is probably more common now than before European settlers cleared much of the forest cover in the south. In Elgin County, it was a common breeder in 1891, 1954, and 2000 (Lancaster et al. 2004). It was common in the Kingston area in 1859, 1909, 1965, 1973, 1989, and 2008

(Weir 2008). Baillie and Harrington (1937) considered it a common breeder in southern Ontario north to Parry Sound District and Ottawa. It was common in the Lake of the Woods area but apparently did not occur between there and Parry Sound District. The first atlas revealed that the range of the Baltimore Oriole was more extensive. It bred in the Kenora area east to the Thunder Bay area, and from the northeast shore of Lake Superior east to the Lake Abitibi area south to the southern boundary of the province. There were gaps in its distribution in the Algonquin Highlands and other extensively forested areas. In more northern areas, it is limited by the dense forest and scarcity of the deciduous trees that it prefers. It was most abundant south of the Canadian Shield, where it was documented in every square, and was widespread in the southern Shield south of the Algonquin Highlands (Flood in Cadman et al. 1987). James (1991) considered it a common summer resident north to Georgian Bay and Ottawa; uncommon north to Kenora, Thunder Bay, and Sudbury; and occasional and rare to Red Lake, Hearst, and Timiskaming District.

The second atlas revealed that the Baltimore Oriole had withdrawn from its more northerly range since the first atlas. It was not detected between Kenora and Thunder Bay or near the northern portion of Lake Superior, and was absent in many squares in the Sudbury–North Bay area where it was present during the first atlas. Its probability of occurrence declined significantly province-wide and in the Great Lakes–St. Lawrence Forest Region, most notably in the Canadian Shield. It was almost completely absent in the Algonquin Park area and declined steadily in the Haliburton area despite the presence of optimum habitat. Declines were consistent with the increase in forest cover and reduction in the amount of open and edge habitat. Most of the population bred south of the Canadian Shield. Highest densities occurred in the Kingston area and much of the Carolinian Forest Region except for the intensively farmed areas of Essex and Lambton counties and Chatham-Kent. High densities occurred in the urban areas of Toronto where it nested in wooded ravines, parks, and residential areas with mature trees. The ecotone along the southern edge of the Shield also supported high densities. This area is characterized by marginal farmlands with numerous hedgerows and tall trees (Cadman in Cadman et al. 2007).

Breeding Bird Survey data indicate that the Baltimore Oriole decreased at annual rates of 1.4% in Canada and 1.15% in Ontario 1970-2021. The trends were annual increases of 2.39% in Canada and 0.712% in Ontario 2011-21. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young can only fly short distances when they first leave the nest but can fly reasonably well 2-3 days after fledging. They follow their parents for approximately 2 weeks and are fed by them during this period (Rising and Flood 2020; Tyler in Bent 1958). Sealy (1980b) described the postfledging period in Manitoba. Brood division occurs, with each adult caring for half the brood. Females abandon their portion of the brood before the male does and begin to move more widely during the last few days of June. Fledglings do not begin moving through the habitat until they have been out of the nest for about 10 days. At this time, they are capable of sustained flight and are presumably independent of the male. In early to mid-July, many males are followed by 3-4 young with few young still with females. Females begin to moult almost immediately after they leave their brood and may move 1-2 km from the nesting territory within 1 or 2 days. Males moult later than females because they remain with the broods longer and remain in their territories until they leave the breeding grounds,

usually in late August. By mid-July when the moult is well underway, females and older males withdraw into dense cover where they are silent, secretive, and essentially cease moving. These birds forage mostly in morning-glories and common hop vines in sandbar willows during this period. Yearling males begin their moult at about the same time as females and begin moving southward early in their moult. One banded on 20 June was found on 10 July 245 km southeast of the banding location. Tyler (in Bent 1958) reported that flocks of juveniles or birds in female plumage frequently occur until birds start to leave in late August. No males were ever seen in these flocks.

Habitat used during the postfledging period is similar to breeding habitat. Flocks of young and adults may occur in these habitats as well as in shrubby pastures (Tyler in Bent 1958). The Baltimore Oriole also inhabits clear-cuts during the postfledging period. In Pennsylvania, Stoleson (2013) netted birds in 3-6-year-old clear-cuts and in adjacent mature deciduous forests 90-100 years old. He captured 12 adult and 3 juvenile orioles in clear-cuts and 0 in mature forests. He considered it a forest edge species. In Ohio, Vitz and Rodewald (2006) netted in clear-cuts 4-7 years old and caught 21 adults and 55 juveniles.

In Kansas, Fitch (1958) observed a pair that arrived in late August with dependent fledglings and remained into early September. During this period, the family group remained within an area of 0.85 ha.

MIGRATION

The Baltimore Oriole is a complete migrant, travelling medium to long distances between the breeding and wintering grounds. Most migration is nocturnal but some diurnal migration occurs. Many appear to migrate at dusk or dawn, and migration continues after dawn. During migration, it may occur in flocks of all age and sex classes (Rising and Flood 2020). Tuck et al. (2018) observed autumn morning departures in Ohio along the southern shore of Lake Erie. Orientation of flights was west to northwest, following the lakeshore. Orioles avoided crossing the lake. Two birds banded in Ontario were recovered in New Jersey and Guatemala 618 km and 3,554 km, respectively, from the banding site. A bird recovered in Ontario had been banded in Honduras 3,298 km away (Brewer et al. 2018).

In Manitoba and Massachusetts, adult males and females arrive simultaneously in spring and yearling males arrive later (Baubock et al. 2012; Sealy 1980b). In most areas, adult males arrive before females by 1-10 days with considerable variation annually at individual sites. Some females arrive before yearling males (Campbell et al. 2001; Edinger 1988; Flood 1984; Leighton et al. 2002; Rising and Flood 2020; Tyler in Bent 1958). At Long Point, mean capture dates were 13.4 May for older males, 17.4 May for yearling males, and 18.2 May for males of unknown age (Stewart et al. 2002).

The Baltimore Oriole arrives in numbers in southern Ontario in early May but birds may appear as early as mid-April (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). In the southern Shield, it arrives in mid-May with some appearing in early May (Mills 1981; Tozer 2012). Over 22 years at Deep River, peak numbers were recorded 13-30 May (Rising and Flood 2020).

Several studies examined spring arrival dates over time to determine the Baltimore Oriole's response to increasing temperatures due to climate change. In New York, Zelt et al. (2017) used first sighting dates for 1888-1939 and 1964-2013. First arrival date decreased significantly at a rate of 0.26

days for all long-distance migrants for 1987-2012. Evidence for longer breeding seasons was weak and nonsignificant. In Manitoba, it arrived significantly earlier over a 63-year period in response to increasing temperatures (Murphy-Klassen et al. 2005). In Massachusetts, the average first sighting was 8 May 1851-1973 and 6 May 1988-2007. The correlation between arrival date and temperature was not quite significant (Ellwood et al. 2010). In Massachusetts, Bauböck et al. (2012) compared mean arrival dates over a 32-year period and reported no change in response to climate change. Its arrival date was associated with temperatures of the current or previous year, with more females in years with higher temperatures. The timing of migration may respond to climate change in different manners in different locations.

Yearling males leave the breeding grounds first before completing their moult. Adult males tend to migrate before females, although flocks of mixed sex and age classes occur. The peak of autumn migration at Deep River was 26 July to 30 August (Rising and Flood 2020). In the southern Shield, most migrants are seen in August with most gone by the end of August, although some remain into early to mid-September (Mills 1981; Tozer 2012). In the south, migration is underway in early August and continues into early September. Most are gone by the end of September, but stragglers may persist into early winter (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

Migration habitat is similar to breeding habitat. The Baltimore Oriole occurs in a variety of habitats but prefers open woodlands, forest edges, and urban parks (Campbell et al. 2001; Rising and Flood 2020). Smith and Hatch (2017) compared its abundance during spring migration in Pennsylvania before and after the viburnum leaf beetle killed most southern arrowwoods, the dominant shrub. Fewer were captured after most of the shrub cover disappeared, but the difference in capture rates was not significant. In Pennsylvania, it was 7 times more abundant in shrubland than forest habitat during spring migration (Smith and Hatch 2008). Suomala et al. (2012) compared its abundance on 2 islands in the Gulf of Maine during autumn migration. One island was predominantly shrubby and the other was more treed. More Baltimore Orioles were captured on the treed than shrubby island. Birds lost mass on the shrubby island and gained mass on the treed island. During spring migration in Wisconsin and Minnesota, Kirsch et al. (2013) compared its abundance in riparian and upland forests. Riparian forests consisted of maple-elm-ash communities; upland forests were steeply wooded hillsides. They did not detect it in upland forests and considered it a riparian species. In Ohio, it was 1 of only 2 species that was significantly more abundant in upland than riparian forests. Upland forests had significantly more shrub cover and less canopy cover than riparian forests (Rodewald and Matthews 2005). It is probable that forest structure is more important than whether the forest is in riparian or upland landscapes.

The Baltimore Oriole is often killed at communication towers and other tall structures during migration (Rising and Flood 2020).

James (1991) considered the Baltimore Oriole a common migrant in Ontario, occasionally wandering north to Moosonee.

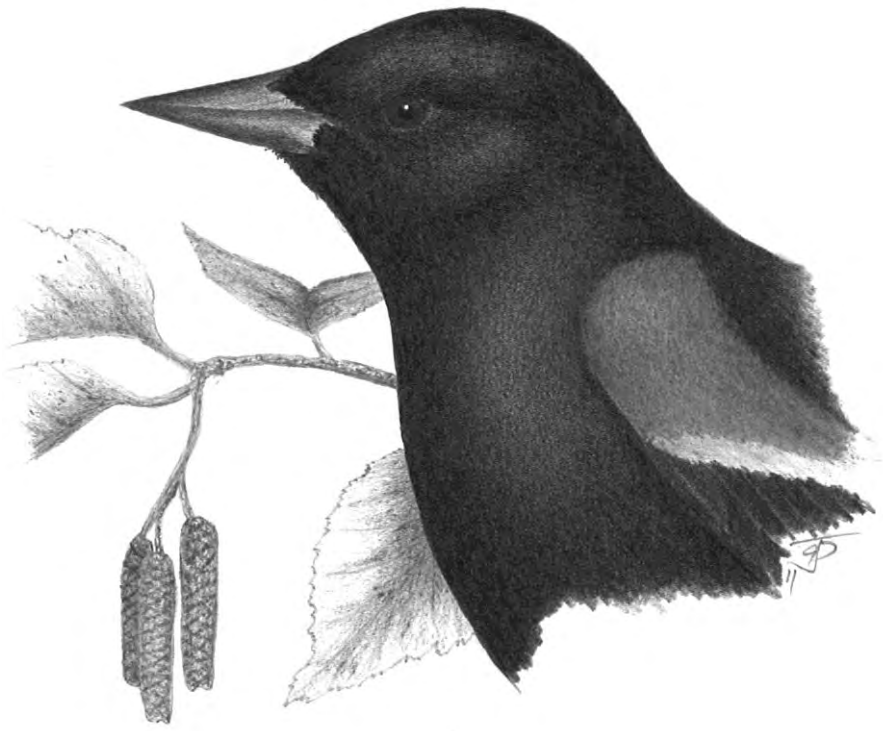
Captures of the Baltimore Oriole at the Long Point Bird Observatory declined at a nonsignificant rate of 0.3% per year 1961-88. Annual trends by period included: 1961-70, +1.0%; 1970-79, –8.2%; and 1979-88, –7.9% (Hussell et al. 1992).

WINTER

James (1991) considered the Baltimore Oriole a rare winter visitor in the south, north to Sault Ste. Marie and Kingston. It is probable that most do not survive the winter. One visited a feeder in Burlington from 3 January to 17 April 1983 where it survived by feeding on oranges (Curry 2006).

Red-winged Blackbird

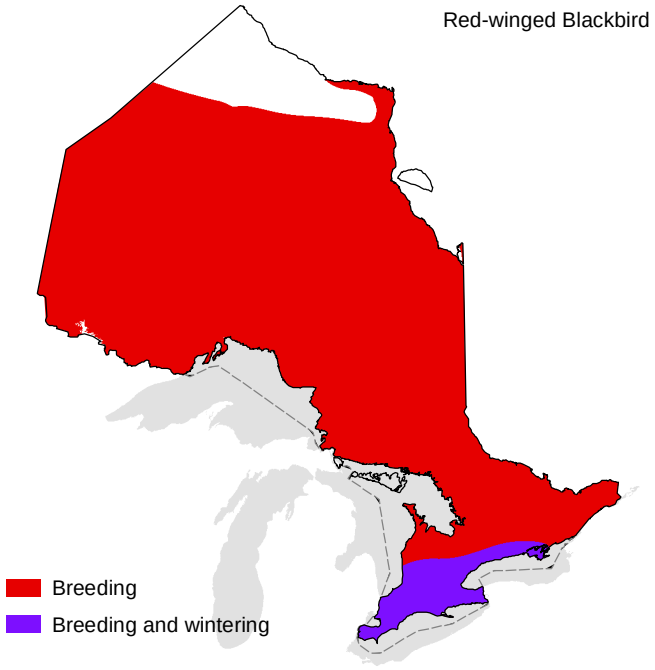
Agelaius phoeniceus



BREEDING SEASON

Habitat Requirements

Ontario Red-winged Blackbird nests were in freshwater marshes (31.5% of nests); in fields, abandoned pastures, river floodplains, and gravel pits (26.0%); in plantations and orchards (16.6%); in roadside ditches, railway rights-of-way, and at shorelines of lakes and rivers (8.2%); in treed swamps and beaver ponds (6.8%); in bogs and fens (4.1%); in gardens and parks (3.6%); on rocky islands (2.0%); and in sand dune areas (1.7%). Marshes that were used were mostly homogeneous cattail stands (90.4% of nests), 4.8% of nests were in mixed shrubs and cattails, 1.6% were in sedges, 1.1% were in rushes, 1.1% were in common reed, and 1.1% were in mixed marsh vegetation. Wooded habitats that it used were usually open and nests were at edges or in clearings. It preferred deciduous stands (65.3% of nests); 27.4% of nests were in coniferous stands and plantations and 7.4% were in mixed stands. Most occupied fields were open but some had limited shrub growth. It preferred wet fields with 57.6% of nests in this habitat (Peck and James 1987).



In the Boreal Forest Region, the Red-winged Blackbird nested in a 3-year-old clear-cut in lowland coniferous forest (Welsh and Fillman 1980).

In the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, the Red-winged Blackbird nested in open bogs, small marshes, and damp meadows in Parry Sound and Muskoka districts (Mills 1981). In Algonquin Park, it occurred in wet and dry bogs with shrubs and snags. It occurred from ground level to a height of 9 m which represented the tops of dead snags outside the treeline (Martin 1960). It also nested in cattail and sedge marshes, lakeshores, beaver ponds and meadows, and wet shrubby clearings (Tozer 2012). North of Kingston, it nested in cattail and cattail-willow marshes surrounded by forest cover and in small (50-100 m^2) patches of cattails adjacent to highways (Shutler and Weatherhead 1991, 1994; Weatherhead 2005).

Near Ottawa in the Great Lakes–St. Lawrence Forest Region south of the Shield, the Red-winged Blackbird nested in uniform stands of cattails (Pribl and Picman 1996) and in 30-100-m-wide grassland strips bordered by a road on 1 side and fields on the other. These territories were covered by short grasses dominated by redtop with scattered small patches of tall vegetation consisting of reed canary grass, Canada goldenrod, and purple loosestrife. Redtop was present at 71.5% of sampling sites but supported only 11.5% of nests. Reed canary grass was present at 15.0% of sites and supported 48.1% of nests; Canada goldenrod occurred at 7.5% of sites and supported 15.4% of nests; and purple loosestrife occurred at 1.9% of sites and supported 5.8% of nests. Common vetch, lesser burdock, and raspberries occurred at 4.17% of sites and supported 19.2% of nests. Nests were in tall vegetation more than expected and in short vegetation less than expected. The distribution of nests was 0% in vegetation 0-25 cm tall, 30% in vegetation 26-50 cm tall (48% availability), 26% in vegetation 51-75 cm tall (equal or greater than availability), and 42% in vegetation taller than 76 cm (only 15% availability). Nests were more frequent in sparse and less frequent in dense vegetation than expected. Ninety-two percent of nests were in vegetation density of 0-10 stems per 0.04 m^2 (30% availability), with the remainder in density of 11-20 stems (less than availability) and 0% in densities of 21-20 or more than 30 stems per 0.04 m^2. Stem thickness was significantly greater at nests than random areas, with 55% of nests in plants with stems more than 3 mm thick (less than 10% availability). Only 1% were in plants with stems 0-1 mm thick. Patch size diameter was significantly less at nests than random sites. Fifty-nine percent of nests were in patches 0-1 m in diameter (1% availability), 30% in patches 2-10 m in diameter (greater than availability), and the remainder were in patches more than 10 m in diameter (less than availability). As patch size decreased, plant height and thickness of their stems increased but plant density decreased. Nest

success was not related to any vegetative features. In eastern Ontario, it nested in beaver ponds and municipal sewage lagoons. Cattails were the dominant vegetation at both habitats, but formed only a narrow band around the perimeters of lagoons (Zimmerling and Ankney 2005). At Luther Marsh in old-field habitat, all nests were in monotypic stands of reed canary grass. Sizes of patches of reed canary grass that it used averaged 1.2 m^2 (range 0.13-5.3 m^2). Twelve ha of the field did not support this grass and were avoided. It was probably attracted to reed canary grass because of its height and density. A second important habitat feature was presence of fence posts that were used as singing perches by males and lookouts by both sexes. Stands of reed canary grass lacking fence posts were unused. The presence of water influenced its distribution. Ten of 12 males were located near 2 ponds in the study area and the other 2 inhabited reed canary grass adjacent to a ditch containing water. Less than 2.9 ha of the 15.4 ha contained all the reed canary grass, fence posts, and water, and only this area was used. Other plant species such as common vetch, bird's-foot trefoil, willow, and Canada goldenrod had little influence on nest placement but became important later because they were a source of caterpillars to feed nestlings (Joyner 1978). In Durham Region, it nested in old fields with bluegrasses and other grasses, asters, and goldenrods with some raspberries and dogwoods; a very young pine plantation still dominated by willow shrubs and meadowsweet; and open forests with standing or running water (Speirs and Orenstein 1967, 1975). McNicholl (1987b) found it nesting in downtown Toronto on the University of Toronto campus. This is a highly urbanized area, but much of the campus consists of well-watered lawns with shrubby plantings.

In the Carolinian Forest Region in Elgin County, the Red-winged Blackbird nests in grassy roadside ditches and winter wheat fields in addition to marshes (Lancaster et al. 2004). In the Hamilton area, it bred almost exclusively in marshes until the 1950s. Since then, it has adapted to nesting in pastures, hayfields, grain fields, and suburban parks (Curry 2006).

In coastal Great Lakes wetlands, the Red-winged Blackbird was positively correlated with wetland cover and the amount of urban and agricultural land in the watershed. It was not correlated with water levels (Tozer et al. 2024).

In Ontario south of the Canadian Shield, it was significantly negatively associated with the amount of forest cover more than 100 m from edge, woodlot size, amount of forest cover within 2 km, and regional forest cover (Austen et al. 2001). It was equally abundant on organic and conventional farms. It was positively correlated with spring grain, hedgerows, hay, rights-of-way, woods, and row crops and negatively correlated with pastures, fences, streams, and trees (Kirk et al. 2011).

Originally, the Red-winged Blackbird was somewhat of a habitat specialist, nesting almost exclusively in wetlands with emergent vegetation. Beal (1897a, 1900) stated that it nested only in swamps and marshes and was absent from large tracts of lands without these features. The same was true in Ontario around this period (McIlwraith 1894). Beginning in the 1950s and 1960s, it adapted to nesting in upland grassy areas and other habitats altered by humans. At that time, it continued to be most abundant in wetlands. Bent (1958) stated that presence of water, or at least its proximity, was essential, but acknowledged that nests were often found in dry uplands a considerable distance from water. In Illinois, its density in mixed hayfields increased by 9.3 times from 1907-08 to 1957-58 (Graber and Graber 1963). In Washington, Orians (1980) observed that it

had recently spread rapidly as a breeder in upland pastures and crops. Dolbeer (1976) stated that most of the Red-winged Blackbird population nested in upland habitat in the Midwestern United States. In British Columbia, most nests continue to be in wetlands. In more boreal areas, it nests in small ponds and muskeg habitats where the traditional emergent aquatic plants it prefers may be absent (Campbell et al. 2001). In the Yukon where upland anthropogenic habitat is scarce, it is not known to nest in upland habitats (Sinclair et al. 2003). In the Boreal Forest Region, it was confined to deep and fertile marshes, wet areas dominated by sedges and low shrubs such as sweet gale and willows, and bogs and fens (Erskine 1977).

The Red-winged Blackbird nests in a variety of natural and anthropogenic wetlands. Marshes are highly preferred over other wetland types. Emergent vegetation must be present to provide nest sites. Open ponds and lakes are unsuitable nesting habitat. Shrub thicket swamps, especially those dominated by willows, alders, and buttonbush that have standing water are also favoured nesting sites. It inhabits bogs and fens at a low density, and some tall isolated shrubs, trees, or snags are usually present in occupied sites. Bogs and fens with some open water may be somewhat more attractive. Treed swamps are unused unless the canopy is very open and standing water is present. To be suitable for breeding, a wetland must have vegetation strong enough to support the nest and provide or be surrounded by suitable foraging habitat. Traditional nesting habitat consists of marshes with robust emergents in ponds, sloughs, beaver ponds and meadows, margins of lakes and rivers, and along sluggish streams. Freshwater, brackish, and salt-water marshes are all used. Wet meadow marshes also provide suitable habitat. Marshes that have bordering shrubs and trees, or woody vegetation close by may be preferred because these provide suitable singing perches, but scattered woody vegetation is preferred to adjacent woodlands. It also nests in sewage lagoons, rice paddies, natural and restored prairie potholes, roadside ditches, and agricultural drains (Bent 1958; Caccamise 1977; Campbell et al. 2001; Delphey and Dinsmore 1993; Hoffman 1989b; Jobin and Gauthier in Gauthier and Aubry 1996; Moulton 1981; Nero 1956a; Orians 1961a; Picman 1980a; Schmidlin and King 1986; Sinclair et al. 2003; Yasukawa and Searcy 2020).

The Red-winged Blackbird nests in several upland habitats. Its only requirement is that there is a small patch of tall grasses or forbs for nest placement, although it may use shrubs and even trees as nest sites. The most commonly inhabited upland sites are old fields and meadows dominated by grasses and forbs such as goldenrods and asters, pastures, and hayfields. It also nests in fields of cereal grains, hedgerows, weedy and shrubby patches, along interstate highways and other roads, tallgrass prairies, grain stubble, field borders with grasses and forbs, surface coal mines, sedge meadows, woodland openings, small woodlands, and forest edges. Conservation Reserve Program (CRP) and Dense Nesting Cover (DNC) lands planted for waterfowl production, clear-cuts in bottomland and northern hardwoods, on or in between sand dunes and beach ridges, orchards, farm shelterbelts, utility rights-of-way, pine and oak barrens, various urban and suburban habitats, and around human habitation and farmsteads may be inhabited. It rarely nests in forests except on edges but may nest in those where the canopy has been opened significantly due to timber management or other disturbances (Albers 1978; Askins et al. 2007; Bent 1958; Camp and Best 1994; Campbell et al. 2001; Conover et al. 2009; Dolbeer 1976; Galligan et al. 2006; Graber and Graber 1963; Hartley 1994; Holcomb 1974a; Hurst and Bourland 1994; Jobin and Gauthier in Gauthier and Aubry 1996; Kerr 1968; Leighton et al. 2002; Mossman 1988; Mossman and Hoffman 1989; Mossman et al.

1991; Noon et al. 1979; Orians 1961a; Paruk 1992; Patterson and Best 1996; Taylor and Taylor 1979; Webb et al. 1977; Yasukawa and Searcy 2020). In Illinois, Walk et al. (2011) reported it in every habitat they surveyed except upland forests and low-density and high-density developed areas.

At the landscape level, the Red-winged Blackbird avoids heavily forested areas where it is restricted to wetlands and other openings within the forest matrix. It is most abundant in grassland and agricultural landscapes, particularly those that have wetlands. In the St. Lawrence River valley, males exhibited a consistent preference for wetlands and avoided forested areas. A preference for hayfields was detected in 1 year. It preferred wetlands and hayfields, fields were used in proportion to their availability, and areas of human occupation, cropland, and forests were avoided. Densities in wetlands varied little over the years with greatest changes in densities occurring in less suitable habitats such as fields and human-occupied areas. Some birds held territories in lower-quality habitat even when the population was low and high-quality habitat was not saturated (Clark and Weatherhead 1987).

Although the Red-winged Blackbird nests both in wetlands and uplands, it prefers its original wetland habitat. Densities and reproductive success tend to be higher in wetlands. In North Dakota, males nesting in wetlands produced significantly more fledglings (5.22) than those nesting in uplands (1.73). Males in wetlands attracted significantly more females which contributed to their higher success rate. These females produced 2.0 times more fledglings than those in upland habitats (Besser et al. 1987). In Connecticut, nesting success was consistently significantly higher in marshes than upland habitats, but the number of young fledged per successful nest was similar. Differences in success were due to factors that resulted in total nest destruction rather than partial brood reduction. Birds in marshes nested in high density, nesting was highly synchronized, and nests had low predation rates. Those nesting in upland habitats nested in low densities, nesting was asynchronous, and predation rates were high. Water beneath nests in marshes deters most predators. Upland nests are accessible to all predators (Robertson 1972). In Illinois, densities were consistently higher in marshes than in upland habitats (Graber and Graber 1963; Walk et al. 2011). In British Columbia, 92% of nests were in wetlands such as marshes, sloughs, lake edges, swamps, and beaver ponds where cattails, bulrushes, sedges or tall grasses grew. Most occupied wetlands were bordered by shrubs, especially willow, but also by sweet gale and steeplebush. Four percent of nests were in upland habitats, including shrubs and deciduous trees along forest edges; 2% were in anthropogenic areas such as ditches, field borders, and orchards (Campbell et al. 2001).

Numerous studies identified the Red-winged Blackbird's habitat preferences and microhabitat requirements in wetlands. Marshes are highly preferred over other wetland types. Marshes with tall robust emergents such as cattails, bulrushes, cordgrass, or broad-leaved sedges are preferred over those with shorter or less robust emergents. Cattails appear to be the overall preferred emergent for nesting. In North Dakota, 23.5% of nests were in cattails. Females nesting in cattails produced an average of 1.13 fledglings per nest compared with 0.88 for all other plant taxa. Higher success rates were also reported in cattails in Connecticut. It will nest in a variety of emergents if the preferred species are not available. These include American three-square bulrush, common reed, bur-reeds, smartweeds, reed canary grass, rushes, arrowheads, rice cutgrass, and horsetails. Marshes with scattered shrubs and trees provide suitable habitat. In North Dakota, nests in American three-square

bulrush, sedges, and common reed produced above average numbers of fledglings. In Michigan marshes, it consistently selected areas with cattails and, to a lesser extent, broad-leaved sedges. It avoided narrow-leaved sedges, reed canary grass, Canada bluejoint, and forbs as nesting substrates (Albers 1978; Bent 1958; Besser et al. 1987; Campbell et al. 2001; Robertson 1972; Sinclair et al. 2003). It prefers edges of marshes to areas distant from shore. Areas with open water dispersed among the emergents are preferred to dense stands of emergents. Even the least preferred areas of a marsh may be occupied, but usually only after the optimum areas have been claimed. Dense stands of emergents preclude sunlight from reaching the substrate of the marsh. These areas typically support no submerged aquatic vegetation and few aquatic insects that could provide a source of food. In a habitat suitability index (HSI) model for the Red-winged Blackbird, suitability was considered 1.0 (optimum) if the wetland had a mix of emergents and open water, 0.3 if the wetland was covered by dense emergents, and 0.1 if the wetland consisted of open water with a few patches of emergents. In 1 cattail marsh, areas where cattails had been burned down to charred stubs were selected over areas where there were dense stands of old cattails (Albers 1978; Devine 1975a; Nero 1984; Orians 1961a; Short 1985). Areas with the tallest vegetation are preferred and are settled first early in the breeding season. In Great Lakes coastal wetlands, it was positively correlated with grass height and density, total vegetation density, submergent vegetation, and presence of open water. It was negatively correlated with bulrushes and shrub density. In New York, it nested in tall emergents and foraged in short emergents and at edges of open water. Presence of residual vegetation early in the spring is important in providing nest sites (Albers 1978; Devine 1975a; Riffell et al. 2001; Short 1985). Permanent wetlands are preferred to those that dry out at some period of the year. This is because most odonates, a preferred prey in many areas, need a year to develop from aquatic nymphs into terrestrial adults. The HSI model considered habitat to be ideal (1.0) if the water is permanent but only 0.1 if the wetland is usually dry at some period of the year. Suitability was 1.0 if the wetland supported odonates and 0.1 if it did not. Nesting occurs in semipermanent wetlands, but birds in this habitat tend to forage more in adjacent upland habitats rather than in the wetland (Short 1985). In a small Kansas pond with emergents around its margins, nesting occurred only in years when the pond retained water (Fitch 1958). In Iowa, its density was significantly higher at natural than restored potholes. This was attributed to the absence of adjacent wet meadows or prairies at restored potholes. This was probably important foraging habitat (Delphey and Dinsmore 1993).

The Red-winged Blackbird also exhibits habitat preferences and has microhabitat requirements in upland habitats. In Michigan upland habitats, it preferred hayfields, pastures, and old fields and occurred infrequently in mowed fields, fallow fields, woodlots, wheat and oat fields, soybeans, edge vegetation (roadsides, field edges, fencerows, and ditches), anthropogenic features (roads, homes, barnyards, and open ponds), and areas of tilled soils. New hayfields were occupied before old hayfields and old fields. In early spring, it had a slight preference for old fields and grasses such as timothy, orchard grass, bluegrasses, fescues, and bromes. It selected areas with the tallest and densest vegetation that restricted visibility. Erect residual vegetation is important early in the season. Although old alfalfa was partially upright in early spring, it was not preferred as consistently as old grass. As the season progressed, vegetation became less important and it also used forbs for nesting. Territories became established in less preferred areas later in the season. Early in the season, field

edges were preferred, but entire fields were used later (Albers 1978). In Illinois, forest edge shrubs, sweet clover, and mixed hay were preferred upland nesting habitats (Graber and Graber 1963). In Iowa, it occurred most frequently in herbaceous vegetation followed by scrub and wooded edges with low frequency in floodplain woodlands, savannahs, and upland woodlands. It was positively correlated with grass-like vegetation and negatively correlated with trees and saplings (Stauffer and Best 1980). In North Dakota, nests in common milkweed produced more fledglings per nest than average. Those in docks, brome grass, and alfalfa produced fewer than average numbers of fledglings. Nest success was lowest in alfalfa (Besser et al. 1987). In Maryland, plots planted to uniform redtop without any woody vegetation that could provide perches supported significantly fewer Red-winged Blackbirds than plots that were not planted to redtop but contained herbaceous vegetation and some trees and shrubs. It preferred areas with tall vegetation and dense grass (Burhans et al. 2010; Furey and Burhans 2006). In Mississippi, Conover et al. (2009) studied its response to field borders planted to native grasses and a variety of forb species. It was the most common species in fields, occurring in 30% of fields. It was significantly more abundant in fields with than without borders and in fields with wide (39-44 m) than narrow (7.3-8.5 m) borders. On restored surface mines in Indiana, it was the most abundant grassland species present. The height of vegetation where the nest was placed was positively correlated with nest success, but only in mixed habitats of grassland with a few areas of shrub or savannah habitat. Vegetation height had no effect on nesting success in open grasslands or shrub-savannah habitats (Gallingan et al. 2006). In Iowa, Camp and Best (1994) studied the Red-winged Blackbird in roadsides adjacent to croplands. Roadsides were 6 m wide with a foreslope descending 1.8 m to the bottom, then rising to a fence. It occurred in all these areas. Nests were positively correlated with coverage by reed canary grass and vegetation height and density. Nest sites had taller, denser vegetation and more forbs than occurred overall. In New Jersey in a shrub transitional area between upland and salt-marsh habitats, hatching success was negatively correlated with the height of the nest and the height of the shrub the nest was in (Caccamise 1977).

Although the Red-winged Blackbird will nest in uniform stands without distinct perch sites, it greatly prefers perches that are elevated above the emergents for singing and territorial defence. Shrubs and trees are highly preferred for perching and linear extensions may be made to territories to include suitable perches. Trees outside territories may be shared by territorial males. If a stick is shoved into the substrate within a marsh with homogeneous cover of emergents, it is immediately used as a perch. It readily uses shrubs 2-4 m tall and trees 10-15 m tall as perches. Artificial perches 1.5 and 2.0 m tall were provided in alfalfa fields. It exhibited no height preference and used both perch types in proportion to their availability. It may use anthropogenic objects as perches such as vertical exhaust pipes of parked trucks, light standards, and utility poles and wires (Albers 1978; Harrison 1977; Nero 1956a, 1984; Schmidlin and King 1986; Weller and Spatcher 1965).

The Red-winged Blackbird is not an area-sensitive species regardless of whether it nests in marsh, grassland, or forested habitat. It will nest anywhere large enough to support a single territory. In Iowa, it nested in 100% of marshes in all size categories (less than 1 ha to more than 20 ha). Brown and Dinsmore (1986) concluded that it was area insensitive. In Illinois grasslands, Herkert (1994a) recorded it on 93% of transects, the most of any species. Its occurrence was significantly negatively correlated with grassland area. Johnson and Igl (2001) studied its area sensitivity in grasslands in

Montana, South Dakota, North Dakota, and Minnesota. Their results were inconsistent and nonsignificant. In Maryland and Delaware, its probability of detection declined significantly as riparian forest width increased, from 46% in 50-m wide forests to 1% in 800-m wide forests (Keller et al. 1993). In Iowa, Fairbairn and Dinsmore (2001a, 2001b) found it in all wetlands they sampled. Its abundance was positively correlated with wetland area. It would be expected that larger wetlands would provide more habitat and support more blackbirds. It was positively correlated with the wetland perimeter to area ratio and area of weak-stemmed wetland meadow vegetation. It was negatively correlated with the percentage of wetland that was open water.

Communal roosts are an important habitat component year-round, but are least important during the breeding season. Very early in spring, flocks of males roost together in marshes, but these may be migrant birds that tend to move on rather than remaining to breed. Arriving resident males do not associate with these flocks and roost on their territories. Members of a pair also tend to roost on the territory. In New York, adults roosted during the breeding season in a small white pine forest on a college campus (Allen 1914; Bent 1958; Orians 1980; Yasukawa and Searcy 2020).

Most Ontario nests (58.3%) were at low heights in dead or living cattails, sedges, rushes, or other nonwoody plants over water or land; 38.6% were in shrubs, trees, or vines; and 3.2% were on or very near the ground. One nest was in a deep cavity in an elm tree, 1 was supported by a fence among cattails, and 2 were on tops of stumps in water. Nests were in 27 species of nonwoody plants; 37 species of deciduous shrubs, trees, and vines; and 6 species of coniferous shrubs and trees. Common nest substrates included cattails (131 nests), willows (51), grasses (40), hawthorns (24), pines (16), dogwoods (16), spiraeas (15), white cedar (15), goldenrods (14), and maples (14). Most nests were attached or woven to several upright stalks or branches of herbaceous or graminoid species, shrubs, and trees; some were in forbs or in crotches; others were suspended from branches or stalks; and a few were on horizontal limbs. Ground nests were in clumps of vegetation and 2 were at bases of shrubs or trees. Nests in cattails and other nonwoody plants were 0.1-1.4 m above water or ground, with most 0.3-0.6 m up. Nests in shrubs and trees were 0.2-11.6 m above water or ground with most 0.8-1.8 m up. One nest was built on top of an old Red-winged Blackbird nest and one incorporated part of an old Baltimore Oriole nest (Peck and James 1987). At Luther Marsh, nests were at a mean height of 15.0 cm (range 10-20 cm) in dead stems of reed canary grass from the previous year's growth that averaged 58.4 cm in height (range 51-71 cm; Joyner 1978). Near Kingston, 64% of nests were in cattails, but nests in cattails were fourth in nest success behind those in purple loosestrife, grasses, and alder-willows (Weatherhead and Robertson 1977a).

Throughout its range, the Red-winged Blackbird preferentially builds its nest in elevated locations in emergent marsh vegetation, but it also uses shrubs as a nesting substrate in wetlands. In upland habitats, it nests near or on the ground in grasses or forbs or higher up in shrubs and trees. Cattails are universally preferred as a nesting substrate, although a variety of emergents may be used in aquatic habitats. Cattails are particularly preferred early in spring because they become less flattened by winter snow than other emergents. As the season progresses, other vegetation becomes sufficiently developed to support nests, and they may be placed in sedges, bur-reeds, horsetails, docks, arrow arum, or other emergents. Softer vegetation such as docks and smartweeds may be preferred later (Allen 1914; Orians 1980). In British Columbia where most nests were in

wetlands, 67% were in emergent aquatic vegetation, including cattails (34%), bulrushes (19%), and reeds (14%). Other nest sites included shrubs (19%), deciduous trees (5%), and grasses and sedges (1.4%; Campbell et al. 2001). In Manitoba, nests were in cattails, common reed, sedges, and willows in shallow water and in patches of snowberry in pastures adjacent to creeks and ponds without emergents (Bird and Smith 1964). In Ohio marshes, 87.9% of nests were in cattails, 7.6% were in gray dogwood, 6.1% were in common elderberry, and 1.5% were in willows. In Michigan marshes, 47.3% of nests were in cattails, 12.5% were in common elderberry, 9.8% were in willows, 8.9% were in rushes, 8.0% were in red-osier dogwood, 3.6% were in gray dogwood, 2.7% were in honeysuckle, 2.7% were in red raspberry, 1.8% were in swamp birch, 0.9% were in shrubby cinquefoil, 0.9% were in white elm, and 0.9% were in dead shrubs (Holcomb and Twiest 1968). In Louisiana, nests were in 30 plant species with 47.1% in buttonbush. Bulrushes were the next most commonly used plant. Nests in buttonbush had higher nest success, probably because buttonbush was sturdier and better at resisting severe weather. Other important nest plants included willows, rushes, cattails, alder, sweet gum, dock, and grasses. Less frequently used species included pine, privet, peach, horse chestnut, oak, common lilac, ironweed, hawthorn, rose, sassafras, blackberry, sumac, boneset, and gray dogwood (Brown and Goertz 1978). In North Dakota, Besser et al. (1987) found 908 nests in 36 plant species: 23.5% in common cattail, 9.4% in American three-square bulrush, 9.4% in alfalfa, 7.9% in dock, 6.4% in sedges, 5.6% in brome grass, 5.1% in common reed, 3.7% in snowberry, 3.6% in big bur-reed, 3.6% in cordgrass, 3.5% in sweet clover, 3.0% in fescues, 2.3% in smartweeds, 2.2% in soft-stemmed bulrush, 2.0% in reed canary grass, 1.8% in willow, 1.4% in wormwood, and less than 1% each in common milkweed, wheat grass, rushes, barnyard grass, squirrel-tail grass, green ash, honeysuckle, Russian thistle, common ragweed, manna grass, daisy fleabane, broad-leaved arrowhead, hybrid cattail, rice cutgrass, prairie rose, stinging nettle, needle grass, Johnson grass, and Canada thistle. Twenty-seven nests were attached to fences for additional support and 8 were attached to 2 plant species. In Iowa, 88% of nests had water under them, 86% were in robust emergents, 75% had open water near the nest, and 75% were in open landscapes (Weller and Spatcher 1965). In upland interstate highway rights-of-way, 61.8% of 358 nests were in woody vegetation and 38.2% were in herbaceous vegetation (Paruk 1992). In upland habitat in Ohio, 39.7% of nests were in goldenrods, 12.8% were in gray dogwood, 10.3% were in white elm, 10.3% were in raspberries, 5.1% were in grapevines, 3.8% were in honeysuckles, 3.8% were in Manitoba maple, 2.6% were in willows, 2.6% were in common elderberry, and 1.3% each were in beech, staghorn sumac, chokecherry, rose, bur oak, meadowsweet, and ash (Holcomb and Twiest 1968). Along roadsides in Iowa, 32.9% of nests were in wire fences, 21.1% were in reed canary grass, 18.4% were in field horsetail, 13.2% were in forbs, 9.2% were in other grass species, and 5.3% were in shrubs (Camp and Best 1994). In upland habitat in Iowa, 20% of nests were in forbs, 48% were in grasses, 19% were in shrubs, 10% were in deciduous saplings, and 3% were in deciduous trees (Stauffer and Best 1980). Other upland species that the Red-winged Blackbird has nested in include poison oak, plum, bayberry, blueberry, cherry, wild currant, gooseberry, white spruce, white cedar, vetch, and peach (Allen 1914; Bent 1958; Devine 1975b; Miller 1968; Orians 1961a). Nests have been reported 0-10 m above ground or water. Nests in aquatic emergents tend to be 20-80 cm above water. In a Michigan wetland, nests were 20-25 cm above water in mid-April and averaged 62.5 cm above water by mid-June as the height of emergents increased. Nests in upland grasses and herbaceous vegetation may be 0-100 cm above ground and average 40-60 cm up. Nests in woody vegetation may be as high as

10 m above ground. In British Columbia, nests were 0-8.0 m above the substrate with 70% 0.3-0.9 m up (Allen 1914; Bent 1958; Campbell et al. 2001; Holcomb and Twiest 1968; Miller 1968; Yasukawa and Searcy 2020). Nest success increases with increasing height above the substrate. Nests over water less than 15 cm deep have lower success than those over deeper water (Brown and Goertz 1978; Holcomb and Twiest 1968). Near Kingston, nests over deeper water had lower incidence of predation; nests 0-40 cm above water were more successful than higher nests. Nests in open areas were more successful than those in dense vegetation (Weatherhead and Robertson 1977a). There are at least 2 records of the Red-winged Blackbird nesting in tree cavities and one of it nesting in a nest box (Nero 1956b; Yasukawa and Searcy 2020).

The Red-winged Blackbird is not known to reuse nests but there is 1 record of a nest being built on top of an old nest. In Washington, one relined an old Baltimore Oriole nest and successfully fledged young (Allen 1914; Bent 1958; Holcomb and Twiest 1968; Miller 1968; Nero 1984; Orians 1980; Yasukawa and Searcy 2020). In Washington, Erckmann et al. (1990) added old nests to experimental plots to determine if females were attracted to areas supporting old nests from the previous season. Females nested preferentially in these plots in 1 year but not in another; results were inconclusive.

The Red-winged Blackbird is often considered colonial because it nests in very high densities in marshes. The fact that it is polygynous can result in large numbers concentrated in a small area. It is not colonial in the traditional sense, with all suitable wetland habitat occupied. The size of the population is determined by the size of the marsh and secondarily by the nature of the surrounding vegetation. Its distribution appears to be the result of nesting habitat distribution rather than gregariousness. In upland habitats, there is no evidence of clumping of territories and solitary territories are common (Orians 1961b; Yasukawa and Searcy 2020).

Males are highly territorial. Territory size and song rate are significantly correlated. A large repertoire of song types is more effective in deterring trespassers than a single song type. The red epaulets of males are important in displays and maintaining boundaries. Males that had their epaulets experimentally blackened often lost their territories to an intruder and these all suffered wounds due to physical combat. Females preferred males with epaulets reddened slightly above the normal range. Chasing is another common method of territorial defence. One Ontario male killed another male by pecking him repeatedly and forcing him under water several times until he died. Males exclude other males from their territory and are particularly aggressive toward yearling males. They also exclude migrating flocks of females, any females that are not their mates, and fledglings of other pairs. Long-term residents know their territory boundaries and respect those of their neighbours. In these cases, there is very little dispute over territorial rights. Boundaries between territories are sharp and can be determined within 30 cm (Nero 1956a, 1980; Nero and Emlen 1951; Orians 1961a; Sabean and Sabean 2017; Yasukawa 1981; Yasukawa and Searcy 2020; Yasukawa et al. 2009).

Females exhibit aggression toward each other, particularly early in the season when they are first settling on territories. When the initial female arrives, she attempts to defend the entire male's territory. When a new female intrudes, the resident female usually vocalizes at it and chases it out of the territory. When the male is present, he often intervenes and courts the intruder and may chase

the resident female away. This may continue for as long as 10 days until the resident female is no longer able to exclude the intruding female who settles in another part of the male's territory and begins nesting. The 2 females subsequently avoid each other, and similar behaviour occurs when new females arrive. Although females are aggressive toward each other, their display perches overlap considerably and nests have been found less than 1 m apart. Females tend to be more aggressive toward harem mates but are also aggressive toward strange females and fledglings. Aggression is strongest early in the season during nest building and egg laying and more prevalent in smaller territories because there is less space to share. Later, females are aggressive only in a small area around the nest (Beletsky and Orians 1991; Blakley 1976; Hurly and Robertson 1984; Nero 1956a, 1956c, 1984; Nero and Emlen 1951; Orians 1980; Yasukawa and Searcy 2020). Whether the aggressive behaviour of females is consistent with territoriality is inconclusive. In Wisconsin, nests of primary females were significantly over-dispersed demonstrating that male territoriality results in over-dispersion. When all nests were considered, they were randomly distributed in 2 years and clumped in 1 year. Results were not consistent with female territoriality (Yasukawa et al. 1992). Near Kingston, females appeared to exhibit territoriality. Female territories were contiguous, aggressive behaviour occurred at boundaries, and trespassers were seldom tolerated. Females appeared to act competitively rather than cooperatively. The purpose of aggression may be to attempt to keep the harem size small, which could result in increased attentiveness of males to females already established within his territory (Hurly and Robertson 1984). Keeping the harem size small may be important in eastern populations where males frequently feed nestlings, but less important in the west where males contribute little to the raising of the young. All females were removed from experimental territories near Kingston. Eleven new nests were initiated in experimental territories compared with 3 in control territories, a significant difference. Hurly and Robertson (1985) concluded that presence of females in a territory inhibited settlement by other females. Early in the season, females respect male territorial boundaries and seldom cross them. They are typically expelled if they trespass onto a neighbouring male's territory. In Wisconsin, nests were experimentally moved into adjacent territories. The male did not alter his territorial boundaries to include these nests. Females readily accepted the new nest locations but became subordinate to both sexes in the other territory. Nests were more important to females than specific locations (Hurly and Robertson 1984; Nero 1984; Nero and Emlen 1951). Roberts and Searcy (1988) placed feeders in males' territories to determine which females within harems were dominant. The earliest female to settle on the territory was dominant in 82.6% of tests. Proximity to a nest at the encounter site was a significant factor in determining dominance. In 66.7% of contests, the female whose nest was closest to the feeder was dominant. When feeders were moved, different females became dominant. Nesting stage and female size and age did not affect dominance.

Upon arrival, males immediately establish territories but spend most of the day foraging away from the territory. They are usually present in the territory only early in the morning and prior to sunset. Gradually they spend more time in the territory until they are there all day. This usually occurs 1-3 weeks before the females arrive and territorial defence is intense at that time. Migratory males may temporarily defend tree perches for a few hours before moving on, but do not attempt to do this in marsh habitat. Territorial defence by resident males typically ceases once their fledglings leave the territory, and the intensity of defence declines before this (Allen 1914; Devine 1975a; Dickinson

and Lein 1989; Hurly and Robertson 1984; Nero 1956a, 1980; Orians 1961a). Boundaries fluctuate considerably early in the season, with early arrivals attempting to hold large territories and withdrawing from parts of them as new birds arrive. Those that previously held small territories usually attempt to enlarge their holdings and frequently succeed. In most areas, territories shrink as the season progresses but in a Michigan area they increased. This may have been due to some birds abandoning their territories, allowing neighbours to expand their territories. Later arrivals at this site may have been relegated to suboptimal habitat where larger territories were required. Some birds attempt to acquire a territory by forcing themselves in between existing territories. Those that are successful alter the boundaries of the neighbours' territories. There are constant attempts to take over territories and birds that die or disappear from their territories are quickly replaced. Birds that are experimentally removed from their territories lose them to other males and few are successful in regaining them after their release. Near Kingston, males defended all nests within their territory equally and did not give preferential treatment to nests of primary females (Albers 1978; Beletsky and Orians 1989; Dickson and Lein 1987; Nero 1956a, 1984; Orians 1961a; Picman 1987; Weatherhead 1990).

High-quality males that sing more frequently and have larger song repertoires have larger territories and males that previously bred in the same territory tend to have larger territories. Territories in high-quality habitat with open water dispersed among emergents are smaller than lower-quality stands of solid emergents. The proportion of food that is obtained in the territory affects its size. Territories are small where all food is obtained outside the territory and large where all food is obtained within the territory. Territories in upland habitat tend to be 1.5-3 times larger than those in marshes because all food is obtained in upland territories and little to none is collected within wetland territories. Territories on highly productive lakes tend to be smaller than those on less productive lakes due to a greater abundance of prey. Territory size may vary annually with changes in male densities, with territory sizes decreasing as densities increase. New territories created by birds inserting themselves between existing territories or by subdividing an existing territory are smaller than territories of displaced males. In Washington, territories were 3 times larger on lakes where Yellow-headed Blackbirds occupied the best habitat. In Michigan, upland territory size was not significantly correlated with landscape or vegetation features. Wetland territory size decreased as the proportion of broad-leaved monocots increased and as vegetation height increased, and increased as the proportion of narrow-leaved monocots increased and vegetation height decreased (Albers 1978; Dickinson and Lein 1987; Nero 1956a; Orians 1961a, 1980; Picman 1987). A large range in territory sizes has been reported, from 46 to 16,932 m^2. In western North America, mean territory sizes in 24 locations ranged from 234 to 2,361 m^2; the overall mean territory size was approximately 2,000 m^2. Largest territory sizes (mean 9,080 m^2) were in a brackish cattail marsh in British Columbia. Other mean territory sizes include 140-160 m^2 in Washington, 233-1,275 m^2 at other Washington sites, 330 m^2 in Wisconsin, 2,936 m^2 in Utah, 384 m^2 in Alberta, 4,000 m^2 in upland habitat in New York, and 771-2,310 m^2 in Manitoba. Territory sizes at a given site vary considerably due to changes in blackbird density and water levels that may affect the distribution and interspersion of emergent vegetation (Beletsky and Orians 1991; Blakley 1976; Dickinson and Lein 1987; Furey and Buchans 2006; Nero 1956a; Orians 1961a, 1980; Orians and Collier 1963; Picman 1980a, 1987; Shutler and Weatherhead 1991; Yasukawa 1981; Yasukawa and Searcy 2020).

The Red-winged Blackbird and Yellow-headed Blackbird are interspecifically territorial and have mutually exclusive territories. The Red-winged Blackbird arrives in marshes first and typically occupies all areas of emergent vegetation. When the Yellow-headed Blackbird arrives, it evicts the Red-winged Blackbird from its preferred habitat. This consists of emergents interspersed with scattered open water and especially the centre of the marsh at the interface between open water and emergents. Red-winged Blackbirds are forced to nest in the periphery of marshes and areas of dense emergents without any open water. Occasionally isolated Red-winged Blackbird territories occur within colonies of Yellow-headed Blackbirds where the microhabitat is not suitable for Yellow-headed Blackbirds. Although the Yellow-headed Blackbird is dominant in deep-water areas of marshes, the Red-winged Blackbird is dominant at the periphery of marshes. The Yellow-headed Blackbird avoids nesting in emergents adjacent to trees, so the Red-winged Blackbird inhabits these areas. The Yellow-headed Blackbird is dominant to the Red-winged Blackbird in upland foraging areas and displaces it from feeders (Miller 1968; Orians and Willson 1964; Weller and Spatcher 1965). In Washington, mean nest height of the Red-winged Blackbird was 22.6 cm compared with 30.8 cm for the Yellow-headed Blackbird (Miller 1968; Orians 1980).

Both sexes of the Red-winged Blackbird, but especially males, are aggressive toward the Marsh Wren. These 2 species commonly occur together in marshes and their territories overlap widely. Blackbird aggression toward the Marsh Wren may represent partial interspecific territoriality. Blackbirds often place their nest nonrandomly so they are as far as possible from a wren nest (Picman 1980b, 1983).

The Common Grackle seldom nests in marshes, but the Red-winged Blackbird is aggressive toward it when it does. The grackle defends a radius of only 0.6-0.9 m around its nest rather than the more expansive territories of the Red-winged Blackbird. Most interactions between the species were initiated by the Red-winged Blackbird as a result of grackles trespassing on their territories, most often in connection with courtship and their attempts to reach their nests or feed fledglings. Grackles that moved more than 3 m into a Red-winged Blackbird territory always elicited a response. Grackles modified their behaviour to conduct courtship displays at Red-winged Blackbird territorial edges and areas of poorly defined territories. Grackle nests were usually at the periphery of Red-winged Blackbird territories but some were well within territories as a result of boundary shifts. Grackles returning to their nests and their fledglings were usually ignored. Grackles were not aggressive to Red-winged Blackbirds unless they approached too close to the nest. The presence of grackles had no effect on Red-winged Blackbird reproductive success. It could not be determined if true interspecific territoriality existed between the 2 species because of the very small and vaguely defined territories of the grackle. Interspecific territorial aggression occurred by both species and even partial territorial exclusion between the species might contribute to successful cohabitation. Grackle nests were usually in somewhat denser cattail clumps and lower than Red-winged Blackbird nests (average 50.8 cm compared with 60.2 cm). Red-winged Blackbird nests were usually exposed and well lit; grackle nests were only somewhat exposed (Wiens 1965).

Natal philopatry rates appear to be quite low. Yasukawa and Searcy (2020) stated that 8% of male and 3% of female nestlings returned to the same series of marshes in Washington to breed. Near Kingston, Shutler and Weatherhead (1994) reported a return rate of nestlings of just over 2% in

marshes along roadsides and less than 1% in marshes surrounded by woodlands. Most fledglings dispersed from the area and were not seen again. Two of 10 fledglings (20%) from roadside wetlands returned in a subsequent year and 11 of 142 (7.7%) from marshes within woodlands returned. Floater birds had low return rates that were approximately the same as for fledglings. Eighty-nine percent of floaters were never seen again. The high rate of floater dispersal may be a mechanism to prevent inbreeding. Of floaters that subsequently acquired a territory, 5 of 14 (35.7%) returned the following year in woodland marshes and 1 of 8 (12.5%) returned to roadside marshes. Dolbeer (1978, 1982) analyzed banding returns of juveniles recovered in subsequent years. Distances between banding and recovery sites were greater than for birds banded in their second or later years. One nestling banded in the Great Plains was recovered more than 1,000 km away.

Adult site fidelity rates tend to be high and males may defend the same territory for several years. Females have high return rates but are more likely to switch territories or even marshes within and between seasons. At a Wisconsin marsh, 28 of 50 adult males (56.0%) returned and 27 of 48 females (56.3%) returned. Of 16 males, 10 returned in 4 years, 3 in 5 years, and 3 in 6 years. Of 16 females, 9 returned for 3 seasons, 4 for 4 seasons, and 1 for 5 seasons (Nero 1956a, 1956c). In British Columbia, 23 of 61 males (37.7%) returned in at least 1 year and 34 returned over the years. Only 2 of the 34 (5.9%) abandoned their original territory to establish a new one. One settled in the adjacent territory and the other established a new territory 600 m away. For 79% of returning males, the overlap between new and previous territories was at least 61% (mean 78%). Most males that returned in consecutive years exhibited strong site tenacity that resulted in similar territory boundaries. Changes in the location of territories were unrelated to the number of young raised, the number of fledglings per female, or harem size. The tendency for males to return to the same territories continues throughout their lives. Yasukawa and Searcy (2020) reported that 87-94% of males return to their same or a neighbouring territory. Meyers et al. (1990) reported return rates of females of 44.2% and 56.0% over 2 years. In British Columbia, 53 of 85 females (62.4%) returned to their original territory the following year in an area defended by their original mate, 26 (30.6%) nested in a territory of a neighbour, and 6 (7.1%) nested in a more distant territory. Seventy-five of 90 females that renested (83.3%) remained in the same territory with their original mate, 14 (15.6%) nested in 2 different territories and were members of 2 different harems, and 1 (1.1%) nested in 3 different territories. The mean distance between previous nests was significantly less within (46.9 m) than between (77.0 m) seasons (Picman 1980a). Albers (1978) concluded that females had strong habitat fidelity within seasons in Michigan. Those that were displaced from upland sites by mowing were reluctant to use a different habitat type. In marsh habitats, females often moved between territories or even marshes in the same or different year. Females may nest repeatedly in the same territory despite successive nest failures, but are more likely to change territories between years following an unsuccessful nesting (Yasukawa and Searcy 2020). In Wisconsin, female movements between years were primarily due to females switching mates because males remained in the same territory. Seven females moved an average of 29.9 m between years (range 4.9-73.2 m). One female was on a territory for 2 weeks then moved to another territory to nest. One nested unsuccessfully twice in 1 territory, then moved to another territory 68.6 m away where she nested successfully and returned the following year. Another deserted a completed nest and renested successfully in an adjacent territory while retaining her original mate (Nero 1956a). In upland habitat in Ohio, females

switched territories in 3 of 27 nesting attempts (11.1%) and another was seen feeding fledglings 220 m from the field. It was hypothesized that the incidence of movement of females in and out of territories was substantial and that females commonly switched territories, perhaps moving considerable distances (Dolbeer 1976). In Washington, Beletsky and Orians (1991) studied 8 marshes that were close enough together that a female could fly between them in a few minutes. Over a 12-year period, 49.2% of renesting females changed breeding territories within seasons and 20.1% changed marshes between breeding attempts. Twenty-two percent changed marshes between their final breeding in 1 year and their first breeding in the next year. Most moves of less than 10 m were within-territory moves, moves of 15-20 m were to adjacent territories, and moves of more than 100 m were associated with marsh changes. Between years, females moved significantly further if their last nest in the previous year was unsuccessful. Females tended to remain on the same marsh for their first and second nesting attempts regardless of their success. Females also tended to return to the same marsh as the previous year for their first nesting attempt. Significantly more females that had been successful the previous year (83.9%) stayed on the same marsh than those that had been unsuccessful (72.5%). The number of familiar males in a marsh appeared to influence whether a female remained. The breeding group may be more important than the individual territory owner. Females may select male breeding neighbourhoods in which they nest for the entire season and copulate with, feed among, and receive cooperative defence from these males. Almost half of females bred on territories other than those of their first mate. Dolbeer (1978, 1982) analyzed recoveries of banded birds. The mean distance between banding sites and recovery sites in a subsequent year was 31 km for males and 34 km for females. Results indicated that most adults were faithful to the general location of their previous breeding areas.

Limiting Factors

Eggs have been found in Ontario nests from the last week of April until the first week of August, with most present from the last week of May until mid-June (Peck and James 1987). In Algonquin Park, nests are under construction from mid-May to mid-June, eggs are present from late May to early July, nestlings occur from early June to late July, and dependent fledglings have been observed from mid-June to mid-August (Tozer 2012). North of Kingston, females arrive in early April at which time they select nest sites but spend very little time in the marsh. Most arrive in late April and begin to build nests shortly thereafter (Hurly and Robertson 1984).

Females arrive in small flocks and males have well established territories by then. Females tend to select territories or neighbourhoods of males over individual males. Yearling females and those new to an area may visit several territories in rapid succession before selecting one. Females familiar with an area may settle on a territory immediately. The pair bond is usually established within an hour of the female's arrival. Once the female has selected a territory, she remains in the territory except to feed in adjacent uplands. Nest building may start immediately or be delayed as long as 2-3 weeks. In Alberta, females spent an average of 4.6 days on a male's territory before building a nest. In Ohio and Michigan, the mean time spent building a nest was 3.1 days; often as long as 6 days is required to build the nest. One to 10 days may elapse between nest completion and egg laying. Eggs are laid at the rate of 1 day (Allen 1914; Bent 1958; Devine 1975b; Dickinson and Lein 1987; Holcomb and Twiest 1968; Miller 1968; Nero 1956c, 1984; Orians 1961a, 1980; Yasukawa and Searcy 2020). Incubation usually begins with the laying of the penultimate egg, but the onset of incubation

is variable, sometimes occurring with the laying of the second egg or not until 1-2 days after clutch completion. In Nebraska, incubation began on the first day of egg laying and the constancy of incubation increased each day. Nocturnal incubation usually began the night after the penultimate egg was laid, with effective incubation beginning with the laying of the last or penultimate egg. Commencement of nocturnal incubation before the clutch is complete results in asynchronous hatching. Nests with earlier onset of incubation are significantly less likely to be parasitized by the Brown-headed Cowbird. The incubation period at 28 Ontario nests was 10-13 days (mean 11.25 days). In eastern Ontario, the incubation period was longer by 0.2 and 0.8 day over 2 years at beaver ponds where prey were less abundant and blackbirds had to forage outside their territories than at sewage lagoons. Elsewhere, incubation periods of 10-13 days have been reported, but most eggs hatch in 11-12 days. Depending upon when incubation was initiated, hatching may occur over a 1-3-day period. The nestling period is 9-12 days, mostly 10-11 days (Allen 1914; Beletsky and Orians 1990; Bent 1958; Brown and Goertz 1978; Campbell et al. 2001; Clotfelter and Yasukawa 1999a; Holcomb 1974a; Miller 1968; Nero 1984; Peck and James 1987; Yasukawa and Searcy 2020; Zimmerling and Ankney 2005).

The Red-winged Blackbird is capable of raising 2 broods in a season and has done so in Ontario and many other areas. Most females raise only a single brood. In Wisconsin, only 3 birds raised more than 1 brood over a 6-year period. In 1 year, 20 females successfully reared their first brood and 0 attempted a second. In Maryland, 3 of 7 females (42.9%) that successfully raised their first brood attempted a second and one was successful. All females that attempted a second brood were adults. In Ohio, 3 of 132 females (2.3%) attempted a second brood and 2 were successful. In Washington, 5.9% of females raised 2 broods. In British Columbia, 108 of 120 females (90%) that nested successfully raised only a single brood; 12 (10%) raised 2 broods. Females may begin building the second nest before the first brood fledges. A Wisconsin female laid the first egg of her second clutch 9 days after the first brood fledged. Nests for second broods are usually close to the first nest, often within 3 m. Usually the same mate is retained (Allen 1914; Dolbeer 1976; Fankhauser 1964; Moulton 1981; Nero 1956b, 1956c, 1984; Picman 1981; Yasukawa and Searcy 2020). The Red-winged Blackbird readily renests if the first nest is unsuccessful. Females may make as many as 5 nesting attempts to try and raise a brood. In British Columbia, 86% of females whose nest failed renested (Picman 1981). In Washington marshes, 45.2% of 1,570 females built 1 nest in a season, 40.7% built 2, 11.1% built 3, 2.4% built 4, and 0.6% built 5 nests. The median distance between successive nests was 10.0 m (Beletsky and Orians 1991). In Maryland, second nests were built within 45 m of the first nest. One female successfully reared a brood in a hayfield and attempted a second. When it was destroyed by mowing, she initiated another nest 550 m away in a marsh (Fankhauser 1964). In Minnesota, 50% of females that renested switched territories and moved considerable distances between successive nests. This type of movement may be common (Moulton 1981). In Ohio, females whose nest failed in early May had the greatest probability of renesting; 0 of 10 females whose nests were lost after 21 May renested (Dolbeer 1976). Peck and James (1987) reported that some replacement clutches were laid in the original nest. Clutches of 2-6 eggs were reported in Ontario and a single 1-egg clutch appeared to be complete. A 7-egg clutch was documented but the eggs had 2 distinct colour patterns and were assumed to have been laid by 2 females. Four-egg clutches were most frequent, followed by 3-egg clutches (mean 3.59 eggs; Peck and James 1987,

1998b). Elsewhere, clutches of 1-6 eggs have been reported, with 2-5 eggs typical. In most areas, 4-egg clutches are most abundant followed by 3-egg clutches. In some areas, 3-egg clutches are most frequent and these are usually in upland habitat. A 7-egg clutch was documented in British Columbia. Mean clutch sizes typically range from 3.38-3.82 eggs, although there is 1 record of a mean clutch size as low as 2.43 eggs. Mean clutch sizes in Alaska were 4.3 and 4.4 eggs. In Ohio, clutch size declined significantly with the season, averaging 3.56 eggs before 10 June and 3.17 eggs later (Allen 1914; Bent 1958; Besser et al. 1987; Brown and Goertz 1978; Campbell et al. 2001; Dolbeer 1976; Ewald and Rohwer 1982; Francis 1975; McGuire 1986; Miller 1968; Moulton 1981; Orians 1961a, 1980; Robertson 1972; Yasukawa and Searcy 2020).

Both sexes are capable of breeding when they are 1 year old. It is probable that all yearling females breed, but few yearling males do. Yearling males are at a disadvantage because most adult males have already established territories by the time they arrive, their testes do not develop fully until about 3 weeks later than adults and they are not as large, and mated females do not display to yearling males. Some yearling males are successful in establishing a territory and mating, usually by nesting in inferior habitat that is unattractive to older males or by taking over a territory when the original owner disappears. Yearling males are occasionally successful in copulating with a paired female, but it is uncertain if these extra-pair copulations result in them actually siring young. Yearling males may initially attempt to hold a territory and subsequently abandon it. One Minnesota yearling male abandoned his original territory and successfully established another 1.4 km away. In Iowa, yearling females began nesting 15 days later than adult females. Yearlings had significantly smaller clutch sizes (3.40 compared with 4.11 eggs) and raised significantly fewer fledglings (0.73 compared with 1.63) than older females. Once a bird breeds, it usually continues to do so for the remainder of its life. Birds as old as 10 years have been documented breeding (Beletsky and Orians 1991; Besser et al. 1987; Crawford 1977; Holcomb 1974b; Moulton 1981; Nero 1956a, 1984; Orians 1961a, 1980; Yasukawa and Searcy 2020).

Most populations include a subpopulation of nonbreeding floater males. These are mostly yearlings, but also include some older birds. These birds try all breeding season to acquire a territory and some are successful in copulating with mated females. Several studies conducted near Kingston involved removal of male territory holders to determine if floaters were successful in acquiring their territories. The first replacement birds were older and only when they were removed did yearlings acquire a territory. In marshes surrounded by woodlands, all original territory holders were older birds and 83% of 410 floaters were yearlings. In roadside marshes, 89 of 90 territory owners (98.9%) were older birds. Only 15% of floaters that claimed a territory after the owner was removed were yearlings. Most floaters left the study area within 10 days indicating that floaters seldom remain within a restricted area. In marshes in the woodland area, 14 of 463 floaters (3.0%) claimed a territory and 5 (1.1%) were captured as a floater in the following year. Forty-nine floaters returned to the roadside marshes; 8 (16.3%) successfully claimed territories and 1 (2.0%) remained a floater. Only 56 of 490 floaters (11.4%) were recaptured or seen holding a territory, with most apparently dispersing. Most territory claimants the next year were newcomers that were probably floaters from outside the study area. Thirteen floaters obtained territories when they were 2 years old, 6 when they were 3 years old, and 1 at age 4 years. Of the original territory owners and their subsequent replacements that were removed, only original territory holders were successful in reclaiming their territory after

they were released; only 50% were successful (Orians 1980; Shutler and Weatherhead 1991, 1992, 1994; Yasukawa 2013).

The mating system is polygynous. The Red-winged Blackbird is the most polygynous species in North America. Although some males mate monogamously, most have 2-5 or 6 females; as many as 33 females have nested in a single territory. The mean number of nesting females within a territory ranges from 1.6 to 5.8. Harem sizes are significantly higher in marshes than upland habitats. In upland areas of Luther Marsh, all males appeared to be monogamous. In Wisconsin, 20% of males were monogamous, 64% had 2 mates, and 16% had 3 mates. Overall, approximately 90% of males are polygynous and 99% of females are in polygynous relationships. Polygyny occurs because of the highly skewed sex ratio dominated by females. This is because all females nest but yearling males mostly do not. Harem size and territory size are not correlated. Higher-quality territories support larger harem sizes. Territories in marshes with open water dispersed among cattails support larger harems than areas of monotypic stands of emergents. High-quality territories habitually support larger harems even if the attending male changes. New males acquiring high-quality territories tend to inherit a large harem (Beletsky and Orians 1990; Besser et al. 1987; Blakley 1976; Dickinson and Lein 1987; Dolbeer 1976; Ewald and Rohwer 1982; Joyner 1978; Nero 1956c; Orians 1961a, 1980; Picman 1980a, 1981; Short 1985; Weatherhead and Robertson 1977b; Yasukawa and Searcy 1981, 2020; Yasukawa et al. 2009). Near Kingston, Weatherhead and Robertson (1977b) found no correlation between harem size and territory quality. Near Ottawa, Pribl and Picman (1996) studied whether females preferred to settle on similar territories defended by bachelors or males already in a monogamous relationship. There were 2 classes of females: older birds that settled early in the season that preferred to mate monogamously, with all selecting bachelor males, and young females that settled later with males that were already mated. Some females may choose mates that are already mated over bachelors if the mated male has a superior territory. New females tended to avoid territories where they would nest synchronously with the resident female and selected territories where they would be nesting asynchronously. The cost of polygyny declines with the season. Resource competition declines due to asynchronous nesting, aggression of resident females declines, and clumping of nests may be beneficial in deterring predation and parasitism. Others have reported that nesting of females within a given male's territory is asynchronous. In Iowa, males rarely acquired more than a single female at the beginning of the breeding season. In most cases, 4-20 days passed before another female settled. In Washington and Indiana, there was no evidence that nest asynchrony declined with the season or that harem size influenced the degree of synchrony (Blakley 1976; Nero 1956c, 1980; Orians 1961a; Yasukawa and Searcy 1981, 2020). Weatherhead and Robertson (1977b) hypothesized that females could either chose a high-quality territory with low female density and a higher chance of nest success or a low-quality, high-density territory where the chances of success were reduced but that any male offspring produced would be expected to have a superior ability to recruit mates. This was termed the sexy-son hypothesis, but there has been limited support for it. In most cases, nesting polygynously does not come at a cost for females. Females in eastern populations that nest polygynously may be at a disadvantage because eastern males tend to assist in feeding of the nestlings. In these cases, only primary females tend to benefit from the care of the male. Western males rarely assist in feeding the nestlings, so polygyny is not a disadvantage for females paired with them (Yasukawa and Searcy 1981, 2020). In

Iowa, most primary females were older birds. Some older females were secondary but in these cases the primary bird was also old. Only 4 yearling females were primary: 2 were in monogamous relationships and in the other 2 cases the secondary females were also yearlings. In no case was a yearling the primary female with a secondary older female in the territory. There was no difference in the clutch size of primary and secondary adult females but primary yearlings laid significantly more eggs than secondary yearlings. Both yearling and older primary females fledged significantly more young than secondary females (Crawford 1977). Polygynous mating is highly beneficial for males. The larger the harem is, the greater the reproductive success of the male. Near Kingston, larger males had significantly larger harems and greater reproductive output. Females appeared to prefer larger and older males (Weatherhead and Boag 1995).

The pair bond dissolves as soon as the female leaves the territory with the fledglings, often as early as June. Many pair bonds do not last throughout the season. Females frequently shift territories and mates between nesting attempts. In Washington, almost half of females bred on territories other than their first mate's. The duration of a pair bond may be no longer than the length of a failed nest attempt. When both members of a pair return in the following year, they may or may not reunite. In Washington, 57% of females bred with another male even when their previous mate was still alive and territorial. Females whose last nest was successful in the previous year were most likely to pair with their old mate, but 50% of these selected a different male suggesting that mate fidelity was unimportant to females. Similar patterns have been observed elsewhere (Beletsky and Orians 1991; Dolbeer 1976; Nero 1956a, 1956c, 1984; Yasukawa and Searcy 2020).

The male commonly attempts to guard his mate by keeping himself between her and neighbouring males (Nero 1956c, 1984; Yasukawa and Searcy 2020). This strategy is ineffective because both sexes actively seek extra-pair copulations and they are an important component of the Red-winged Blackbird's mating strategy. About 50% of nests contain extra-pair young. The rate of extra-pair young varies among populations: 26% in Ontario, 24% in New York, 31% in Wisconsin, 31% in Washington, and 40% in Kentucky (Yasukawa and Searcy 2020). Roberts and Kennelly (1980) tested the promiscuity of females by vasectomising their mates so they could not fertilize eggs. Phase 1 birds were vasectomised before the females arrived and phase 2 males were vasectomised after breeding began. Over 2 years, 100% and 86% of clutches in territories of phase 1 males were fertile and 36% and 100% of phase 2 birds were fertile. Overall 70% of clutches in territories of vasectomised males were fertile. Promiscuity declined as the season advanced. North of Kingston, females fledged fewer young as the proportion of extra-pair young in their nests increased, probably because males defended their nest less vigorously when they contained illegitimate young. Weatherhead and Boag (1995) assessed the parentage of 617 nestlings from 203 nests in 103 territories. A total of 25.6% of nestlings were extra-pair: 20.1% of young that fledged and 39.2% of those that did not fledge. Approximately 19% of illegitimate nestlings were sired by nonterritorial floaters: 4.9% of all nestlings and 4.3% of those that fledged. Larger males sired more young on their own territories and had higher success at siring extra-pair young. Older males sired significantly more young on other males' territories. Males were consistent in their breeding success on their own territories annually but their success in obtaining extra-pair copulations was not. Male body size was the only secondary sexual trait that affected reproductive success. Large males were more successful because more females nested on their territories and they tended to sire more extra-pair

young. Age was only weakly linked to reproductive success. Large males were more successful on their own territories, but older males were more successful at extra-pair fertilizations. Gray (1977a, 1977b) studied extra-pair copulations in Washington. Females actively sought extra-pair copulations; 17-21% of observed copulations were extra-pair. An average of 30% of females engaged in extra-pair copulations. Thirty-five percent of nestlings were extra-pair and 50% of broods contained extra-pair young. Neighbours sired 111 of 117 extra-pair young (94.9%) and the remainder were sired by nonadjacent territorial males nesting in the same marsh. Females that copulated with neighbours benefitted because the neighbouring male allowed them to forage on his territory. Females that engaged in extra-pair copulations were significantly less likely (32%) to have their nests depredated than faithful females (54%). Males that copulated with a neighbouring female aggressively defended her nest against predators. Age and breeding experience did not influence whether a female engaged in extra-pair copulations. Females appeared to select extra-pair partners based upon their harem size. They benefitted by hatching and fledging a significantly higher proportion of their eggs. They may also copulate with multiple males to ensure fertility of all their eggs because male sperm supplies become depleted as the season advances. Some males are effectively sterile later in the season. There was no evidence that extra-pair copulations were costly to females.

Intraspecific nest parasitism is a rare mating strategy. In some populations, 0.5% of nests contain parasitic Red-winged Blackbird eggs. In other areas, no intraspecific parasitism has been reported (Yasukawa and Searcy 2020). Eggs in an Ontario 7-egg clutch were apparently laid by 2 different females (Peck and James 1987).

The Red-winged Blackbird forages in both aquatic and terrestrial habitats. Those that nest in marshes may forage exclusively in their territories, in both their territories and adjacent uplands, or only in upland areas. Birds are most likely to forage within their territories if they are larger or highly productive, with areas of open water and abundant emerging aquatic insects. Best wetland foraging areas are the outer edges of emergents and shores of marshes where there are no emergents. Shorelines with emergents and interior patches of emergents are inferior foraging areas. Females foraging within marshes are usually confined to their mate's territory, but those who engage in extra-pair copulations with neighbouring males are allowed to forage on their territories. Birds that nest in upland areas have much larger territories that encompass the feeding areas. In addition to marshes with emergent vegetation, birds may feed in meadow marshes bordering cattail marshes, in hayfields, open areas with scattered trees, grain fields, at edges of deciduous woods, in old field and meadow habitats, pastures, prairies, lakeshores with exposed mud, on bare ground, on tree trunks, on floating mats of vegetation, on floating logs and snags, and even on the back of a turtle (Bird and Smith 1964; Gray 1977a; Hurly and Robertson 1984; Nero 1956c, 1984; Orians 1961a, 1980; Orians and Collier 1963; Sinclair et al. 2003; Wiens 1965; Yasukawa and Searcy 2020). In eastern Ontario, females nesting in beaver ponds foraged in forest edges. Those nesting in sewage lagoons foraged mostly in their territories in cattails around the margins of the lagoons, but also on the shorelines (Zimmerling and Ankney 2005). It is a highly versatile forager that can exploit a wide range of food resources. It is adept at feeding in trees and shrubs, can cling to vertical stalks of emergent vegetation, and also forages on the ground. In aquatic habitat, it turns over stones weighing as much as 45 g to reveal stoneflies and fly larvae. It frequently moves floating debris among stones and

aquatic vegetation by a sideways movement of the head and bill. This motion is also used in grasslands to move dead vegetation from the ground and extract spittle bugs from their froth. In cattails and grasslands, it inserts its bill into the vegetation to expose insects and seeds. In trees and shrubs, it gleans among the leaves. It may split open ragweed stalks to expose pupae of the ragweed borer moth. It captures insects on the wing and emerging odonates when they ascend stalks of emergents. It has been observed feeding on insects on Canadian waterweed 2-3 cm below the surface of water. It landed on the waterweed and fluttered with its wings or walked with the legs and tail partially submerged while capturing insects. Foraging may occur in the flowers of water-lilies where it captures flower flies. In New York, females broke tern eggs open and ate the contents. It feeds on white ash seeds by seizing and dropping them and squeezing the fruits to obtain the seeds. It may follow tractors discing or plowing fields to feed on exposed invertebrates, including orthopterans, beetles, caterpillars, and earthworms. It also preyed upon young leopard frogs, and nestling and juvenile voles. As the tractor moved forward, birds at the rear of the flock flew to the front and resumed feeding. While feeding on spittle bugs in a field of sweet clover, it took leaves or small stems into its beak and moved them forward slowly over and past the froth, exposing the bugs. It occasionally flips over cow dung to obtain insects. It obtains seeds by picking them off the ground and may use a double-scratching motion with its feed to uncover food under the litter layer. It occasionally hovers at trees while gleaning caterpillars and may fly as far as 800 m to obtain cankerworms to feed its nestlings. It feeds on white pine seeds and pulls pine seedlings from the ground to eat the seeds. In Wisconsin, birds learned to fly 800 m to visit a zoo where they fed on bread (Beasley and Crothers 1974; Bent 1958; Macklin 1958; Nero 1950, 1984; Orians 1961a; Orians and Horn 1969; Pessino 1968; Richardson 1947; Snelling 1968; Yasukawa and Searcy 2020). Birds quickly learn to avoid unpalatable foods and other flock members learn to avoid these foods more quickly when experienced birds are present (Avery 1994).

The foraging techniques of the Red-winged Blackbird were compared with those of the Western Meadowlark, Yellow-headed Blackbird, and Brewer's Blackbird. There was very little overlap with the Western Meadowlark because it obtains most of its food by digging in the ground. The Red-winged Blackbird forages on the ground, but not by digging. Both the Red-winged Blackbird and Yellow-headed Blackbird are adept at feeding from vertical surfaces of emergents, but the Red-winged Blackbird also forages in shrubs and trees, habitat that is avoided by the Yellow-headed Blackbird. The Yellow-headed Blackbird forages on aquatic prey all day whereas the Red-winged Blackbird forages in upland habitat in the afternoon. Due to their interspecific territoriality and their different foraging habitat preferences in afternoons, these 2 blackbirds are almost always spatially segregated. In addition, they use different foraging techniques in marshes. The Red-winged Blackbird forages swiftly through the vegetation 0.3-0.9 m above the water. The Yellow-headed Blackbird forages near the water line by slowly moving around clumps of cattails and by searching on floating dead vegetation. The Brewer's Blackbird forages mostly by walking on bare ground or over short sedges bordering lakes and streams. It is not adapted to foraging from vertical stalks of emergents. The Red-winged Blackbird has shorter legs and has trouble walking through the short sedges that the Brewer's Blackbird prefers to feed in. In sagebrush, the Red-winged Blackbird readily climbs through the shrubs to forage. The Brewer's Blackbird forages on them by leaping up from the ground or walking on top of them. The Brewer's Blackbird is subordinate to the Red-winged

Blackbird and is not permitted to feed in their territories (Orians 1980; Orians and Horn 1969; Voigts 1973).

In western populations, most male Red-winged Blackbirds do not feed their nestlings and spend their time attempting to attract additional females. In Washington, 1.2-9.3% of males fed nestlings over a 6-year period. Other reported rates of males feeding nestlings in western populations include 0% in upland habitat in Iowa, 6% in Washington, and rare in Michigan, California, New York, and British Columbia. A higher proportion of males feed their nestlings in the east: 46.7-87.5% near Kingston, Ontario, 59% in Indiana, 45.5% and 88% in New York, and 87% in Wisconsin. In both New York and Wisconsin, males rarely fed nestlings in some populations; most males provisioned their young in other populations (Allen 1914; Beletsky and Orians 1990; Blakley 1976; Muldal et al. 1986; Nero 1956c, 1984; Orians and Collier 1963; Patterson 1991; Yasukawa and Searcy 2020). In most populations, males preferentially feed their primary brood and tend to feed secondary broods only if the nest of the primary female fails. Near Kingston, males were equally likely to assist primary and secondary females, but rarely assisted tertiary females. In other areas, nests of primary and secondary females may be asynchronous enough so that the male can provision both sequentially. One male fed at 2 nests simultaneously, alternating trips between nests. Near Kingston, no male assisted more than 2 females on his territory. Nests that were assisted by the male fledged more and a significantly higher proportion of nestlings than unassisted nests. Starvation of the youngest nestling may be common, particularly in larger harems. Starvation seldom occurs in nests where the male feeds the young. Males assist older females with larger broods, selecting females that have the greatest reproductive potential. In Indiana, territories of feeding males were larger and contained more edge interface between open water and marsh vegetation. These areas were much more productive in producing aquatic insects. If the female dies, the male is capable of rearing the brood on his own (Beletsky and Orians 1990; Francis 1975; Muldal et al. 1986; Orians 1980; Patterson 1991; Yasukawa and Searcy 2020). In Michigan, males that were not feeding young began to do so when the brood size was artificially increased. Males that fed young spent less time singing and intruding into other territories, reducing their efforts to acquire additional females and extra-pair copulations (Whittingham 1993). Nesting in many locations is timed so that the period of peak emergence of odonates or grasshoppers coincides with the nestling period. When feeding nestlings, females tended to feed those that were larger, in the best condition, and that begged the loudest. At fledging, male nestlings are 30% heavier and need nearly 30% more energy than females, so this strategy helps sustain male nestlings (Krauss and Yasukawa 2013; Miller 1968; Orians 1961b; Patterson 1991). Males that had fertile mates did not respond to nestling hunger and may withhold parental care at 1 nest to protect paternity at another (Whittingham and Robertson 1993).

In Manitoba, adults foraged for nestlings' food in both marsh and upland habitats. Arthropods in the marsh were significantly larger than those in the upland and the representation of orders of insects differed significantly in the 2 habitats. Nestlings were fed significantly larger prey than were available in both habitats. There was a significantly higher proportion of nymphs and larvae in nestlings' diets than was available in the marsh. The apparent selection for these might be attributed to their soft bodies and their ease of capture (Wilson 1978). The food provided to nestlings in Connecticut consisted of 100% animal matter, predominantly insects with some spiders, molluscs, and miscellaneous items. In marshes, young were fed 55% terrestrial food items (42% caterpillars);

upland young were fed 98% terrestrial food items (26% caterpillars). Aquatic prey comprised 33% of the food items for nestlings in marshes (21% odonates) and 1% in uplands, which were all odonates. Some marsh nestlings had both aquatic and terrestrial prey in their esophagus (Robertson 1973). In New York, nestlings were fed insects almost exclusively, with mayflies, caddisflies, and caterpillars most important in the diet (Allen 1914). Bent (1958) reported that nestlings were fed wireworms, crickets, beetles, grasshoppers, five-spotted hawk caterpillars, and geometer moth caterpillars. In Quebec, Bendell and Weatherhead (1982) studied the diet of nestlings in 2 upland areas. One was in grain, hay, and pasture and the other was along a railway near a river. Nestlings were fed insects from 27 families in 9 orders as well as spiders, isopods, snails, and grain. In every collection of samples, 1 insect order comprised more than 50% of the diet. June samples at both sites were dominated by caterpillars, especially owlet moths, and samples from the area near the river also contained a high proportion of mayflies. Samples collected at the first site 23 July to 2 August differed markedly from the June samples. Caterpillars, mayflies, and beetles were absent in the diet and were replaced by orthopterans and orb-weaver spiders. Females were selective in the prey that they fed their nestlings, preferring passive slow-moving species with no escape reactions. These required a high degree of searching but little active pursuit. The slow-moving long-horned grasshoppers were taken preferentially over the more abundant agile short-horned grasshoppers. The most important prey were herbivorous insects taken from grasses, alfalfa, and clover. Insects that inhabited soil and surface litter were strikingly absent in the diet. It preferentially preyed upon owlet moth caterpillars, the clover leaf weevil, and the European skipper. In Washington, prey delivered to nestlings in a marsh was 76% aquatic invertebrates even though they were not abundant in the environment; the marsh was surrounded by coniferous forest. If spiders were considered aquatic, most of which were taken from emergents, then the diet consisted of 90% aquatic items. The most important prey were beetles (leaf, whirligig, rove, ground, and marsh beetles) followed in order of decreasing abundance by flies (midges, biting midges, crane flies, and flower flies), spiders, lepidopterans (owlet moths, leafroller moths, twirler moths, and snout moths), snails, odonates, soft-winged bugs (froghoppers, aphids, and fulgorid planthoppers), hymenopterans (braconid wasps and sawflies), springtails, green lacewings, stoneflies, millipedes, and annelids. At 1 lake in 1 year, there was limited emergence of damselflies and an unusually high number of nestlings starved (Orians 1980). In an Alabama hayfield, 93.2% of prey brought to nestlings was terrestrial. Soft-winged bugs, mostly froghoppers and leafhoppers, were most prevalent in the diet. Caterpillars were also important, especially owlet moths with some geometer moths. Other prey consumed in small amounts included springtails, adult skimmer dragonflies, short-horned and long-horned grasshoppers, spiders, and snails (Orians 1980).

Voigts (1973) compared the diets of nestling Red-winged and Yellow-headed blackbirds in Iowa. Narrow-winged damselflies were the most important food item for both species all day. For both species, there was increased use of marsh foods and decreased use of upland foods during midday. Narrow-winged and spread-winged damselflies and larval shore flies were selected more between 0900 and 1659 h with fewer treehoppers, aphids, and owlet moths consumed at midday. In addition, they ate leaf beetles, crickets, ground and scarab beetles, snout moths, crane flies, midges, flower flies, anthomyiid flies, and spiders. As the season progressed, the Red-winged Blackbird tended to forage more in marshes and the Yellow-headed Blackbird more in uplands. Before 20 June, owlet

moths gathered in shrubs and trees were the most important prey for the Red-winged Blackbird. Important food items for the Yellow-headed Blackbird at this time included narrow-winged damselflies, larval soldier flies, and adult midges. After 20 June, the Red-winged Blackbird fed less on terrestrial prey and the importance of damselflies and soldier flies increased in the diet. The total overlap in food by volume of the 2 species was 46-49%. The least overlap in diet occurred 0900-1259 when most teneral damselflies were available. The 2 species selected many of the same foods, but at different times during the nesting season. In Washington, Orians and Horn (1969) compared the diets of nestling Red-winged, Yellow-headed, and Brewer's blackbirds. The Red-winged Blackbird ate approximately equal amounts of odonates, flies, and lepidopterans early in the morning. By 1000 h, its diet consisted of 75% odonates with equal numbers of the other groups. At noon, the diet consisted of 40% odonates, 2-3% flies, 30% lepidopterans, and almost 30% other items. At 1600 h, the diet consisted of 20% odonates, 5% flies, 35% lepidopterans, and 35% other items. At 1800 h, the diet consisted of 20% odonates, 30% flies, 20% lepidopterans, and 10% other items. Other items included small snails, spiders, and insects that exhibited no diurnal variations in abundance. The percentages of food items fed to nestlings by Red-winged, Yellow-headed, and Brewer's blackbirds, respectively, were: odonates, 56%, 37%, and 34%; orthopterans, 1%, 2%, and 7%; leafhoppers, 1%, 3%, and 1%; lepidopterans, 4%, 30%, and 24%; flies, 24%, 13%, and 21%; other insects, 7%, 5%, and 7%; spiders, 4%, 7%, and 5%; and other items, 3%, 3%, and 1%. Orthopterans and cicadas were numerically insignificant but contributed a major proportion of the total energy delivered to nestlings. Most of the lepidopterans were very small plume moths and the flies were small so they contributed little energy even though they were eaten in large numbers. Odonates were important in both numbers and calories delivered. The overall diet overlap for all blackbird species was high for all periods of the day, especially during midmorning when all species were feeding almost exclusively on emerging damselflies. The overlap was also high for Red-winged and Brewer's blackbirds in the afternoon when both fed mostly on caterpillars and orthopterans from sagebrush and grasses. Despite the large overlap in prey, competition among the 3 blackbird species was reduced because of partial spatial segregation and differing foraging techniques, and, in the case of the Yellow-headed Blackbird, interspecific territoriality. In 1 spring, there was an invasion of cicadas and they comprised 25% of the energy provided to Red-winged Blackbird nestlings and 10% of the energy for Brewer's Blackbird nestlings. The Yellow-headed Blackbird did not attempt to capture them.

In a Wisconsin marsh, Snelling (1968) compared the diets of nestling Red-winged Blackbirds and Common Grackles. The diet of Red-winged Blackbirds consisted of 92.1% animal matter and 7.9% vegetable matter. Nestling grackles consumed 33.4% animal matter and 66.6% vegetable matter, which was mostly white bread. There were no differences in the mean size of prey items for the 2 species: 10.09 mm for the Red-winged Blackbird and 9.79 mm for the grackle. By volume, the diet of nestling Red-winged Blackbirds consisted of 31.99% owlet moths, 28% geometer moths, 5.76% skimmer dragonflies, 4.95% narrow-winged damselflies, 3.65% soldier flies, 3.17% darners (dragonflies), 2.64% spiketails (dragonflies), and 1.59% fishflies. Small amounts of nematodes, leeches, spiders, isopods, ground and marsh beetles, other lepidopterans (snout, leafroller, and ermine moths), flies (midges and crane, flower, fruit, and bristle flies), and soft-winged bugs were consumed. The vegetation that was eaten consisted of green leaves, bread, and peanut chips. From

11 June to 30 July, locusts (43.21% by volume) and 8.53% brush-footed butterflies, including the red admiral, were important in the diet. By this time, the grackle had completed its nesting. During the period of overlap in the nesting of the 2 species, lepidopterans were most important in the Red-winged Blackbird's diet, with geometer and owlet moths comprising 63.73% of the total volume. Fall webworms comprised 11.32% of the total volume. After the grackle finished feeding its young, locusts, owlet moths and narrow-winged damselflies constituted 62.08% of the Red-winged Blackbird's diet. The change in diet was due to differences in prey abundance and not competition with the grackle. Prey was not limiting for either species and they foraged in different areas so competition was minimal.

The Red-winged Blackbird has a highly diverse diet, yet shows some distinct preferences with these differing in aquatic and terrestrial areas. During the breeding season, it is predominantly insectivorous. In eastern Ontario, birds nesting at sewage lagoons fed predominantly on midges and those at beaver ponds fed mostly on owlet moth caterpillars (Zimmerling and Ankney 2005). McNicol et al. (1982) studied its diet in Frontenac and Leeds counties and collected samples from wetlands in mixed forest and agricultural landscapes. The overall diet was nonspecialized and consisted of 31% corn, 18% weed seeds, 6% oats, 40% insects, 2% other animal matter, and 3% unidentified material. When habitats, sexes, and seasons were considered separately, some specializations were apparent. When males returned in spring, few insects were available and their diet consisted almost exclusively of waste grain and weed seeds. Despite limited amounts of crops in the forested landscape, males were still able to obtain a significant proportion of their diet from waste grain. During the breeding season, both sexes in both habitats dramatically increased their consumption of insects, but waste grain remained an important component of the diet throughout the breeding season. The breeding season diet of males in the agricultural landscape consisted of 51% insects, 42% waste grain, 4% weed seeds, and small amounts of other animal material and oats. Insects were most important during the nestling period, least important during incubation, and of intermediate importance during the fledgling stage. In the forested landscape, males consumed 84% insects, 7% weed seeds, and 3% waste grain with insects most important during the nestling and fledgling stages. Females in the agricultural landscape consumed 67% insects, 21% waste grain, 4% weed seeds, and 4% non-insect animals. Females in the forested landscape ate 79% insects, 9% non-insects, and 8% weed seeds. In Algonquin Park, it feeds on spruce budworms during outbreaks (Tozer 2012). In Manitoba, the June and July diet consisted of 70% animal material in agricultural landscapes and 100% animal material in a large marsh; young were fed animal food exclusively. Differences in food items in different areas were due to local differences in food abundance. Diet in a marsh consisted of 3% vegetation (sunflowers), 96% animal food, and 0.5% grit. The animal food included 37% orthopterans, 14% lepidopterans, 14% beetles, 9% flies, 2% damselflies, 1% harvestmen, a few snails, and 4% unidentified matter (Bird and Smith 1964). Potvin et al. (1976) determined that its overall diet consisted of 23.3% corn, 17.4% barley, and 21.0% beetles in Quebec. From 10 to 19 May, the diet consisted of 46.8% vegetation, 29.1% insects, and 24.2% unidentified: 42.0% grain, 4.8% smartweeds, less than 0.1% sheep sorrel, 2.1% grasshoppers, and 20.7% beetles (weevils and scarab, leaf, click, cedar, and sap beetles). From 14 to 29 July, the diet consisted of 25.6% vegetation, 43.4% insects, and 31.0% unidentified: 24.8% grain, less than 0.1% sheep sorrel, 0.8% dock, 7.9% grasshoppers, 3.9% flies, 8.0% weevils, and 23.6% other beetles (ground, rove, sap, and

click beetles). From 12 August to 16 September, the diet consisted of 61.3% vegetation, 17.3% insects, and 21.4% unidentified: 55.3% grain, 3.6% smartweed, 0.6% sheep sorrel, 1.8% perennial sow thistle, 4.3% snout moths, 4.3% stink bugs, 4.3% aphids, and 4.4% stag beetles. Although it is not the case in all marshes, in Washington and British Columbia, Orians (1980) reported that emerging aquatic insects were the most important prey, and that their abundance was a function of water chemistry, marsh depth and permanence, the types of predators present, and the distribution of emergent and submergent vegetation. The most important prey was damselflies, mostly taken as tenerals as they emerged on stalks of emergent vegetation. These also swim to shore where blackbirds prey upon them and they are easy to capture in upland habitats early in the morning before they become active. Predatory arthropods such as spiders were sometimes major components of the diet, but midges were second in importance to odonates. Mayflies were irregularly abundant and formed a trivial portion of the diet. At 1 lake where there was almost no emergence of odonates or flies, aquatic leaf beetles were a major food item for nestlings. In a New York marsh, the breeding season diet was initially dominated by caterpillars but later by green lacewing larvae, weevils, and other beetles, and finally by aquatic leaf beetles when they constituted 100% of the diet. It ate some fly larvae, spiders, and ground beetles (Allen 1914). In some areas, odonates are the staple of the diet but they are consumed in negligible numbers in other areas. This is probably because most odonate nymphs take at least a year to metamorphose into adults. Permanent wetlands may produce large numbers of odonates; wetlands that dry up may not produce any. Beal (1897a, 1900) examined 1,063 stomachs. Upon arrival in spring, the diet consisted of grubs, caterpillars and other larvae, beetles, cutworms, earthworms, crickets, aphids, and weevils. The nonbreeding season diet consists of 90% vegetation in spring and again in autumn through the winter, with the breeding season diet consisting mostly of animal matter. Later on in the summer, it eats fruits of blackberries, raspberries, gooseberries, snowberry, hackberry, blueberries, wild strawberries, and wild cherries. The annual diet consisted of 73.4% vegetation and 26.6% animal matter, with animal matter comprising 1.4% of the January diet, increasing gradually to 88.2% in June, and dropping to less than 1% in November. Oats were the preferred grain, which constituted 6.3% of the diet, but it also ate corn, wheat, and barley. Grain formed 13.9% of the annual diet; peak consumption was in July and August. Forage crop species such as timothy, sorghum, and clover were unimportant in the diet. Weed seeds were the favourite food item, comprising 54.6% of the annual diet, especially in spring and autumn. Weed seeds comprised only 3% of the June diet. The most abundant weed seeds eaten were those of barnyard grass followed by smartweeds, ragweed, panic grasses, docks, wild rice, paspalum, sunflowers, chickweeds, amaranths, goosefoots, gromwells, and plantains. Some birds were collected while they were picking pine seeds from the tops of trees. One bird each had eaten beechnuts and sedge seeds. Beetles were the most important animal prey, comprising 10% of the diet, with a maximum of 22.4% in June. These were mostly weevils but also included ground, click, leaf, and June beetles. Caterpillars constituted 5.9% of the annual diet, with a maximum of 20% in May, almost 0% in August when grasshoppers were abundant, and increasing again in September. Caterpillars it commonly consumed included armyworms and tent caterpillars. Grasshoppers were important animal foods, constituting 4.7% of the annual diet with a peak of 17% in August. Other animal foods of minor importance included ants, wasps, bugs, flies, dragonflies, spiders, and centipedes. In terrestrial habitat in Manitoba, the diet consisted of 57% vegetation, 35% animal food, and 8% grit in an agricultural landscape.

Vegetation included 23% sunflowers, 6% wheat, 6% oats, 0.5% barley, 2% corn, 1.5% wild oats, 13.5% green foxtail, 1.5% black bindweed, 1% sedges, 1% smartweeds, and 2% unidentified. The animal food included 8.5% grasshoppers, 7% beetles, 3.5% lepidopterans, 3% crickets, 3% ground beetles, 2% flies, 2% spiders, 1% damselflies, traces of snails, and 2% unidentified. Birds from another agricultural landscape with a different mix of crops consumed 58.5% vegetation, 20.5% animal material, and 11% grit. Vegetable matter consisted of 37% wheat, 13% oats, 9% barley, 7% green foxtail, 2% wild oats, and 0.5% sedges. Animal food consisted of 6% beetles, 5.5% orthopterans, 2% ground beetles, 1.0% lepidopterans, 3% unidentified, 1.0% flies, and 0.5% each of harvestmen, damselflies, crickets, and hymenopterans. Wheat and oats were taken mostly as waste grain but were also removed from the ripening heads in the milk and dough stages. Sunflowers were very attractive to it and it concentrated on them from when the kernels formed until the seed coat became too tough to break. Green foxtail seeds were eaten in great quantities, with 984 found in a single stomach (Bird and Smith 1964). The Red-winged Blackbird may eat newts (Bent 1958).

Two studies (Ewald and Rohwer 1982; Wimberger 1988) provided supplemental food in territories to determine the effects of unlimited food. In both cases, supplemental feeding significantly advanced the breeding season suggesting that food availability limits when breeding can commence. At 1 site, harem sizes were significantly larger in territories with supplemental food. In the other area, the supplemental food attracted predators and resulted in higher predation rates and reduced harem sizes because males had to spend more time defending the territory and less time trying to attract additional females.

The Red-winged Blackbird is a common host of the Brown-headed Cowbird. It readily accepts cowbird eggs and incubates clutches comprised solely of cowbird eggs. It also accepts artificial cowbird eggs, strangely coloured artificial eggs, and miniature and over-sized eggs (Ortega and Cruz 1988; Ortega et al. 1993; Ward et al. 1996). In Illinois, Red-winged Blackbirds removed cowbird eggs in 43.5% of nests (Paruk 1992). The Red-winged Blackbird's primary defence against parasitism is to exhibit high levels of aggression toward cowbirds, and it is more aggressive toward female than male cowbirds. Clustering of nests reduced parasitism rates, with nests close to each other less likely to be parasitized than those distant from other nests. Nests where nesting density is high are less likely to be parasitized than those in low-density areas. Nests at the periphery of a colony are more likely to be parasitized and those in upland habitats are usually parasitized at a significantly higher rate than nests in adjacent marshes (Clotfelter and Yasukawa 1999b; Henger and Hauber 2014; Nickell 1955; Ortega and Cruz 1988; Robertson and Norman 1976, 1977; Strausberger 2001; Yasukawa et al. 2016). Nest abandonment is another antiparasitic behaviour. Females typically abandon the nest if a cowbird lays an egg in the nest before it contains any blackbird eggs. In Wisconsin, nest abandonment rates were significantly higher for parasitized than unparasitized nests. No nests were abandoned if they were parasitized after the blackbird clutch was complete (Clotfelter and Yasukawa 1999c; Yasukawa and Searcy 2020). One Ontario nest had a cowbird egg buried in it (Peck and James 1987). Parasitism reduces the reproductive success of the Red-winged Blackbird, with parasitized nests having significantly smaller clutch sizes and fledging significantly fewer young. The smaller clutch size is due to direct removal of eggs by the cowbird and cracking of blackbird eggs. Eggs may be cracked by the thicker-walled cowbird eggs rolling around in the nest or by the female blackbird inadvertently damaging her eggs while trying to strike a cowbird

egg. Females that abandon their nests due to parasitism and renest raise fewer fledglings than they would have if they had incubated their original clutches. This is due to lower nesting success later in the season. Later nests are less likely to be parasitized because the cowbird laying season ends earlier than that of the Red-winged Blackbird. In some cases, the female cowbird does not remove an egg, resulting in a higher than normal clutch size. Larger clutches may be inefficient to incubate, resulting in lower fledging rates. The cowbird may also destroy eggs and nestlings in unparasitized nests, presumably to prompt the bird to renest and offer an opportunity for parasitism (Blankespoor et al. 1982; Clotfelter and Yasukawa 1999c; Granfors et al. 2001; Orians et al. 1989; Ortega and Cruz 1988; Rivers et al. 2010: Yasukawa and Searcy 2020). Parasitism rates of 0-74% have been reported. Parasitism rates may vary considerably at a given site annually. There are many factors that affect parasitism. Low parasitism rates in marshes along an interstate highway in Illinois were attributed to a lack of nearby suitable foraging habitat for the cowbird. In South Dakota grasslands, the odds that a nest would be parasitized decreased by 6% for every 1% increase in tree cover within 1 km. Bird densities were higher in wooded areas and provided a higher density of potential hosts. In the same state, marshes with a high edge to area ratio had higher parasitism rates. Cowbird density also affects parasitism rates with higher rates where the cowbird is more abundant (Besser et al. 1987; Blankespoor et al. 1982; Galligan et al. 2006; Linz and Bolin 1982; Paruk 1992; Pietz et al. 2009; Yasukawa and Searcy 2020). Peck and James (1998b) reported that 170 of 6,554 Ontario nests (2.6%) were parasitized. Near Kingston, 49 of 2,039 nests (2.4%) were parasitized (Robertson and Norman 1976). In Wisconsin, 222 of 1,320 nests (16.8%) were parasitized including 24.8% at a wet-mesic prairie and 14.3% in an old field (Clotfelter and Yasukawa 1999c) and 18% of nests at another Wisconsin site were parasitized (Yasukawa et al. 2016). In Illinois, 46 of 356 nests (12.9%) in marshes along an interstate highway were parasitized (Paruk 1992); Strausberger (2001) reported that 52 of 139 nests (37.4%) in upland habitats were parasitized compared with 2 of 101 nests (2.0%) in marshes. In Michigan, 7 of 1,300 nests (0.5%) were parasitized (Nickell 1955), 0 of 35 New York nests were parasitized (Hahn and Hatfield 1995), 4 of 263 Indiana nests (1.5%) were parasitized (Galligan et al. 2006), 40 of 309 nests (12.9%) at natural wetlands and 0 of 34 nests at restored wetlands in Iowa were parasitized (Delphey and Dinsmore 1993), 2 of 239 Maryland nests (0.6%) were parasitized (Burhans et al. 2010), 2 of 73 nests (1.6%) in South Carolina and Georgia were parasitized (Kilgo and Moorman 2003), and 12 of 755 nests (1.6%) in Louisiana were parasitized (Brown and Goertz 1978). Parasitism rates tend to be higher in the west where the cowbird is more abundant: 109 of 258 nests (42.2%) in North Dakota (Linz and Bolin 1982), 186 of 873 nests (21.3%) in Kansas (Rivers et al. 2010), 14 of 19 nests (73.7%) and 14 of 34 nests (41.2%) in South Dakota (Blankespoor et al. 1982), 0-40.9% in Colorado (Ortega and Cruz 1991), and 18 of 1,416 nests (2.0%) and 29 of 258 nests (11.2%) in British Columbia (Campbell et al. 2001).

There are 2 cases of the Yellow-billed Cuckoo parasitizing the Red-winged Blackbird. The blackbirds accepted cuckoo eggs and fed the cuckoo nestlings. In 1 case, the cuckoo nestling appeared to have fledged. The other nest was depredated (Nickell 1954; Yasukawa 2010).

The Red-winged Blackbird has experienced loss and degradation of both its aquatic and upland nesting habitats. Wetlands may be drained and filled to improve agricultural production and fragmented by roads and other infrastructure. It has been estimated that 70-80% of the original wetlands in southern Ontario have been lost. Loss of wetlands is a universal problem in its range. In

some areas most of the population breeds in upland habitats due to the scarcity of wetlands. Marshes are dynamic ecosystems and their balance is easily upset. Water levels define the extent and configuration of emergent vegetation and they fluctuate naturally seasonally. When this process is altered, water levels may become too deep or shallow to support productive populations of emergents. When water levels are too high, emergents may be drowned out. When they are too low, the emergents become dense monotypic stands without the openings that this blackbird prefers. If there is no standing water beneath the emergents, fewer birds nest in them and those that do have reduced reproductive success due to better access for predators. Introduction of carp into wetlands greatly reduces their quality. Carp uproot aquatic vegetation and result in reduced populations of aquatic invertebrates. Turbidity from stormwater and runoff from fields and roads reduces light penetration into wetlands, killing submergent vegetation and decreasing the abundance and diversity of aquatic insects (Graber and Graber 1963; Jobin and Gauthier in Gauthier and Aubry 1996; McCracken 2003b; Orians 1980; Weller and Fredrickson 1973; Weller and Spatcher 1965; Yasukawa and Searcy 2020).

European settlers created upland habitats that provided suitable nesting habitat for the Red-winged Blackbird. Initially, these were predominantly hay and pasture fields with some fields planted to cereal grains. The composition of the agricultural landscape has changed considerably, with most lands that were in forage crops being converted to small grain and corn fields. Corn and soybeans are now the dominant crops in southern Ontario, with lesser amounts of small grain crops and limited areas in pasture and hay. Most hayfields are now alfalfa rather than the original hay crops of grasses and clovers. Alfalfa fields are not particularly suitable for nesting for this blackbird. CRP and DNC fields provide nesting habitat, but they are typically sinks, and early mowing of hayfields greatly reduces productivity (Jobin and Gauthier in Gauthier and Aubry 1996; Walk et al. 2011; Yasukawa and Searcy 2020). Clark and Weatherhead (1986) and Clark et al. (1986, 1988) chronicled the population changes of the Red-winged Blackbird in the St. Lawrence River valley in eastern Ontario and western Quebec and related them to the crops that were grown. The greatest increase in this species in North America for 1966-76 occurred within this area. During this period, there were significant changes in Quebec including a decline in the area planted to hay and oats and an increase in corn, wheat, and barley. The only significant change in Ontario was a decrease in oats. There was a clear association between the abundance of the Red-winged Blackbird and cereal grains, particularly corn, which provides energy in the form of waste grain through spring and summer. The sole function of cornfields is to provide food; they are not used for nesting. Where hayfields are common but corn production is limited, the population is limited by food. Where cornfields are common, food is abundant but breeding sites are scarce. At some intermediate mix of hay and corn, production should be at its maximum. Further corn production may lead to declines in Red-winged Blackbirds and these declines have already started.

Mowing of hayfields is detrimental to the Red-winged Blackbird. In Michigan, breeders remained in their territories more than 48 hours after mowing but did not establish territories or attempt to nest in cut fields after the vegetation grew back (Albers 1978). In Iowa, birds did not recolonize alfalfa fields after they were cut. By the time the vegetation had re-established itself, its nesting season was over (Frawley and Best 1991). In Arkansas, cutting hay early (26-31 May) had a strong negative effect on nest survival with no nests surviving. The effects of late haying (17-26 June)

were trivial (Luscier and Thompson 2009). In Maryland, mowing destroyed most nests (Fankhauser 1964). In Nebraska, grazing had no apparent effects on it (Kim et al. 2008).

Agricultural chemicals may have adverse effects on the Red-winged Blackbird. Several were found dead adjacent to a North Carolina cornfield where carbofuran had been applied (Augspurger et al. 1996). Myers et al. (1990) administered a single dose of methyl parathion, an organophosphorus insecticide, to free-living females attending their nests. It caused ataxia, lacrimation, and lethargy, and significantly depressed cholinesterase activity, but there were no apparent effects on reproduction. There were no significant differences in weights of nestlings of treatment and control females. There were no significant differences in return rates of females by treatment in the next year: 5 of 11 controls (45.5%), 6 of 6 birds (100%) given a low dosage, and 6 of 12 (50.0%) given a high dosage returned.

Where the 2 species are sympatric, the Marsh Wren is a significant predator of Red-winged Blackbird nests. Wrens peck eggs and nestlings and may cause complete brood failures. Blackbird nest success is significantly lower for nests closer to a wren nest and significantly higher for nests closer to an active blackbird nest. Proximity to a wren nest may be a factor that females consider when selecting a mate. In Washington, all Red-winged Blackbird nests in Marsh Wren territories failed. Blackbirds nesting with wrens may reduce their impacts by both sexes aggressively attacking them, nesting in sparse vegetation where it is easier to defend against the wrens, females nesting in a clumped pattern to better protect nests, and females selecting older, more experienced males thereby increasing their potential nest success. Protection against the Marsh Wren may be another reason for females to nest polygynously (Milks and Picman 1994; Orians and Willson 1964; Picman 1980a, 1980b, 1981; Picman et al. 1988).

Red-winged Blackbirds may be affected by the amount of rainfall received and temperatures. Rainfall determines how many wetlands there are in the landscape, water depths in wetlands and consequently the distribution of aquatic plants, and the permanence of ponds and the resulting aquatic invertebrate populations they support. In North Dakota, its abundance was positively correlated with the number of ponds present in the current and previous years (Niemuth et al. 2008). In the Prairie Pothole Region of Canada, its abundance was strongly affected by the previous year's precipitation and spring temperature. Below-average temperatures affected nesting success because of exposure and a reduction in food supplies (Forcey et al. 2007). In California, clutch size was significantly lower in dry seasons and declined throughout the season (Fletcher and Koford 2004). In Nebraska, its abundance varied significantly with drought indices, but there were no clear trends. It appeared to decrease with increasing wetness, but only slightly (Kim et al. 2008). Heavy rains early in the season may result in nests being flooded (Campbell et al. 2001).

In Minnesota, Hanowski et al. (1977b) applied methoprene and Bti to cattail marshes to control mosquito larvae. There were no apparent effects on the Red-winged Blackbird. In North Dakota, Linz et al. (1996) treated 50%, 70%, and 90% of wetland areas with glyphosate to control cattail growth and reduce numbers of breeding Red-winged Blackbirds. Two years post-treatment, density was higher in control wetlands than in 90% treatment wetlands, but not significantly. Its abundance was positively correlated with the percent coverage by live vegetation during the 2 post-treatment years

and negatively correlated with the percent coverage by dead vegetation in the year following treatment.

Status

The Red-winged Blackbird has always been common to abundant in Ontario. McIlwraith (1894) stated that it bred throughout the province. Baillie and Harrington (1937) considered it common in suitable marshy areas from the southern portion of the province north to at least the transcontinental railway and west to western Kenora District. A specimen from Moose Factory suggested that its breeding range extended northward to James Bay. The first atlas revealed that its range extended from the south northward to include the entire Boreal Forest Region and it also occurred in the Hudson Bay Lowland along the west shore of James Bay north of Akimiski Island. It was observed in every square south of the Canadian Shield and in most squares in the Shield portion of the Great Lakes–St. Lawrence Forest Region. It was abundant in agricultural landscapes, becoming uncommon to rare north in the Boreal Forest Region (Weatherhead in Cadman et al. 1987). James (1991) considered it an abundant summer resident in the south, locally common in the north to Sandy Lake and Moosonee, and rare north to Hudson Bay.

The second atlas indicated that there had been no substantive changes in the range of the Red-winged Blackbird since the first atlas. It was documented in a few more blocks in the Hudson Bay Lowland but not in some blocks in the northern Boreal Forest Region where it was present during the first atlas. Its probability of observation declined significantly since the first atlas province-wide and in the Great Lakes–St. Lawrence and Boreal Forest regions. It experienced a nonsignificant decline in the Carolinian Forest Region and a nonsignificant increase in the Hudson Bay Lowland. It was most abundant from southwestern Ontario north and east through Cornwall and the Ottawa Valley. Lower densities occurred in urban Toronto where there are few wetlands and along the heavily forested Niagara Escarpment. Some of the highest densities occurred at sewage lagoons where there is an abundance of insects. Densities dropped off sharply in the Canadian Shield and areas further north (Zimmerling in Cadman et al. 2007).

During European settlement, the population of the Red-winged Blackbird probably declined initially due to wetland drainage and market hunting. The population increased significantly when it adapted to nesting in upland habitats. Populations are now declining due to habitat loss, changes in land use and management practices, climate change, and efforts to control its depredation on crops. It is still the most abundant bird species in North America, with the population estimated at 100-400 million. According to the Breeding Bird Survey (BBS), the Ontario population peaked in 1976 and has been declining significantly since. During 1966-2015, the North American population declined at a significant rate of 0.93% annually with the negative trend more pronounced in the east (McCracken 2003b; Yasukawa and Searcy 2020; Zimmerling in Cadman et al. 2007). BBS data indicate that it decreased at annual rates of 0.11% in Canada and 0.845% in Ontario 1970-2021. Trends for 2011-21 were an annual increase of 1.83% in Canada and an annual decrease of 1.11% in Ontario. All results were highly reliable (A.C. Smith et al. 2023). In Great Lakes coastal wetlands, it increased at an annual rate of 3.8% 2011-21 (Tozer et al. 2024).

POSTFLEDGING PERIOD

Fledglings remain in the marsh for approximately 2 weeks during which time they may be fed by both adults. In Washington, only 1.1-11.7% of males fed their fledglings in each year; 24.1% of males that fed their nestlings also fed the fledglings. After 2 weeks, fledglings are led to uplands by the female where she feeds them for another 2 weeks. In 1 case, the youngest fledgling was too small and weak to leave the territory. It remained in the territory and was fed by the male (Beletsky and Orians 1990; Nero 1956c, 1984; Nero and Emlen 1951; Orians 1961a; Yasukawa and Searcy 2020). After independence, juveniles join flocks with older females; males remain in discrete flocks. At this time, juveniles forage in uplands during the day and roost in marshes at night. During the moult, juveniles may remain in marshes all day. Later in the season, juveniles form roosts with adults of both sexes (Yasukawa and Searcy 2020).

The sexes segregate as soon as the female leaves the territory with the young and they remain in separate flocks during the postfledging period into autumn migration. Juveniles initially occur in flocks of females, but later may join male flocks, and male flocks may include scattered females. Most birds move into agricultural landscapes at this time. Marshes surrounded by forests may be completely abandoned but those in agricultural landscapes may be used as night roosts by flocks. In Matchedash Bay and the Kingston area, large flocks form in mid-July and are present in the St. Lawrence River valley by late July. In Presqu'ile, flocks occur as early as late June. Flock sizes are initially small but quickly swell and remain large until they gradually diminish during autumn migration. Most birds disperse in late October or early November. At Presqu'ile, flocks abandon the park by mid- to late August and move to surrounding cornfields. Most leave Algonquin Park in August to seek more favourable foraging areas (Clark et al. 1986; LaForest 1993; McNicol et al. 1982; Nero 1984; Somers et al. 1981; Tozer 2012). During the moult in August, birds may remain in marshes all day and hide in dense emergents until they replace their tail and flight feathers (Bent 1958; Bird and Smith 1964; Nero 1984; Orians 1961a; Yasukawa and Searcy 2020).

Postbreeding flocks congregate in large roosts overnight. To be suitable, roosts must be within a few kilometres of abundant food sources. At Matchedash Bay, birds fed in areas as far as 13 km from the roost. In California, birds flew as far as 32 km from the roost to forage. Marshes with emergent vegetation are preferred roost sites. In Ontario, they are typically dominated by cattails or common reed. Marshes are preferred elsewhere as well, with cattails and common reed preferred but wild and cultivated rice and bulrushes are also used. A major requirement of roosts is that they must offer dense cover. Roosting habitat may also include deciduous thickets and coniferous stands. Roosts may contain other species of birds, particularly European Starlings, Brown-headed Cowbirds, and Common Grackles. At a roost in Niagara Region, all these species roosted with the Red-winged Blackbird along with swallows and a few Rusty Blackbirds. Large roosts in the Matchedash Bay and Kingston areas routinely support as many as 100,000 birds. Individual roosts in the southeastern United States frequently support several millions of birds, particularly in autumn and winter (Besser et al. 1987; Bird and Smith 1964; Black and Roy 2010; Brugger 1988; Brugger and Dolbeer 1990; Joyner et al. 1980; Orians 1961a; Short 1985; Somers et al. 1981; Weir 2008; Yasukawa and Searcy 2020).

Each day birds fly from the roost to foraging areas that are predominantly agricultural fields. At the Matchedash Bay roost, there was a progression in the use of habitats from 16 July until the fourth week of September with the use of cornfields becoming increasingly important throughout the summer. Sightings in pastures, wheat stubble, and other fields were infrequent after the first week of August. Oat fields were important foraging areas from mid-July to mid-August. The Red-winged Blackbird visited wheat stubble fields but not those in which winter wheat was growing. Adult and juvenile males were frequently seen together. Males were active at mean distances of 3.2-4.4 km from the roost. Two males moved 3.9 and 7.6 km to new foraging areas. Some birds were sighted as far as 13 km from the roost. In morning, birds moved directly from the roost to foraging areas. Movements of the sexes were similar. There may be a large turnover of individuals foraging in a given field (Somers et al. 1981). At a California roost, birds left the roost early in the morning but returned to the marsh after the morning feeding and made another major feeding flight in mid-afternoon before returning to roost overnight. There was steady movement in and out of the roost, with individuals probably feeding at least once a day in addition to the 2 major feeding flights (Orians 1961a). Birds store food in the gullet on foraging trips, presumably for consumption during the night (Bird and Smith 1964).

Dolbeer (1978, 1982) summarized banding recoveries of the Red-winged Blackbird during the postfledging period. It was fairly sedentary in the Great Lakes area and the Midwest, but in New England, it often moved 200-350 km from the nesting area by August.

During the postfledging period, the Red-winged Blackbird switches from a predominantly insectivorous diet to one dominated by vegetable matter, particularly agricultural crops. In Frontenac and Leeds counties, oats were briefly exploited in late July, then replaced in the diet by corn and weed seeds, with males concentrating on corn and females on weed seeds. By the time they migrated in October and November, the diet was similar to that observed immediately following spring arrival. During early postbreeding and autumn flocking, the male diet consisted of 56% corn, 24% seeds, 11% insects, 5% oats, and some waste grain and other vegetable matter. The female diet consisted of 44% weed seeds, 28% corn, 15% insects, and 10% oats. Eighty to 90% of the insects that were consumed were injurious to agricultural crops. Few insects contributed more than 5% of the diet and only forest tent caterpillars and tawny-edged skippers constituted more than 20% of the diet. Insects that contributed 5-20% of the diet included weevils, leafhoppers, and froghoppers. Insects comprising less than 5% of the diet included click beetles, scarab beetles, leaf beetles, long-horned beetles, flat bark beetles, geometer moth caterpillars, owlet moth caterpillars, corn borers, aphids, flies, chinch bugs, and short-horned grasshoppers. The percentage of the total number of seeds consumed by males and females, respectively, was: foxtails, 19% and 59%; barnyard grass, 4% and 19%; smartweeds, 6% and 3%; gromwell, 4% and 0%; chicory, 0% and 1%; American three-square bulrush, 34% and 9%; water-lily, 6% and 0%; and traces of quack grass, chickweed, common dandelion, panic grass, redroot amaranth, and lamb's-quarters. At no time during their 8-9 month residency in eastern Ontario did grain comprise less than 25% of the diet. Males appeared to be responsible for most of the crop damage. Females are much more likely to be beneficial because they eat less grain and more weed seeds, are more abundant, and also prey on insects to feed nestlings and fledglings (McNicol et al. 1982). In Oxford County, the Red-winged Blackbird commonly fed on the seeds of giant ragweed during the postfledging, autumn migration, and

winter periods. Flocks as large as 600 were seen suggesting that it may be a valuable source of food (Dance et al. 2012).

Considerable research has been undertaken on Red-winged Blackbirds foraging in cornfields and the damage it inflicts on both sweet and field corn. It feeds extensively on the northern corn rootworm, a serious pest that may be abundant in silky tassels and leaves. It also preferentially feeds on the European corn borer by slitting open the husks and removing them from infected ears. It is attracted mostly to fields that support these pests and feeds heavily on them in the period before the corn is ripe. Fields infested with these insects are more likely to sustain crop damage from blackbirds because birds continue to visit these fields once the corn crop ripens. Field experiments demonstrated that corn in plots treated to kill these insects is less likely to suffer blackbird depredation than untreated plots in the same field. The apparent benefit from blackbirds feeding on these insects is outweighed by the damage they do later to the crop. In Quebec, the reduced density of corn borers due to predation by blackbirds only compensated for about 20% of the damage that they inflicted. Approximately 1% of the entire North American corn crop is destroyed by the Red-winged Blackbird, predominantly in localized areas, mostly within 8 km of a roost. Fields close to a roost may sustain 5% or more damage. Fifteen days after silking, corn kernels enter the milk stage and this is when they are first vulnerable to blackbirds. Field corn is allowed to mature and dry, so it is vulnerable for several weeks. Sweet corn is usually harvested 16-20 days after silking, so it is vulnerable for only a few days. Red-winged Blackbirds feeding in cornfields during the silking period should be considered beneficial but management may be required during the milk stage. In North Dakota cornfields, males ate more corn and less foxtail seeds than females. Aphids were the most prevalent animal prey in cornfields, followed by spittle bugs, green lacewings, and spiders. Most damage to corn crops is by males (Bendell et al. 1981; Bernhardt et al. 1987; Bollinger and Caslick 1985; Dolbeer 1990; Linz et al. 1984; Straub 1989).

The Red-winged Blackbird may inflict serious damage to sunflower crops. Odds of a field receiving damage were 2.1-3.9 times higher in 2 years for fields adjacent to marshes than for fields distant from marshes. Birds avoided fields with plowed fields adjacent to them if no wetlands were present. If wetlands were present, this cancelled out the negative effects of plowed fields (Otis and Kilburn 1988). In North Dakota sunflower fields, more than 75% of bird damage occurred in the first 18 days after antithesis and then gradually decreased until harvest. Forty percent of damage occurred 3-4 days after antithesis. Soft seeds received 86% of the damage indicating that this stage was preferred (Cummings et al. 1989). In North Dakota sunflower fields, there was no difference in the diets of adults and juveniles. Males ate significantly more sunflower seeds and fewer foxtail seeds than females. From 12-25 August, males in sunflower fields ate 25% animal matter compared with 28% for females. In the following 10 weeks, animal matter comprised only 4% of the male diet and 5% of the female diet. The animal food included 20% beetles, 16% aphids, 13% leafhoppers and spittlebugs, and 6% green lacewing larvae. Weevil larvae were commonly consumed from 23 September to 20 October. Males were largely responsible for damage to sunflowers (Linz et al. 1984).

In Oklahoma, Goddard (1969) studied the diet of the Red-winged Blackbird in sorghum crops. The percent occurrence of food items was 93% sorghum, 75% ragweed, 36% insects, 36% sunflower seeds, 24% Johnson grass, 10% foxtails, 10% lamb's-quarters, 10% amaranths, 7% croton, 5% panic

grass, 2% sand dropseed, 2% grama grass, and 1% each smartweed, bush-clover, and bluestems; 11% of material was miscellaneous or unidentified. Sorghum crops harvested by mid-October sustained little damage but considerable damage occurred when the harvest was delayed due to poor weather. In California, it concentrated its foraging in late summer on seeds of barnyard grass. It also feeds on rice seeds that are coming into the milk stage at this time. Considerable damage to rice crops is sustained then. They continue to feed on it until it is harvested and on waste grain after harvest. The Red-winged Blackbird also forages in newly sprouting alfalfa fields where it captures insects (Orians 1961a). In New York before agriculture consisted of extensive monocultures of row crops, the diet consisted of 82% vegetable matter, with aquatic leaf beetles and weevils dominating the animal prey. The vegetable matter was dominated by seeds of yellow foxtail with lesser amounts of ragweed, bindweed, and other grass seeds. Later in autumn, the food consumed in upland areas was almost 100% vegetation, mostly foxtail and ragweed seeds with a little grain (corn, wheat, and oats; Allen 1914)).

Because of its crop depredation, the Red-winged Blackbird is considered a serious agricultural pest. The most significant limiting factor to it during the postfledging, autumn migration, and winter periods is mortality due to humans. In the days of the early settlers, many states offered a bounty for killing it. Other jurisdictions ascribed a quota to landowners who were fined if they did not kill enough Red-winged Blackbirds (Allen 1914; Beal 1897a). An amendment to the 1918 *Migratory Birds Convention Act* allowed both lethal and nonlethal control of blackbirds to protect resources such as ornamental or shade trees, crops, livestock, or wildlife and human health. Lethal control methods included dynamiting, shooting, trapping, poisoning with pesticides and avicides, and spraying with surfactants. Surfactants are detergents that cause the birds' feathers to lose their waterproofing ability. Following aerial spraying of surfactants, bird roosts were sprayed with cold water resulting in them dying of exposure. From 1974 to 1992, 38.3 million birds were killed using surfactants, 13% of which (5 million) were Red-winged Blackbirds. DRC-1339 was a nonpersistent organochlorine pesticide that shuts down liver and kidney functions. It was applied as bait on the ground or seeds were coated with it. Millions of Red-winged Blackbirds were killed with this chemical. Largest kills occurred at winter roosts. Because birds from a wide geographic area were represented at winter roosts, these massive kills had no apparent effects on any breeding populations. The use of surfactants and DRC-1339 has since been discontinued, but millions are still killed each year (Bent 1958; McCracken 2003b; Yasukawa and Searcy 2020).

Several nonlethal control methods have been attempted. These include habitat management, integrated pest management, bird-resistant sunflowers, decoy crops, chemical frightening agents and repellents, mechanical scaring devices, propane exploders, chemosterilants to lower reproduction, and Avitrol, a chemical that causes birds to behave abnormally and emit distress calls when they ingest it. Most of these methods are time consuming and ineffective and often cost more to implement than the value of the crop that is damaged. Cost-benefit analyses suggest that local control may be effective only for the most damaged fields (Dolbeer 1990; Yasukawa and Searcy 2020). In Simcoe County, Joyner et al. (1980) tested the effectiveness of methiocarb as a repellent in field corn. It was ineffective, with approximately 75% of ears damaged in both treated and untreated areas. The overall mean damage per ear was 29% for treated corn and 30% for untreated corn. The costs of applying methiocarb exceeded the benefits.

MIGRATION

Most populations of the Red-winged Blackbird are migratory but some in the western United States and along the Gulf Coast are resident. Those breeding in the Great Lakes region travel approximately 1,200 km to their wintering grounds. Adult females migrated 187-300 km further south than adult males (mean 247 km). Juveniles migrated 200-350 km further than adult males, about the same distance as adult females. Southern Ontario birds overwinter in Alabama, Georgia, South Carolina, and Florida. Ontario birds also winter in coastal and adjacent states from Maryland south to Florida (Brewer et al. 2018; Dolbeer 1978, 1982; Yasukawa and Searcy 2020). Burtt and Giltz (1974) analyzed 10,664 banding recoveries. Birds in the Atlantic Flyway flew southwest, those in the Mississippi Flyway flew south, and those in the Central and Pacific flyways flew south and southwest. Those in the first 3 flyways wintered mostly along the north coast of the Gulf of Mexico. Knittle et al. (1987, 1996) analyzed spring migration from winter roosts in Missouri, South Dakota, and Minnesota. Birds from Missouri travelled through a broad corridor from eastern Montana to eastern Wisconsin, a distance of about 3,000 km. Breeders from this roost were also found in east-central Alberta, southern Manitoba, and southwestern Ontario. These birds dispersed over an area of about 18,000,000 km^2. Many South Dakota birds nested locally and dispersed over a smaller area of 405,000 km^2, to east-central Alberta, central Saskatchewan, and Manitoba. Most birds from Minnesota concentrated in southern Saskatchewan, northeast North Dakota, and northwest Minnesota. Distances travelled from the South Dakota and Minnesota roosts were 856-1,093 km. It is a diurnal migrant that tends to move in flocks smaller than 100 birds (Yasukawa and Searcy 2020).

In the western United States, spring migration was correlated with the 1.7°C isotherm (Dolbeer 1978, 1982; Miller 1968; Yasukawa and Searcy 2020). In Wisconsin, males arrived over a period of 9-43 days per season (mean 29.2 days). Arrival dates of individual males varied as much as 20 days over the years (average 13.6 days). Certain males were consistently early arrivals; others were consistently late. Males that previously held territories at the site were usually the first to arrive (Nero 1956a, 1984). Males usually arrive 1-3 weeks before females. Yearling males usually do not arrive until adult birds have initiated nesting and yearling females may not arrive until a week after yearling males (Bent 1958; Bird and Smith 1964; Devine 1975b; Nero 1984). In Michigan, the time lag between male territory establishment and arrival of females on territories varied by habitat: at least 4 weeks for pastures; 1-3 weeks for old hayfields, old fields, and wetlands; and females arrived as soon as males established territories on new hayfields (Albers 1978). At a spring roost at Beauharnois, Quebec, the population was almost exclusively males in late March but there was equal representation of the sexes by the end of April. In late March, the male population consisted almost entirely of adults but yearling males predominated in late April. Territorial males became established in marshes at the same time that representation by adults in the roost declined (Greenwood and Weatherhead 1982). Allen (1914) broke spring migration into 7 periods in New York: arrival of vagrants, migrant adult males, resident adult males, migrant females and yearling males, resident adult females, resident yearling males, and resident yearling females. Vagrants arrived in February when marshes were still frozen and there was snow on the ground. The first true migrants were adult males that arrived an average of 13 days after the vagrants. They stopped briefly then continued migrating. Migrant males continued to arrive for about 2 weeks and then the resident breeding males arrived. The first migrant females and yearling males arrived a few days before the resident females; the first females travelled

with adult and yearling males. As numbers of females increased, flocks comprised solely of females occurred. Resident adult females arrived in the early part of the first week of April, yearling males arrived around the first week of May after most adult males had begun nesting, and yearling females began to arrive around mid-May.

In southern Ontario, the Red-winged Blackbird arrives in mid- to late February. Larger numbers arrive after the first week of March and waves of migrants continue to arrive through May. Females usually do not arrive until early April (Curry 2006; Hurly and Robertson 1984; LaForest 1993; Lancaster et al. 2004; Weir 2008). Birds arrive in the St. Lawrence River valley in eastern Ontario in late February or early March but do not disperse to territories until early May (Clark et al. 1986). Arrival in the southern Shield is in mid- to late March (Mills 1981; Tozer 2012).

At Delta Marsh in Manitoba over a 63-year period, the Red-winged Blackbird arrived significantly earlier in later years in response to warmer temperatures (Murphy-Klassen et al. 2005).

Autumn migration to wintering roost areas does not begin until October, and most birds arrive on the wintering grounds in November. Males migrate later than females in autumn (Dolbeer 1978; Yasukawa and Searcy 2020). Most leave the southern Shield by mid-November. Birds may remain at feeders into late November or the first week of December (Mills 1981; Tozer 2012). Migration out of the St. Lawrence River valley is nearly complete by early November (Clark et al. 1986). Most leave the Kingston area in early November (Weir 2008). In the Hamilton area, large numbers are recorded in early November and late migrants may occur until early December (Curry 2006). In Elgin County, autumn migration is evident from late October to mid-November when mixed flocks of thousands of blackbirds migrate westward along the Lake Erie shoreline (Lancaster et al. 2004).

During spring migration, the Red-winged Blackbird mostly inhabits marshes and other habitats typical of breeding habitat. It may visit parks and gardens, stubble fields, beaches, small islands, wet fields, airfields, and pipeline rights-of-way to forage (Campbell et al. 2001; Sinclair et al. 2003). During spring migration in Pennsylvania, it was significantly more abundant in shrubby habitat than in forests (Smith and Hatch 2008). In Wisconsin and Minnesota, it was significantly more abundant in mature floodplain forests than mature upland forests during spring migration (Kirsch et al. 2013). During autumn migration, the habitat that is used is the same as during the postfledging period, with birds concentrating in agricultural fields to feed.

Roosts are important during spring migration. In some areas, the Red-winged Blackbird simply roosts in the marshes that are subsequently used for breeding. During the day, they spend most of their time away from the marsh foraging in upland habitats. The sexes may roost together but tend to segregate early in the season (Orians 1961a; Orians and Collier 1963; Yasukawa and Searcy 2020). In some areas, large numbers of Red-winged Blackbirds, often in the company of starlings, cowbirds, and Common Grackles, form large spring roosts before nesting commences. At Beauharnois, the roost area was devoid of birds in mid-March, built up to a peak population of about 100,000 birds on 9 April, and continued to be used until at least late May when observations were terminated. The population gradually declines as birds move to their territories (Greenwood and Weatherhead 1982). Roosting habitat usually consists of marshes with emergent vegetation, particularly cattails and common reed (Greenwood and Weatherhead 1982; Orians 1961a). In Kansas, spring migrant flocks roosted in tall grass (Fitch 1958). Roosts used during autumn migration are similar to those used

during the postfledging period. Many postfledging roosts continue to be used through migration with migrating birds joining postfledging flocks in roosts.

During spring migration, the Red-winged Blackbird commonly visits bird feeders to obtain seeds. Before insects are abundant, waste grain may form a large proportion of the diet. Once insects are plentiful, it quickly switches to an insectivorous diet, with most prey captured in upland habitats. In New York during spring migration, the diet of birds feeding in uplands consisted of 66% vegetable matter and 34% animal matter. Seeds of yellow foxtail and common ragweed were the most important vegetable foods, with traces of corn and rye. The animal food was dominated by caterpillars followed by ground beetles, centipedes, grasshoppers, and other insects. Food obtained in marshes consisted of 19% vegetation (all cutgrass seeds) and 81% animal food. Weevils were the most important animal prey followed in order by caterpillars, ground beetles, spiders, centipedes, and fly larvae (Allen 1914). During spring at Presqu'ile, it feeds on flooded lawns and in the marsh (LaForest 1993). In September and October in Algonquin Park, it commonly forages with other blackbird species in areas such as campgrounds, clearings, and marshes (Tozer 2012).

James (1991) considered the Red-winged Blackbird an abundant migrant in Ontario. Flocks of 10,000 are fairly common in the south, and flocks as large as 50,000 have been observed.

WINTER

In Ontario, most Red-winged Blackbirds occur singly or in small flocks in winter, usually near a food source such as a feeder or corn crib. They may also occur in cattail marshes (Curry 2006; LaForest 1993; Lancaster et al. 2004). In the core of its winter range, it prefers cornfields, shrubbery of all types, pastures, feedlots, garbage dumps, sewage lagoons, stubble fields, unharvested grain fields, and feeders (Campbell et al. 2001; Graber and Graber 1963).

Due to its scarcity in winter in Ontario, no large roosts of Red-winged Blackbirds occur. Major roosts, often in common reed, occur in the southeastern United States from Texas to southwest Indiana east to the Atlantic Coast and north to Maine, with some roosts in California. Most birds wintering in Kentucky, Tennessee, and Alabama come from the Great Lakes region. Some roosts support 20-30 million birds and 1 in Arkansas supported 40 million birds in 1965. There are approximately 150 roosts in the United States that support at least a million birds (Nero 1984; Root 1988; Yasukawa and Searcy 2020).

Banding recoveries suggest that the Red-winged Blackbird is fairly sedentary within winter, with most recoveries in the same year within 25 km of the banding site. Only 6% of recoveries within the same year were more than 100 km from the roost where the bird was banded. Birds may travel as far as 80 km from the roost to forage, but distances travelled are usually much less. The distance between banding and recovery locations was further between years, with a mean of 88 km in 1 study and 154-231 km in another. It is much less faithful to wintering than breeding areas (Dolbeer 1978, 1982; Yasukawa and Searcy 2020). It spends an average of only 4 nights at a particular roost before moving on to a different roost, typically 4.8-13.6 km from the previous roost, although some may move 5 times that distance (Dunn and Tessaglia-Hymes 1999).

The Red-winged Blackbird may use some different foraging strategies in winter. In North Carolina, a flock of 2,000 fed in a dense stand of pines. Some extracted seeds from cones. Others

searched for insects on terminal buds or beneath bark. While searching for prey under bark, it pecked in a manner similar to a woodpecker or nuthatch. Most searching under bark was done on limbs and not on trunks (Meanley 1966). In New York, it often fed on the seed capsules of sweetgum. After a heavy snowstorm, it fed on standing giant ragweeds, splitting the stalks open with the bill to obtain small leafroller caterpillars (Fischer 1953). In Wisconsin, it preyed upon larvae of the cattail borer moth. It also commonly ate cocklebur seeds (Nero 1984). The diet of birds in a Tennessee winter roost consisted of 38% corn, 36% weed seeds, and smaller amounts of sorghum, wheat seeds, tree seeds, and insects. The weed seeds were from 15 genera of plants, with those of ragweeds and rough cocklebur most important. Weed seeds comprised 62% of the diet from November to March (Yasukawa and Searcy 2020).

Highest numbers of Red-winged Blackbirds at feeders occur during spring migration. Smaller numbers use them throughout the winter, mostly where agricultural crops and weedy fields are scarce, or when snow covers food resources. Its favourite feeder foods include mixed seeds, millet, sunflowers, and cracked corn, and probably milo. It infrequently consumes safflower, whole corn, hulled peanuts or hearts, suet, bird puddings, fresh fruit, baked goods, wheat, and oats (Dunn and Tessaglia-Hymes 1999).

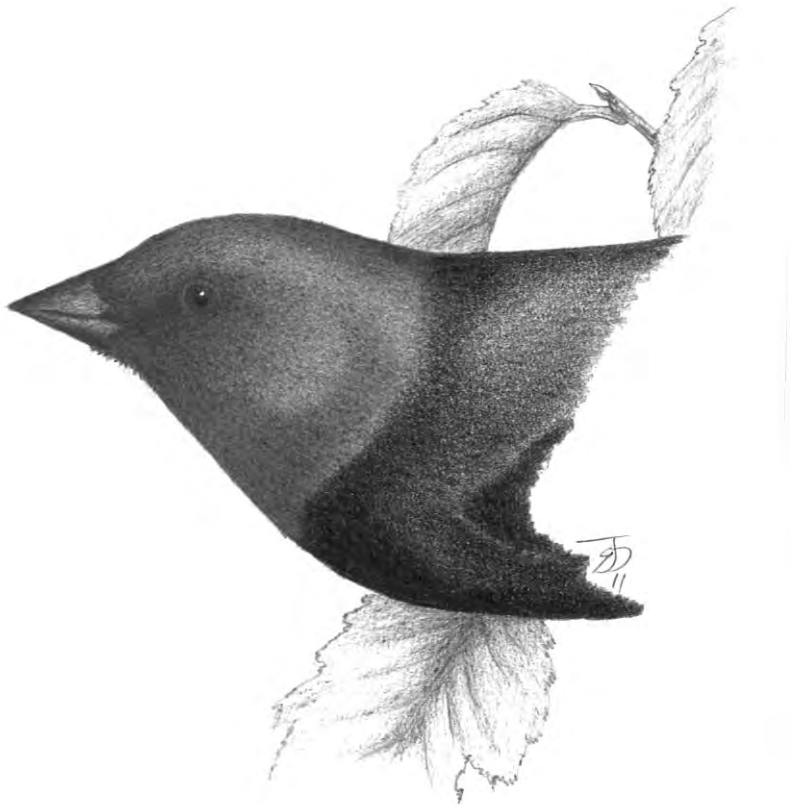
Severe winter weather may cause significant mortality. In Kentucky, 25 cm of snow fell over a week, making it difficult for birds to find food, and the overnight temperatures dropped to −24.4°C. The Red-winged Blackbird represented 0.9% of the birds at a roost but 6.3% of the dead birds found. Its mortality rate was 7 times higher than other species in the roost (Stewart 1978). In Illinois, heavy snow and extreme cold occurred during a January storm. Its density in bottomland forests declined by 10.9% after the storm and some carcasses were found (Graber and Graber 1979). North of Kingston, Weatherhead (2005) documented a steep decline in the breeding population from 1974 to 1995. Harem sizes were negatively correlated with variation in the North Atlantic Oscillation Index in the previous 6 months. Harem size and male return rates were significantly correlated. He concluded that more frequent or severe winter storms could be causing the decline.

James (1991) considered the Red-winged Blackbird an uncommon winter resident in the south north to Toronto, and occasional and rare north to Thunder Bay and Moosonee.

There are some indications that the Red-winged Blackbird has increased as a wintering species over historical conditions, and that the core of its wintering range may have shifted northward. This may be due to the current abundance of cereal crops which were formerly much less common, and the proliferation of bird feeders. McIlwraith (1894) was aware of no winter records for the province. Freedman and Riley (1980) analyzed Christmas Bird Counts (CBC) for southern Ontario for 1929-77. It demonstrated an irregular increase in abundance and frequency of occurrence beginning in 1958, but total annual numbers continued to be low. CBC data indicate that it decreased in Ontario at annual rates of 0.86% 1970-2021 and 0.14% 2009-21 (National Audubon Society 2022).

Brown-headed Cowbird

Molothrus ater

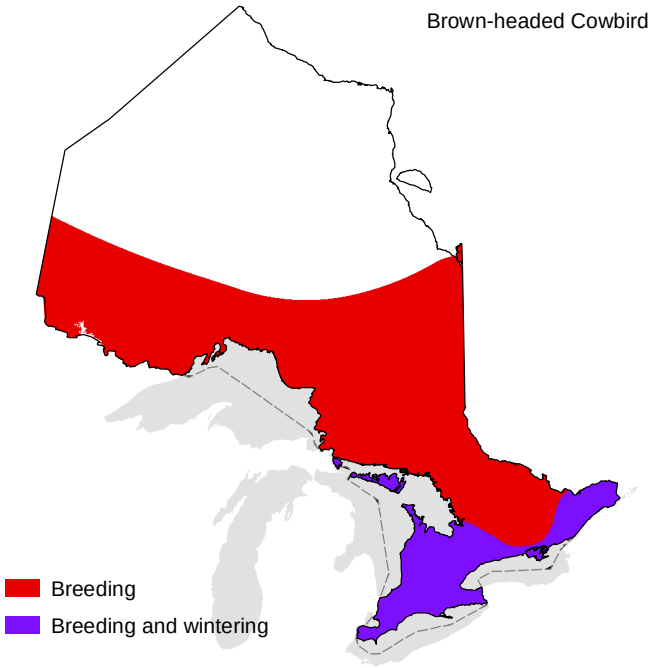


BREEDING SEASON

Habitat Requirements

The Brown-headed Cowbird is Ontario's only obligate brood parasite. It lays its eggs in nests of other species and leaves the rearing of their young to the host species. Because of its parasitic behaviour, the cowbird has been much maligned. Some birders and even ornithologists illogically think that it should have human morals (Bent 1958; Ortega et al. 2005). Many people remove cowbird eggs from nests and cowbird control programs (which consist of killing them) have been implemented in many areas. Instead of being cast as a villain, the cowbird should be viewed as a native species that is in significant decline and that has some very interesting physiological and behavioural adaptations to support its parasitism.

Cowbird parasitism always has an adverse effect on the reproductive success of the host. Hosts that accept eggs typically raise fewer of their own eggs to fledging. Many smaller hosts typically raise only cowbird young when they are parasitized. Hosts that are smaller than the cowbird and those with long incubation periods are affected the most. Parasitism may also affect species that



reject cowbird eggs. The female cowbird may remove one of their eggs, thus reducing the clutch size of hosts. Ejectors may also damage their own eggs while attempting to eject a cowbird egg. If eggs are pierced in the nest, the leaked contents may glue the host's eggs together and to the nest, resulting in poor hatching success. For species that abandon parasitized nests, there is a loss of energy and time as a result of this activity. Replacement nests tend to have smaller clutch sizes than first nests, so there is often a loss of reproductive success as a result of nest abandonment. Nest desertion does not guarantee that the replacement nest will not be parasitized. Time and energy costs may be slightly less for species that that build a new layer in the lining of the nest and bury the cowbird egg. These species also often bury some of their own eggs with a resultant loss in reproductive effort. The mere presence of cowbirds may result in nest losses because the distress responses of the potential host often attracts predators, and the noisy vocalizations of cowbird nestlings may also attract predators (Grzybowski and Pease 1989; Peer et al. 2005; Rothstein 1975; Rothstein and Peer 2005; Smith 1999; Zanette et al. 2007).

A good parasite should not harm its host population; if the host population declines so will the parasite. Parasites tend to be rare in relation to their host so that the host population is not adversely affected by parasitism. The Brown-headed Cowbird meets both these criteria. It has not been confirmed causing the decline of any host species, and its population is approximately 3% of the population of suitable host species. Brittingham and Temple (1983) did a major disservice to the cowbird by suggesting that it might be responsible for recent declines in songbirds. This paper is still widely cited but contains a major flow. They used Christmas Bird Count (CBC) data for the southeastern United States where most cowbirds overwinter to determine its population trend. Instead of calculating the actual number of cowbirds counted, they simply tallied the number of counts it was detected on 1900-80. The number of counts it was observed on increased over this period and they interpreted this as an indication that its populations was increasing. Actual CBC data and results of the Breeding Bird Survey (BBS) indicated that it was declining in their study period. Their conclusion that increasing cowbird populations were adversely affecting songbird populations was incorrect. There is no evidence that the cowbird has caused the decline of any of its host species, but it has been accused of causing the decline of Kirtland's Warbler, Least Bell's Vireo, Southwestern Willow Flycatcher, Black-capped Vireo, and Golden-cheeked Warbler. Populations of these species are or were previously low and parasitized heavily by the cowbird. This lead to cowbird control programs which included killing cowbirds and removing cowbird eggs from nests. The Kirtland's Warbler is the best studied example, with the population declining to an estimated 201

singing males. After 18 years of cowbird control, the male population was still 200 indicating that the population was at carrying capacity. A further study of the Kirtland's Warbler population revealed that most nest mortality was due to predation and that mortality related to parasitism was only 16.8% of the total. The Kirtland's Warbler population did not recover until an out-of-control prescribed burn created about 100 km^2 of new habitat. The Least Bell's Vireo population is the only one that increased during cowbird control. The population began to rebound before the control program was initiated due to increased habitat availability following extensive wildfires. Despite the lack of evidence that cowbird control programs are effective in endangered species recovery, no major control program has been terminated. In all cases, the species of concern are endangered due to limited availability of suitable habitat. The cowbird gets blamed for habitat loss and fragmentation caused by humans. Although parasitism exerts costs on individuals that are parasitized, there are no effects on the host population as a whole. Failure to recognize this fact explains much of the lack of understanding between advocates and opponents of killing cowbirds in control programs (Chace et al. 2005; Lowther 2020c; Martin 1992; Mayfield 1977a; Ortega et al. 2005; Peer et al. 2005; Rothstein and Peer 2005; Schweitzer et al. 1998; Smith 1999).

The Brown-headed Cowbird is a generalist parasite, laying its eggs in a variety of bird species' nests. As of 2005, it had been documented parasitizing 228 species; 87 host species were confirmed in Ontario (Peck and James 1998b). Many hosts are parasitized rarely or only accidentally; only 132 of the 228 hosts (57.9%) have successfully raised a cowbird (Chace et al. 2005). To be a suitable host, the species should be altricial and not precocial; its manner of feeding should not depart greatly from the normal passerine method; and it should feed its young insects, worms, soft seeds, and other typical passerine foods. Most suitable hosts are within 4 families: tyrant flycatchers, vireos, sparrows, and warblers; thrushes are also frequently parasitized. Almost all nonpasserine species are unsuitable hosts as are many passerines. The Mourning Dove is unsuitable because their young thrust their bill into the adult's throat instead of vice versa. Swallows may raise a cowbird while it is in the nest but it probably dies after fledging because fledglings are trained to catch prey in the air. Most finches feed their young a granivorous diet and cowbird nestlings rarely survive without the protein in insects that they require. Birds nesting in cavities (woodpeckers, certain wrens, nuthatches, chickadees, and bluebirds) are seldom parasitized because the cowbird prefers open-cup nests and may not be able to access nests with small cavity entrances. Species that regularly eject eggs are unsuitable hosts. Poor hosts are a major source of reproductive loss for the cowbird. The breeding success of the cowbird is much lower than that of its most important hosts (Friedmann 1929, 1963).

Parasitism by the Brown-headed Cowbird has resulted in the evolution of antiparasitic behaviours by hosts and, in some cases, further adaptations by the cowbird to offset these strategies. Avoiding parasitism is the best defence, but this is seldom achievable. Eastern Kingbirds aggressively defend their nests and Red-winged Blackbirds mob cowbirds. These strategies may reduce the incidence of parasitism but do not completely eliminate it. In response to this, the cowbird lays its eggs very early in the morning before dawn when the host is usually not at the nest. The most common defence against parasitism is rejection of the parasitic egg by ejecting it, burying it in the nest, or deserting the nest. The cowbird's response to this is mimicry of the most common hosts'

eggs, particularly those in the central portion of the continent where the species have been in contact the longest (Rothstein 1975).

Habitats in which parasitized nests have been reported in Ontario provide an indication of the cowbird's habitat preferences. Most nests were in dry open or semiopen areas with growths of deciduous (49.2% of nests), mixed (41.2%), or coniferous (8.8%) shrubs or small trees a predominant feature. Breeding areas included farmlands (54.5% of nests) dominated by overgrown fields and fencerows (26.9%), young conifer plantations and orchards (20.7%), and open fields (6.9%); woodland areas (14.3% of nests) including wooded edges (12.6%), second-growth woods (1.2%), mature woods (0.4%), and swamps (0.1%); residential areas (14.1% of nests), including gardens, parks, and streets; shrubby edge areas (13.2% of nests), including shorelines and floodplains (8.8%) and roadsides (4.4%); and wet areas (3.9% of nests), including cattail marshes, sedge meadows, fens, bogs, and muskegs (Peck and James 1987).

The cowbird avoids extensive tracts of forest. In Algonquin Park, it avoided forests and inhabited shrubbery and more open country (MacLulich 1938). It has been essentially absent as a breeder in the park since the 1980s. The habitat is almost completely unsuitable for it due to the lack of agricultural lands for foraging and the nearly contiguous forests now present due to natural succession (Tozer 2012). In the Boreal Forest Region of Ontario, it avoided most coniferous forests, occurring regularly only in stands dominated by white pine or red pine. It was characteristic of artificial grass and shrub habitats within agricultural areas. It occurred in low densities in stands dominated by balsam fir, poplar and/or white birch, and maple-beech, and in urban suburbs (Erskine 1977). In the agricultural and urban landscapes of southern Ontario, it is almost ubiquitous because of the variety of habitats that its hosts prefer. Near Kingston, 6 habitats supported cowbirds: sugar maple–beech-elm–white pine–red pine mixed forest; shoreline areas of alder, staghorn sumac, cattails, and ferns; open grassy areas with shrubs and saplings; grassy areas with scattered tall trees; mixed open areas with both shrubs and scattered trees; and short-grass areas such as lawns or cattle pastures (Teather and Robertson 1985). In Durham Region, it occurred in very young and mature pine plantations, a black spruce bog surrounded by red maple–poplar swamp, a variety of open deciduous and mixed forests in both upland and lowland areas, and mature deciduous woods. Speirs and Orenstein (1975) considered it a mid-successional species but it occurred in all stages of succession. On the University of Western Ontario campus in London, its habitat consisted of lawns interspersed with trees and shrubs and a narrow strip of second-growth shrubby woodland growing between the campus and the Thames River (Darley 1983; Scott 1977). These are just a few examples of the habitats it occupies in southern Ontario. It has a high preference for agricultural lands, particularly where livestock is common.

In Ontario forests south of the Canadian Shield, the cowbird was positively correlated with the amount of forest more than 100 m from edge and negatively correlated with woodlot size, the amount of forest within 2 km, and the amount of regional forest cover. The negative relationship with the amount of regional forest cover was highly significant. The other relationships were nonsignificant (Austen et al. 2001).

The Brown-headed Cowbird has 3 main habitat requirements during the breeding season: nesting, feeding, and roosting areas. These areas may be considerable distances from each other

rather than confined within a small territory. What is unique about the cowbird is that it completely abandons the nesting area in late morning and does not return until dusk or the next morning. It is able to do this because it does not have to attend to a nest. The habitat of the breeding and feeding areas is quite different. The breeding area consists of shrubby or forested lands where it spends most of its time in elevated perches. Feeding areas have very short vegetation and cowbirds spend most of their time on the ground foraging. In highly fragmented landscapes, all 3 habitat components may be found in a small area. In contiguous landscapes, cowbirds may commute long distances between forested areas that provide breeding habitats and openings that provide a source of food. Good breeding habitat that is too far from a suitable feeding area is not occupied. Even excellent feeding areas will not be used if they are not within commuting distance of a breeding area. Distance from feeding areas appears to be one of the most important determinants of its breeding abundance, having greater influence than forest type or host density (Chace et al. 2005; Curson et al. 2000; Friedmann 1929; Gates and Evans 1998; Goguen et al. 2005; Rothstein et al. 1980, 1984; Thompson 1994). Distances travelled between breeding and feeding areas vary depending upon the distribution of habitat within the landscape. In many areas, daily commuting distances tend to be 1-3 km: 1.2 km in Missouri and Illinois, 2.27 km in Maryland, 4.1 km in California, and 1.47 km at a forest-prairie ecotone in New Mexico. At another New Mexico site in a bison-grazed landscape, female commuting distances averaged 7.24 km (range 0.16-11.81 km). In Michigan, no cowbirds were found in potential breeding habitat further than 3 km from agricultural land that provided feeding habitat. Another New Mexico study reported mean commuting distances of 11.8 km (range 9.3-13.2 km) for females. For 3 females, the mean distance between roosts and breeding areas was 19.0 km (range 17.8-20.6 km). It was previously thought that the maximum commute distance was about 7 km. This study demonstrated that the cowbird can penetrate forest tracts to breed considerably further. Only a small proportion of the population consisted of long-distance commuters. In California, the mean distances between daily activity centres were 2.27 km (range 0.30-6.14 km) between breeding and feeding areas, 2.96 km (0.29-9.84 km) between feeding and roosting areas, and 1.35 km (0.08-4.91 km) from roosting to breeding areas. Females usually had 2 feeding, 1 breeding, and 1 roosting home range. Occasionally feeding and roosting areas, breeding and roosting areas, and breeding and feeding areas overlapped. In New Mexico, 70% of hosts were parasitized in areas close to grazed pastures, but only 33% were parasitized at distances of 8-12 km from pastures (Chace et al. 2005; Curson et al. 2000; Gates and Evans 1998; Goguen and Mathews 2000; Goguen et al. 2005; Rothstein et al. 1984; Stribley and Haufler 1999; Thompson 1994).

Numerous studies examined the habitat preferences of the Brown-headed Cowbird at the landscape scale. Most dealt with the amount of forest cover in the landscape. It is generally believed that the cowbird avoids heavily forested landscapes, but this is not always the case. Chace et al. (2005) examined factors affecting its distribution and abundance at continental (greater than 50 km), regional (10-50 km), and landscape (1-10 km) levels. Because it may travel 15 km between breeding and feeding sites, forests would have to be larger than 700 km^2 to entirely exclude cowbirds. Results at the 50-km and 10-50-km scales were ambiguous suggesting that it did not make habitat selection decisions at these scales. At the 10-km scale, its abundance and parasitism rates on host species showed a consistent negative relationship with the amount of forest cover surrounding the study area. Parasitism declined linearly as forest cover at this scale increased from

6% to 95%. When the amount of forest cover was considered at the 1-10-km scale, the most significant relationships were at the 10-km scale for both sexes combined and only at 3-5 km for females. Abundance and parasitism rates increased with the proportion of grassland and agriculture in the landscape at the 3-km scale. In Michigan, the most important habitat variable determining cowbird abundance was the presence or absence of agriculture within 3 km. It was 3-3.5 times more likely to occur in a forest stand where agriculture occurred within 3 km. The probability of finding it dropped considerably when the nearest agricultural lands were no closer than 2 km (Stribley and Haufler 1999). Hochachka et al. (1999b) examined 23,448 nest records for the cowbird across the United States. Sites with higher forest cover tended to have a lower probability of parasitism, although the pattern only approached significance. The probability of parasitism was not significantly affected by the amount of forest cover at the 50-km or 10-km scales. There was a 95.3% probability that increased forest cover within 10 km resulted in a decreased incidence of parasitism. Hosts were parasitized at a lower rate where there was greater forest coverage. A 10% increase in forest cover was predicted to result in a 1% decrease in the proportion of nests that were parasitized. In Montana and Idaho, 73% of points where it was detected were within 10 km of agricultural areas and almost 90% were within 20 km. It was found closer to developed areas and in landscapes with more open and xeric forests and less coverage by subalpine and mesic forests. Proximity of upland shrub areas, such as clear-cuts, was not related to its occurrence (Young and Hutto 1999). In Saskatchewan, it was more common than expected in fragmented landscapes but was not influenced by the amount of forest cover within 5 km (Hobson and Bayne 2000). In North Dakota, Pietz et al. (2009) studied the influence that woody vegetation had on parasitism rates of grassland birds. A previous study determined that 14% of grassland passerine nests were parasitized in treeless landscapes compared with almost 0% in grasslands within aspen-parkland landscapes. In their study, the relationship between the percent tree cover within 2 km of nests and the probability of parasitism was negative for all grassland species. For every 1% increase in tree cover within 2 km, the probability that a nest would be parasitized decreased by 12%. The cowbird is less likely to target grassland species in landscapes with sufficient tree cover to provide alternative hosts in woodlands. In Vermont where 77% of the area was forested, higher probability of cowbird occurrence was associated with the number of food sources within 7 km and the distance to the nearest disturbance (maintained wildlife openings, residences, hayfields, pastures, and ski areas). Large disturbance areas and clustered patches of them had a higher probability of occurrence. It preferred landscape elements that produced edge, so the larger the area of disturbance, the higher the probability that it would be used. It tended to occur in disturbance patches close to other disturbance patches. Distance to the nearest livestock area was not an indicator of cowbird abundance, but the number of them within 7 km was. Areas isolated from livestock areas (the preferred feeding areas) and chronic disturbance areas had a low probability of being occupied. It was largely absent from heavily forested regions, so it may prefer to travel within these landscapes along corridors of chronic disturbances. Large continuously forested areas may act as a barrier to its movement (Coker and Capen 1995). Males preferred landscapes that were 42-75% forested in North Dakota; no areas supported more than 75% forest cover. Females preferred landscapes that were 8-40% forested. In New York, males preferred landscapes with 39-60% forest cover (Cunningham and Johnson 2019). In Quebec, its distribution corresponds with open habitats, especially those created by agriculture. It nests in almost all settled landscapes. Its relative abundance is highest in the St. Lawrence

Lowlands where agriculture, urban, and suburban habitats predominate. It becomes less common where forest cover increases (Houle and Choiniere in Gauthier and Aubry 1996; Michaud in Robert et al. 2019).

The Brown-headed Cowbird lays its eggs in nests in a variety of habitats. It breeds in nearly every major habitat type in North America. It has bred in deciduous, mixed, and coniferous forests, urban and suburban areas, riparian vegetation, tallgrass and short-grass prairies, shrublands, shrubsteppe communities, agricultural fields, savannahs, bottomlands, clear-cuts and other logged areas, meadows and old fields, fencerows, utility and road rights-of-way, pastures, hayfields, Dense Nesting Cover and Conservation Reserve Program (CRP) grasslands, pine and oak barrens, coniferous plantations, small stream corridors through forests, marshes, prairie potholes, willow and alder thickets, forest burns, windthrows in forests, urban parks and green spaces, fens with scattered trees, orchards, farmyards, and tundra (Bielefeldt and Rosenfield 1994; Campbell et al. 2001; Chace et al. 2005; Delphey and Dinsmore 1993; Faanes and Andrew 1983; Falardeau et al. 1999; Grundel and Pavlovic 2007b; Hartley 1994; Hoffman 1989a, 1989b; Morris and Thompson 1996; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991; Niemi and Hanowski 1984a; Noon et al. 1979; Norris 1947; Robinson et al. 1999; Samson 1979; Sinclair et al. 2003; Temple et al. 1979; Walk et al. 2011; Whitmore 1977; Wood et al. 2013; Yahner 2003).

Although the Brown-headed Cowbird breeds in almost every habitat type, it prefers habitats with more complex structure, such as forests, savannahs, shrublands, and old fields. These habitats support a higher diversity and abundance of hosts than grasslands and marshes. They also provide elevated perches from which they can search for host nests (Chace et al. 2005). Forests are highly preferred over grasslands. In Oklahoma, nests in open habitats were usually not parasitized, with most parasitized nests on edges of adjacent low shrubby thickets (Wiens 1963). In Pennsylvania prior to 15 May, the cowbird was never seen in forested areas and it parasitized birds nesting in open habitats. Later, when forest songbirds returned, most cowbird eggs were laid in nests of woodland species, although it continued to parasitize some open-country birds (Norris 1947). In New York, Hahn and Hatfield (1995) studied parasitism rates in a 1,300-ha forest and old-field habitats adjacent to the forest within commuting distance. The parasitism rate in the forest (32.3%) was significantly higher than in the old fields (6.7%). The Eastern Phoebe occurred in both forested and open habitats. In forest, 42.1% of its nests were parasitized compared with 0% in the open. Habitat was the only significant variable predicting parasitism rate. Both the species that are traditional hosts and the field-edge community, which is often considered its preferred habitat, were conspicuously underused compared with species nesting in forest interior further than 50 m from edge. There was no relationship between parasitism and proximity to edge, consistent with their observations of cowbirds throughout the forest. In North Dakota, parasitism rates of grassland birds declined as the amount of forest cover increased, indicating that it preferred hosts inhabiting forests (Pietz et al. 2009). In heavily forested landscapes of Vermont, it significantly preferred permanent forest openings to temporary regenerating openings such as clear-cuts, shelterwood cuts, or group-selection cuts. Its preference for permanent openings was probably due to the presence of short grass. Lawns and other areas that are maintained as short grass may provide feeding areas as well as breeding habitat at forest edges (Coker and Capen 1995). In Illinois, highest densities occurred in shrubs at edges of forests and in shrublands and hedgerows (Graber and Graber 1963). Illinois

parasitism rates were higher in forests than in shrublands, edges, and grasslands. Grasslands consistently had the lowest abundance of cowbirds and savannahs had the highest abundance. Parasitism rates were significantly higher in shrublands and savannahs than in forests; parasitism rates in grasslands were significantly lower than in any other habitat type. Grasslands may be difficult for it to search for nests because of the scarcity of perches, dense grass cover, and the cryptic behaviour of these host species near their nests. Grasslands that have some woody vegetation that provide perches have elevated parasitism rates, but these are still lower than for other habitats. The preference for savannahs may have been because of the numerous perches and lack of dense ground cover (Robinson et al. 1999). It was more abundant in forests than in shrublands in southern Illinois but equally abundant in these habitats in the remainder of the state (Walk et al. 2011). In British Columbia, it preferred open habitats with low or scattered trees. It preferred forest-field ecotones over extensive forests or fields. Thirty-four percent of parasitized nests were associated with rural habitats, including cultivated farmland (12%), farmyards (11%), orchards (7%), and pastures (4%); 30% were in forests including deciduous (13%), coniferous (9%), and mixed (8%) stands; 16% of nests were in riparian areas; 11% were in suburban and urban areas; and 6% were in shrublands. Specific habitats included 33% backyard and farmyard gardens and residential areas; 29% mature and second-growth forests and regenerating clear-cuts, forest edges, and road edges through forests; and 25% riparian habitats including forested shores of lakes and watercourses, cottonwood bottomlands, and willow thickets. Orchards, urban parks, sagebrush shrublands, and transportation corridors were used to a lesser extent (Campbell et al. 2001).

The Brown-headed Cowbird exhibits habitat preferences within the major breeding habitat categories. Forest age may be a factor in its habitat selection in certain areas. In Pennsylvania, it occurred in 36.5% of old-growth forests, 87.7% of forests statewide, and 83.4% of forests in the Appalachian Plateau. Haney (1999) considered it to have a negative affinity with old-growth forests. In Alberta, it was significantly more abundant in young and old-growth than mature trembling aspen stands (Schieck et al. 1995); results were similar in British Columbia (Campbell et al. 2001). In the Prairie Provinces, it was associated with young mixed or deciduous forests. These tended to be on moist nutrient-rich soils (Kirk et al. 1996). In South Dakota green ash stands, it was significantly more abundant in late than early seral stages. Bird abundance was greater in late seral stands, so its habitat preference may have been related more to the abundance of potential hosts rather than stand age (Rumble and Gobeille 1998). In Saskatchewan, it was significantly more abundant in trembling aspen stands than in white spruce stands and mixed woods (Hobson and Bayne 2000). In Montana and Idaho, it occurred at 1.3% of points in old growth, 5.1% in mature forests, 5.6% in young forests, and 10.0% in selectively cut forests. It was common in extensively logged areas but more abundant in partially logged stands than clear-cuts. It occurred in all major habitats except hemlock-cedar, but did not use all cover types equally. It was largely absent from dense old growth and high-elevation forests. It was abundant in open coniferous forests, grasslands, agricultural areas, and riparian cover. Grasslands and agricultural areas were used much more than clear-cuts. The distribution of potential hosts was similar to that of cowbirds (Young and Hutto 1999). Evans and Gates (1997) sampled 6 habitat types in a 15,699-ha forest in Maryland: forest–power line edges, forest–open-canopy road edges where there was less than 10% canopy cover at the centre of the dirt road, forest–closed-canopy road edges with more than 90% canopy cover at the centre of the

road, forest-brush edges, forest-stream edges, and forest interior 250 m or more from edge. The cowbird was detected in all habitats except forest interior. Its frequency of occurrence was 50% at forest-brush edges, 46.4% at streams, 33% at power lines, 14.3% at open roads, and 10.3% at closed roads. Host species richness was lowest at closed roads and highest at brush and power line edges. Host abundance was significantly higher at power lines and open roads than at streams, closed roads, and forest interior. Habitat where it was most frequently detected had both high mean snag basal area and total vegetation volume. It was found near visible openings, ranging from narrow road and stream corridors to larger clearings. Both high numbers of snags and high vegetation volume were required to attract high densities of cowbirds. If one of these factors was low, the frequency of use was also low. It was attracted to distinct edges formed by canopy openings and secondarily by the occurrence of high snag basal area and total vegetation volume. These may be cues that direct the cowbird to habitats with the potential for supporting high host nest densities. In Iowa, it parasitized a significantly higher proportion of Red-winged Blackbird nests at natural than restored prairie pothole wetlands. Delphey and Dinsmore (1993) attributed this to the presence of trees around the perimeter of natural wetlands, providing observation perches for cowbirds.

Several studies examined microhabitat preferences of the Brown-headed Cowbird. Microhabitat preferences can be subdivided into those selected in forests and grasslands. Its distribution is influenced by plant species diversity, tree density, canopy closure, and vegetation cover or volume at various height classes. Some studies determined that host nest concealment affects parasitism rates; other studies found that nest concealment is not a factor. Many studies concluded that abundance of potential hosts is more important than habitat. Others found that habitat is selected rather than potential hosts. Individual host species may be parasitized at different rates in adjacent old fields and forests, and this may be related to the degree of nest concealment. Parasitism rates on individual species vary geographically, with suitable abundant hosts such as the Red-winged Blackbird not being parasitized in some areas and heavily parasitized in others. As a result of all these factors, it is difficult to definitively define its microhabitat requirements (Chace et al. 2005; Hauber and Russo 2000).

Most information on the cowbird's microhabitat preferences is for forested habitat. In Michigan, its abundance could be predicted based on 5 habitat variables: presence of agricultural land within 3 km, total percent non-agricultural openings within 0.5 km, percent vertical cover 0-1 and 1-7 m from the ground, and mean canopy height. Areas with mean basal area less than 16 m^2 per ha were significantly more likely to support it than denser forests. Where agriculture was present in the landscape, lower occurrence occurred in stands with more than 70% canopy cover. The percent cover 0-1 m from the ground was the most significant predictor of occurrence after agricultural lands (Stribley and Haufler 1999). In Montana and Idaho, ground cover was the most important predictor of its occurrence. Ground cover was high where it occurred, both in forests and grasslands (Young and Hutto 1999). In Wisconsin, parasitized nests were characterized by a more open subcanopy (3-10% coverage) and canopy, and more cover 0-0.5 m from the ground than unparasitized nests. Associated with these differences were a significantly higher density of low shrubs and saplings and a lower density of shrubs taller than 5 m and small trees (7-14.5 cm diameter at breast height [DBH]) around parasitized nests. The number of shrubs and saplings was higher around parasitized nests, but not significantly. The number of dead trees did not vary between

parasitized and unparasitized nests and the percentage of nests parasitized was similar for nests closer or further than 11.3 m from a snag. An open canopy and subcanopy would enable the cowbird to attain an elevated perch with an unobstructed view of nest-building activities. Snags below the canopy do not provide better observation sites than exposed branches of living trees, which may explain why nest distance from a snag did not affect parasitism rates (Brittingham and Temple 1996). In Indiana, it was significantly associated with the density of dead trees (Grundel and Pavlovic 2007a). In Illinois, it was positively correlated with shrubs and negatively correlated with sugar maple and basal area (Blake and Karr 1987). In New York, parasitism rates were higher on forest-host nests 1 m or less from the ground than on higher nests. There was a high rate of parasitism on species that nested on the ground and short heights above it, consistent with observations that it frequently moved about in the lowest vegetation strata, both by walking on the forest floor and perching at heights of 1 m or less. Ground nests that were particularly well concealed, such as those of the Ovenbird, Black-and-white Warbler, Louisiana Waterthrush, and Carolina Wren, experienced a high rate of parasitism. The bulky and conspicuous nests of the Wood Thrush experienced much lower rates of parasitism, but its nests were higher. In adjacent old fields and edges in New York, nest height had no effect on the rate of parasitism (Hahn and Hatfield 1995). In the mid-Atlantic states, it was positively correlated with foliage density 0.3-1 m from the ground and the number of trees around the point count station (Robbins et al. 1989). In Illinois, the rate of parasitism on ground nests (41.2%) was less than on nests in shrubs, saplings, and the canopy (75.0%; Robinson 1992). In Wisconsin, its density in forests was inversely related to the distance to openings in the canopy 0.2 ha or larger. It occurred at 40% of points at an opening, 30% 200 m from an opening, 20% 300 m from an opening, and 15% of points 400 m from an opening. Parasitism rates decreased with distance to the nearest opening: 65% at 0-99 m, 46% at 100-199 m, 36% at 200-299 m, and 18% for 300 m and further. Parasitism rates were greater near openings 0.2 ha or larger than near openings smaller than 0.1-0.2 ha. The type of forest opening (agricultural field, recently logged area, or brushy second growth) did not influence parasitism rates. The frequency of parasitism increased significantly as the amount of open habitat within 200 m of a nest increased: 38% at 0-20% open habitat, 50% at 21-40%, and 92% at more than 40% open habitat. It preferred open habitat near areas where it searched for nests (Brittingham and Temple 1983). In New Jersey, Rich et al. (1994) examined its abundance at forest interior 300 m from edge and at 3 types of corridors cutting through the forest: power lines, 16-m-wide paved roads, and 8-m-wide unpaved roads. It was significantly more abundant at paved roads than in forest interior adjacent to these corridors. For power lines and unpaved roads, there was no difference in its abundance at the corridor and in adjacent forest interior. It was significantly more abundant at points with mowed grass (along paved roads) than at sites with shrubs or saplings. It preferentially selected corridors with mowed grass where both sexes often foraged, and males often displayed from power line poles. With an abundance of hosts near the forest edge, grassy corridors through the forest appeared to provide optimum habitat. In Wyoming, it was absent in subalpine areas, most abundant in lowland woods, and common in mid-elevational shrublands. Its abundance was negatively correlated with shrub density. It showed an affinity for areas with a more open understorey (Finch 1991a).

Less information is available on the cowbird's microhabitat preferences in grasslands. In North Dakota, litter depth was greater, the percent coverage by aspen was much greater, and the percent

cover by native herbaceous vegetation was less where it was present than absent. It was positively correlated with the amount of aspen within 100 m but negatively correlated with the amount of aspen within 500 m. Several other parameters had no influence on its presence or absence. These included maximum vegetation height, percent live vegetation, shrubs taller or shorter than 1 m, and amount of Kentucky bluegrass, brome grass, and sweet clover within 100 m (Grant et al. 2004). In Saskatchewan, its occurrence was affected by the amount of residual vegetation. It was positively correlated with the density of standing dead vegetation within 10 cm of the ground and negatively correlated with the amount of dead standing vegetation at greater heights (Davis 2004). Chapman et al. (2004) studied native grasslands that were being invaded by red cedar in Oklahoma. It was associated with shrubs and its density increased as coverage by cedar increased.

The Brown-headed Cowbird is considered an edge species in both grasslands and forests. This tends to be true only where there are large tracts of habitats that are not fragmented by roads, houses, or other disturbances. In fragmented habitats, it tends to parasitize hosts throughout habitat patches. Although it may occur in the interior, parasitism rates and its abundance tend to be higher near edges due to the greater abundance and diversity of hosts and host species. In Midwestern forests, parasitism rates were lower in patches 200-3,000 ha. Only at very large scales (greater than 30,000 ha) are forest-interior habitats likely to be entirely free of parasitism. As the cowbird population density increases, so does the distance that it penetrates into forest interior (Chace et al. 2005). In New York, parasitism occurred in all areas of a 1,300-ha forest. Parasitism rates were not higher closer to edge (Hahn and Hatfield 1995). In large riparian treed wetlands in Michigan, it was equally abundant in interior and edge (Inman et al. 2002). In Illinois, cowbird abundance and parasitism rates were high throughout forests 19-65 ha in size (Robinson 1992). It was abundant and widespread throughout the Great Cypress Swamp in Delaware, Maryland, and Virginia. Heckscher (2000) concluded that even the largest forest patch (5,000 ha) was too small to reduce parasitism effects. In New Jersey, it was common 300 m from forest edge (Rich et al. 1994). In Michigan, it was significantly less likely to occur at distances more than 300 m from edge, but it still occurred in the interior (Stribley and Haufler 1999). In Maryland, Gates and Giffin (1991) studied its distribution relative to a 3.4-m wide stream through a 270-ha forest. It was recorded most frequently near the stream and was absent further than 240 m from it. In riparian forests in Maryland and Delaware, the cowbird was equally abundant in all widths of forests, which ranged from 50 to 800 m (Keller et al. 1993). In Maryland, 94.4% of fixes of radiotracked females were 220 m or closer to forest edge. Females often moved hundreds of metres into the interior, but were often less than 50 m from an edge. Based on point counts, forest interior more than 250 m from edge was not used. Forest interior had a significantly more closed canopy, higher numbers of small trees and snags less than 30 cm DBH, and fewer seedlings and saplings than core breeding areas. Gates and Evans (1998) concluded that it would likely penetrate more than 600 m into the interior in highly fragmented landscapes. When feeding in grazed pastures, females were most often 50-100 m from edge where livestock grazed most frequently.

The Brown-headed Cowbird is not an area-sensitive species. It is mostly uninfluenced by forest and grassland size and tends to occur at higher densities in smaller patches. Johns (1993) considered it area sensitive in trembling aspen groves in Saskatchewan, although it occurred in woodlots as small as 0.1 ha. In Illinois, Blake and Karr (1987) concluded that its abundance was related to woodlot

size. They studied woodlots 1.8-600 ha in size. Their results were more an indication that it did not avoid forest interior than it was area sensitive. In Saskatchewan forests, Hobson and Bayne (2000) did not consider it area sensitive and Hayden et al. (1985) reached the same conclusion in Missouri. In CRP grasslands in Montana, North and South Dakota, and Minnesota, it favoured smaller patches. The interior of these grasslands lacked perches and the grasses were too tall to provide foraging habitat (Johnson and Igl 2001). In Saskatchewan pastures, Davis (2004) considered it area insensitive. It was more abundant in irregularly shaped patches with a greater density of shrubs, but patch size had no influence on its occurrence.

Feeding areas are the second important component of the habitat of the Brown-headed Cowbird. Birds move to feeding areas in late morning (1000-1100 hours) and remain until near dark. It has a high propensity to feed in association with large grazing ungulates. It was originally known as the buffalo-bird but became the cowbird after bison numbers were greatly reduced and they were replaced by cattle. It forages to a lesser extent with other wild and domestic ungulates such as elk, pronghorns, horses, pigs, and domestic sheep. Corrals with horses are often favoured feeding areas because the feed provided also provides food for cowbirds; manure may also be an important source of insects. The large grazing species provide foraging opportunities by creating feeding microhabitats, decreasing vegetation height thus facilitating foraging, increasing insect abundance, and flushing insects while they are grazing. The backs of large ungulates may provide sites for social interactions and displays and possibly perches for females searching for nests (Chace et al. 2005; Gates and Evans 1998; Goguen and Mathews 1999; Goguen et al. 2005; Payne 1973; Rothstein et al. 1980, 1987; Sinclair et al. 2003; Thompson 1994). In New Mexico, females fed with bison 77.0% of the time and with elk 9.9% of the time. Most of the times when they did not feed with bison occurred when there were few within 10 km of the breeding area. In cattle-grazed landscapes, the cowbird fed almost exclusively (98.7% of the time) with cattle or horses at active livestock corrals (Goguen et al. 2005). In Illinois and Missouri, 57% of 1,351 feeding observations were associated with livestock (Thompson 1994). In Maryland, 82.9% of fixes of radiotracked feeding females were in grazed pasture and 97.5% were in agricultural land (Gates and Evans 1998).

Although feeding areas associated with grazing or penned ungulates are highly preferred, the cowbird forages in a variety of habitats. These may include row crops, agricultural fields, ungrazed grassy fields, lawns, golf courses, cemeteries, urban yards, bird feeders, campgrounds, dry lake beds, open short-grass prairie, and mowed verges of roads. Where cattle are present, row crops are unimportant as feeding areas, but may be important where cattle are scarce. The cowbird makes extensive use of late-planted soybean fields in Illinois. These continue to provide bare ground habitats favourable for foraging long after corn has grown to a height so that it is no longer suitable for foraging. Urban and suburban habitats provide important feeding habitats in many areas (Chace et al. 2005; Gates and Evans 1998; Goguen et al. 2005; Rothstein et al. 1984; Thompson 1994). The distribution, abundance, and quality of feeding areas are important in determining the cowbird's distribution and abundance.

Morris and Thompson (1998) examined cowbird usage of 5 habitats for foraging in Missouri. These included short (2-20 cm) grazed grass, short (2-10 cm) ungrazed grass such as lawns and mowed hayfields, tall (5-30 cm) grazed grass, tall (more than 30 cm) ungrazed grass such as uncut

hayfields, and feedlots lacking grass where cattle were fed processed feed or grain. They also measured invertebrate biomass and density to determine if habitat preferences and foraging success were related to food availability. Flock sizes were greatest in short grazed grass and smallest in tall ungrazed grass. Density was significantly higher in feedlots than all other habitats, but density was artificially high due to their small size. Density in short grazed grass was higher than in tall grazed grass, and density in tall grazed grass was higher than in the other 2 habitats. Flock size and the number of females were positively related to invertebrate density but male numbers were unrelated to invertebrate density. There were no relationships between invertebrate biomass and either sex. Short grazed grasslands were the primary habitat used for foraging. Intermediate use was made of feedlots because of the readily available food, but females had to also seek invertebrates in short and tall grazed grass to meet their nutritional requirements. Cowbirds appeared to select short grazed grass because of the high density of invertebrates. Cattle were an important component of foraging habitat. Grass height was less important than cattle, but within grazed habitats short grass was preferred.

Roosts are the third important habitat component. These may be either in the breeding or feeding areas or at a disjunct site. In Illinois and Missouri, roosts were often in single trees or fencerows in agricultural areas or in developed areas. A communal roost consisted of a stand of flooded dense sapling-sized silver maples along a drainage ditch. It supported at least 200 cowbirds and 1,000 Common Grackles. The other roosts supported solitary birds (Thompson 1994). In New Mexico, females roosted individually in coniferous forests or riparian woodlands, or colonially in a cattail marsh. The colonial marsh supported 600-1,000 cowbirds and lesser numbers of Yellow-headed Blackbirds, Red-winged Blackbirds, and Common Grackles (Curson et al. 2000). Cowbirds roosted in marshes in California and females roosted communally in trees at edges of woods (Payne 1965, 1973). Friedmann (1929) reported that roosts may be in urban areas and on university campuses. Bent (1958) stated that grasses and reeds in large meadows were favourite roosting sites. It also roosted in dense coniferous trees and other thickets. In California, 1 male roosted alone in a patch of brush all 3 nights he was detected. Three nonbreeding males roosted in a blackbird roost on a shrubby hillside. The roost was used mostly by Brewer's Blackbirds. No females or breeding males were found at this roost (Rothstein et al. 1984). In Maryland, roosts occurred in a range of habitat types but particularly in deciduous forests. Some roosting occurred on developed land near houses. Nearly all roosts were in trees with 60% in deciduous woods, 6-10% each in mixed and coniferous woods and developed areas, and less than 1% in grazed pasture. Most roosts supported a single or only a few individuals (Gates and Evans 1998). In New York, all females roosted solitarily on their breeding home range (Hahn et al. 1999).

Near Kingston, the cowbird used 3 techniques to find nests. The most frequent method was to perch at the tops of trees or shrubs for 9-21 minutes and watch hosts' activities. In every case where Norman and Robertson (1975) observed this behaviour, a nest 4.6-7.6 m from the perch was parasitized the following morning. The second technique was to walk silently over the forest floor, looking about and sometimes stopping to watch birds in the canopy. The third technique was to make a series of short flights just above the shrubbery, landing abruptly in the leaves with considerable wing flapping. One female worked her way along the shrubby edge of a woodlot until she flushed a Chipping Sparrow. The sparrow's nest was parasitized the next morning. In Ohio, no

artificial nests with quail eggs in them were parasitized, but natural nests experienced a high rate of parasitism. This indicated that host activity was important in finding a nest (Thompson and Gottfried 1976). Strausberger (1998) observed a female flying in a hovering fashion less than 1 m above 15-cm tall grass. It flew in a circular pattern looking down, or occasionally dropping to the ground without feeding, then flew up and repeated the process about 20 cm away. The next morning a Song Sparrow nest within 0.5 m of where the female had been walking and hovering was parasitized. In the case of Ovenbirds, cowbirds found nests by watching the host build it (Hann 1941). Watching hosts is the most common form of nest searching but actively flushing hosts from nests also occurs (Chace et al. 2005; Mayfield 1961). Presence of the host in the vicinity of the nest appears essential to nest finding. Hackemack et al. (2016) determined that nest shape and size were not factors determining whether a nest was parasitized.

The cowbird is confined to parasitizing hosts that nest within its home range, so this may limit the possibility of preferentially selecting hosts (Hahn et al. 1999). Some individuals or populations are selective. In Georgia and South Carolina, all host species nested in shrubby habitat or in the understorey of deciduous forests. No species that nested on the ground or in tree canopies were parasitized. Parasitism rates were low, which may have allowed cowbirds to select preferred hosts (Kilgo and Moorman 2003). In Kentucky, it preferentially parasitized Dickcissel nests, parasitized vireo nests according to their availability, and parasitized Red-winged Blackbirds and other host nests less than their availability, indicating avoidance of them. The Dickcissel may have been preferred because it nests later into the season than other birds, readily accepts eggs, and can fledge as many as 5 cowbirds. Vireos are capable of fledging only a single cowbird and often desert heavily parasitized nests. The Red-winged Blackbird can fledge 2 cowbirds but may effectively defend its nest against parasitism (Rivers et al. 2010). Elliott (1977) studied a population in Kansas where most parasitized nests contained more than 1 cowbird egg. The first eggs of individuals were not randomly distributed among host nests, suggesting that some degree of selection or avoidance was being exercised. Subsequent eggs were randomly distributed. In most areas, the cowbird parasitizes a variety of host species, exhibiting no particular preferences, but some individuals may exhibit preferences. A female in Michigan laid all her 18 eggs in Yellow Warbler nests but other females used a variety of species (Friedmann 1929). The cowbird has been confirmed selectively parasitizing older and more experienced Willow Flycatcher and Song Sparrow nests. The female cowbird may inspect nests that she parasitized later in the season to determine the nest fate. Birds that successfully fledged cowbirds the previous year may be preferentially parasitized (Arcese et al. 1996; Smith 1981; Smith and Arcese 1994).

In Ontario, the 10 host species with the largest numbers of parasitized nests, in decreasing order, were Chipping Sparrow, Song Sparrow, Yellow Warbler, Red-winged Blackbird, Eastern Phoebe, Red-eyed Vireo, American Goldfinch, Veery, Cedar Waxwing, and Northern Cardinal. These hosts accounted for 67.6% of all cowbird nest records (Peck and James 1987). Four of these abundantly parasitized hosts are of interest. The Yellow Warbler is a poor host. It raises few cowbirds because of its high propensity to reject eggs. In Michigan, the success rate of cowbird eggs laid in Yellow Warbler nests was only 18% (McGeen 1972). The American Goldfinch is also a poor host that rarely raises a cowbird due to the diet it provides the young (Middleton 1991). The cardinal is another poor host that rarely raises cowbirds in Ontario (Graham 1988). The Cedar Waxwing is a known rejecter

species (Rothstein 1975) so the incidence of parasitism on it may have been higher. The 26 Ontario hosts with more than 20 parasitized nests comprised 87.9% of all cowbird nest records; 30 species with more than 15 parasitized nests comprised 90.2% of records; and 38 species with more than 10 parasitized nests comprised 93.3% of records. Species with the highest percentages of parasitized nests in descending order were House Finch, Purple Finch, Red-eyed Vireo, Chipping Sparrow, Yellow-rumped Warbler, and Yellow Warbler. Those with the lowest percentages included Tree Swallow, Barn Swallow, Eastern Bluebird, Common Grackle, Spotted Sandpiper, and American Robin (Peck and James 1987). Of the 6 most frequently parasitized species, 3 are poor hosts for the cowbird: the Yellow Warbler and the 2 finch species. Cowbirds that hatch in finch nests almost always die because of the granivorous diet they are fed (Kozlovic 1998; Peck and James 1987; Wootton 2020).

In Ontario, 80.4% of hosts' nests were elevated and the remainder were on the ground. Of 1,690 elevated nests, 57.0% were in living deciduous trees and shrubs, 33.2% were in living coniferous trees and shrubs, 0.7% were in dead trees and stumps, 5.4% were inside or outside buildings, 1.7% were on bridges, and 1.7% were in cavities in trees, bird houses, fence posts, and light fixtures. Nests in deciduous trees, shrubs, and vines (47 species, 63.2% of nests) were selected more frequently than those in coniferous trees and shrubs (8 species, 36.8%). The most frequent nest substrates were hawthorns (253 nests), pines (232 nests), spruces (131 nests), maples (116 nests), white cedar (114 nests), raspberries (84 nests), willows (63 nests), and apple (51 nests). Ground nests were in clumps of grasses, weeds, cattails, and ferns (59.6% of nests); at bases of trees and shrubs and among roots (22.9%); in or under brush, dead branches, and leaves (5.5%); under overhanging rocks (4.0%); in sphagnum moss hummocks (2.5%); in rock crevices (2.5%); under rocks, logs, and boards (1.5%); beside logs (0.8%); and in upturned roots (0.8%). Elevated nests were 0.2-19.8 m from the ground, with most 0.9-1.2 m up. Of 1,925 nests, 29.4% were 0.2-1.1 m from the ground, 42.8% were 1.2-3.0 m from the ground, and 8.2% were at heights of 3.4-19.8 m (Peck and James 1987). In British Columbia, Campbell et al. (2001) reported nests 0-15.0 m from the ground, with most 0.9-2.1 m up. The cowbird prefers to nest in the shrub and sapling layer, although it may nest from the ground to the top of the canopy. It has nested as high as 24 m from the ground (Friedmann 1929).

Both the male and female maintain a distinct home range which may or may not be defended. What is unusual about the cowbird is that the female defends the territory and not the male. The female parasitizes nests within her home range. Whether the female defends the home range is dependent upon the density of host nests and also the cowbird density. Territoriality may be unnecessary at low densities of hosts or cowbirds and would be energy inefficient with limited rewards. At high densities of cowbirds, it is too difficult and energetically expensive to defend the entire home range. It is only at moderate densities of cowbirds in areas of moderate to high densities of hosts that defence of an area is viable. Territoriality is most prevalent in the east where cowbird densities are moderate. Where home ranges are defended, there is limited overlap in them but home ranges overlap considerably where they are not defended due to high cowbird densities. Most cases of parasitism by multiple females in a single nest occur where territories overlap or home ranges are undefended and overlap widely. Home ranges appeared to be defended in London but not in the Kingston area (Darley 1983; Dufty 1982; Friedmann 1929; Gates and Evans 1998; Hahn et al. 1999; Laskey 1950b; Rothstein et al. 1984; Teather and Robertson 1985; Yokel 1989). In London and New York where home ranges were defended, most aggressive encounters occurred at mutual

boundaries, with less aggression within the boundaries and outside the home range. At Kingston where home ranges were not defended, most aggressive behaviours by females occurred in the centre of their activity centres. Home ranges are maintained throughout the egg-laying season and aggression may continue until the home range is abandoned (Darley 1983; Dufty 1982; Hahn et al. 1999; Laskey 1950b; Teather and Robertson 1985). Males also have distinct home ranges but do not defend them. Instead, they establish dominance hierarchies with the dominant male mating with the resident female. Occasionally the sexes have the same home range boundaries. In the case of polygynous males, their home ranges overlap those of all females they are mated with. The overlap in the home ranges of the sexes is largely because males closely guard their females from other males. Males accompany their females most of the day, including in the afternoon feeding ranges. Movements of mated males may be restricted by their attendance to females but they occasionally move as far as 900 m outside their home range. Both sexes are within the breeding home range from just before sunrise until 1000-1100 hours, although some birds roost overnight within the breeding home range (Darley 1978, 1982, 1983; Dufty 1982; Elliott 1980; Gates and Evans 1998; Rothstein et al. 1984; Teather and Robertson 1986).

At London, the mean size of home ranges for mated males was 7.9 ha (range 0.4-25.0 ha). Ranges of unmated males were significantly larger and averaged 8.7 ha. Females had mean home ranges of 4.5 ha (range 0.9-13.4 ha). These was no significant difference in the home range sizes of yearling (4.4 ha) and adult (4.8 ha) females (Darley 1982, 1983). Near Kingston, the 90% core ranges of females averaged 8.58 ha or 9.89 ha using convex polygons. The range of members of a monogamous pair was similar, although the male's home range was larger (5.45 compared with 3.48 ha). The range of a bigamous male was 4.69 ha and encompassed most of his mates' home ranges which were 2.52 and 3.18 ha. The range of a trigamous male was 4.94 ha and overlapped the ranges of all 3 females, who had ranges of 1.95, 2.55, and 3.06 ha (Teather and Robertson 1985, 1986). In Illinois, female breeding home ranges averaged 9.10 ha, not significantly different from those of males (12.38 ha). Home ranges of the sexes overlapped by a minimum of 68% (Strausberger and Ashley 2003). In New Mexico, breeding home ranges averaged 38.5 ha in bison-grazed landscapes and 53.8 ha in cattle-grazed landscapes (Goguen et al. 2005). In New York, the average home range size of females was 9.38 ha (range 2.6-32.3 ha, median 7.6 ha). Six females that returned in the subsequent year used almost the same home ranges; they averaged 8.0 ha (Hahn et al. 1999). Another New York study reported breeding home ranges of 3-14 ha (Hahn and Fleischer 1995). In Ohio, home ranges were typically 7.3-8.1 ha, but occasionally as large as 12.1 ha (Nice 1937). In New York, 12 home ranges averaged 20.4 ha (range 11.0-29.7 ha). Ranges of the male and female of 1 pair were identical (Dufty 1982). In California, breeding home ranges averaged 68 ha. The smallest home range was in dense riparian habitat which appeared to be preferred habitat. The larger home ranges were probably related to the low density of both cowbirds and hosts (Rothstein et al. 1984). In Maryland, home ranges averaged 1,592 ha (range 105-6,958 ha). Although home ranges were large, most of the area was little used by females. Core home ranges were much smaller, covering a mean of only 3.5% (range 0.7-11.3%) of the home range. Average core home range was 31.6 ha (range 11.8-56.7 ha; Gates and Evans 1998).

Feeding home ranges are usually not occupied before 1100 hours except by nonbreeders. Birds remain at feeding areas until dusk when they move to the nocturnal roosts. Neither sex defends the

feeding home range although males may continue to display to each other and monogamous males may guard their mates (Darley 1983; Dufty 1982; Laskey 1950b; Rothstein et al. 1984). In some cases, home ranges were combined, with roosting home ranges occurring in both breeding and feeding home ranges and occasionally breeding and feeding home ranges were combined. Single-use core ranges were often oval or elongated in shape with a higher edge-to-area ratio than multiple-use core ranges. The long axis of core ranges often paralleled a habitat edge formed by an opening in a forest such as a stream or road. Roosting core ranges were longer and narrower than other types of core ranges and had significantly higher edge-to-area ratios. Core ranges used for more than 1 activity tended to be circular in shape. Mean core range sizes were 9.5 ha for breeding, 21.8 ha for breeding and feeding, 16.5 ha for feeding, 11.2 ha for feeding and roosting, 1.8 ha for roosting, 9.8 ha for roosting and breeding, and 31.6 ha overall. Breeding and feeding core ranges were significantly larger than roosting home ranges (Gates and Evans 1998). In New Mexico, the overall home range of cowbirds averaged 3,238.3 ha in bison-grazed landscapes and 740.3 ha in cattle-grazed landscapes (Goguen et al. 2005). California males were highly mobile both in the morning and afternoon. One male's movements covered 510 and 550 ha in 2 days. Males used more feeding home ranges (mean of 3.0) than females (1.6) and occasionally visited 3 feeding areas in a single afternoon. Males had larger total home ranges (195-385 ha for yearlings and 350-1,025 ha for adults) than females, with a range of 70-435 ha (Rothstein et al. 1984).

Limited information is available on natal philopatry rates. In Kansas, 2 of 13 nestlings (15.4%) returned (Elliott 1978). In Michigan, 12 of 15 young were recovered the next year in the same 10-minute block and the other 3 were recovered within 40 km of the natal area (Payne 1972). In California, 110 of 1,393 juveniles (7.9%) returned. These were banded as independent fledglings in feeding areas that were as far apart as 50 km and supported birds from a wide geographic area (Anderson et al. 2005). These results may not give an accurate representation of the proportion of birds that return to their natal area.

Adults tend to have high site fidelity. At London, 75.0% of mated males returned, 77.8% of unmated males returned, and 31.0% of nonresident males returned. The 2 nonresidents that returned and mated the following year settled 300 and 600 m away from their previous ranges (Darley 1982). Darley (1971) estimated the mortality rates from autumn to spring at 38% for males and 55% for females. The higher mortality rate of females may be due to egg laying, with the energy in a single egg representing 9% of the female's weight. At Delta Marsh, 65.5% of resident males and 46.6% of resident females returned in a subsequent year. Hahn et al. (1999) noted that site fidelity makes it likely that the female will encounter many of the host birds that bred there in the previous year. This allows it to monitor the progress of its young in host nests and preferentially select superior birds in subsequent years. In New York, females returned to the general area of their previous home range. Six returning females used nearly the same 8.0-ha home range. Another female was present in 3 years. In the second year, her home range overlapped with 53% of the year-1 home range. In the third year, her home range overlapped 89% with the areas used in years 1 and 2. Dufty (1982) also reported birds returning to the same home ranges in New York. In grassland habitat in Kansas, only 4.5% of males and 9.4% of females returned (Verheijen et al. 2017). Anderson et al. (2005, 2012) reported return rates of 10.2% and 12.1% in feeding areas in California. Because these were feeding areas that attracted birds over a large regional area, they do not represent breeding site fidelity rates.

In California, Elliott (1978) reported that only 3 of 14 adults (21.4%) returned to grassland habitat. This was a breeding area where a high proportion of nestlings returned. It is possible that adult fidelity rates to grasslands are lower than in other habitats. Rothstein et al. (1984) only attempted to find a single bird in a subsequent year and found the female in the same feeding area as the previous year. Breeding birds have strong homing instincts when displaced from their breeding ranges, with males more likely to return. Birds transported as far as 550 km have returned to their breeding home ranges within the same season. No transplanted juveniles returned (Manwell 1962; Wood 1952).

Limiting Factors

The Brown-headed Cowbird has evolved several adaptations for its parasitic behaviour. The parasitic cowbirds are the only North American species that are indeterminate egg layers. It can lay an egg a day for extended periods, similar to the domestic chicken. This allows it to lay eggs throughout the entire breeding season of their primary hosts (Jackson and Roby 1992; Payne 1965; Scott and Ankney 1980, 1983). Timing of egg laying is another adaptation. The cowbird lays its eggs very early in the morning, usually before it is light. At London, egg laying occurred an average of 9.14 minutes before sunrise. In Manitoba, females laid their eggs an average of 35.6 minutes before sunrise. By laying its eggs very early in the morning, it is considerably less likely to encounter the host at the nest. During the early egg-laying period, most hosts are absent from the nest. In order to parasitize a nest in the dark, the cowbird may check a nest for several days in advance before parasitizing it. In this manner, it knows where to deposit its egg a day in advance. Another adaptation is that the cowbird lays its eggs very quickly, spending only 5-10 seconds to slightly over a minute in the host's nest. This lessens the odds that the host and cowbird will encounter each other. A final adaptation is that eggs are typically laid during the host's egg-laying period, usually after there is at least 1 egg in the nest and before the host's clutch is complete. This ensures that the cowbird's egg is in the same timing sequence as those of the hosts. If the cowbird egg is the first egg in the nest, this increases the probability that the host will abandon it. Eggs laid once the host has started incubation may not have time to hatch. Cowbirds are often forced to lay in hosts' nests out of the preferred timing. This may occur if there is a shortage of host nests or if the nest that was selected for parasitism the previous day is unavailable due to predation or other factors. Cowbirds are completely silent in the morning, another adaptation to reduce the probability of detection by hosts. They do not vocalize until egg laying is complete in the morning (Ellison et al. 2019; Friedmann 1929; Hann 1941; Neudorf and Sealy 1994; Norris 1947; Scott 1991; Sealy 2015). The egg itself is highly adapted for parasitism. It closely mimics those of its traditional grassland hosts in the Midwest. There was no difference in the mean ground cover, colour, and density of maculation in cowbird eggs and those of Sprague's Pipit, Vesper Sparrow, Savannah Sparrow, Baird's Sparrow, Chestnut-collared Longspur, and Western Meadowlark in Saskatchewan. The cowbird has evolved a generalized egg appearance that mimics the eggs of multiple species in grassland communities (Klippenstein and Sealy 2010). Mimicry reduces the likelihood that cowbird eggs will be rejected by the host because hosts may have trouble distinguishing their eggs from those of the parasite (Peer et al. 2005). The cowbird's egg is 40% thicker than expected based upon its volume and can withstand approximately 2 times the amount of pressure than comparably sized eggs. The cowbird egg is also more rounded in shape than most eggs. This makes it more difficult for hosts to pierce cowbird eggs. Hosts often damage their own eggs while trying to pierce a cowbird egg through deflection of the blow. The cowbird

also drops its eggs into the nest from a height of 4-8 cm. The stronger eggshells prevent damage when laying and may damage hosts' eggs when dropped into the nest, thereby reducing competition for the cowbird nestling (Ellison et al. 2019; Picman 1989, 1997; Rohwer and Spaw 1988; Spaw and Rohwer 1987; Weatherhead 1991). The thickened eggshell has the potential to impeded gas flow to the developing embryo. Cowbird eggs have 1.9 times more pore area than those of the Red-winged Blackbird and significantly greater gas flux than those of comparable species. This adaptation allows cowbird eggs to hatch significantly earlier than expected (Jaeckle et al. 2012). Cowbird eggs typically hatch 1 or more days before those of the host, thereby conferring a significant competitive advantage to the cowbird nestling over the hosts' nestlings (Peer et al. 2005). For smaller hosts, the presence of the larger cowbird egg may reduce the amount of heat hosts' eggs receive. The cowbird egg may receive a disproportionate amount of the heat, thereby hastening its hatching. Cowbird eggs hatch faster even than the much smaller eggs of the Yellow Warbler. In Manitoba, the incubation period per ml of egg was 4.22 days for the cowbird and 8.92 days for the Yellow Warbler (Briskie and Sealy 1990; Friedmann 1929; McMaster and Sealy 1998). In order to provide additional competitive advantage to the cowbird egg, the female cowbird often removes host eggs or punctures them. It tends to remove eggs when there are 2 or more host eggs present. The last host egg is not usually removed because this may stimulate nest desertion. Eggs are typically removed from hosts' nest 1 or more days after it is parasitized. Removal of hosts' eggs fulfils 2 functions. The first is that the addition of the cowbird egg may increase the clutch size to the point where the host cannot adequately incubate the clutch. The second is that this results in 1 less host nestling that the cowbird nestling has to compete with. Removed eggs may be eaten, but many are just dropped or placed on the ground, indicating that eggs are not removed to obtain food (Carey 1986; Granfors et al. 2001; Hann 1941; Mayfield 1961; Peer et al. 2005; Scott et al. 1992). Female cowbirds may remove eggs and kill nestlings in unparasitized nests. The purpose of this appears to be to induce the host to renest, thereby providing another opportunity for parasitism (Elliott 1999; Granfors et al. 2001; Norris 1947; Peer et al. 2005). Cowbird nestlings usually grow faster than hosts' nestlings because they hatch earlier. Because they are larger, they also receive a disproportionate amount of the food that the adults provide. Host nestlings tend to beg for food only when an adult approaches the nest. Cowbird nestlings are much louder than host nestlings and beg continuously, ensuring that they get most of the food.

Females establish home ranges immediately upon arrival and pair formation occurs shortly thereafter (Darley 1983; Lowther 2020c; Teather and Robertson 1985). Eggs have been reported in Ontario nests from mid-April until the first week of August, with most present from the middle of the last week of May until slightly after mid-June (Peck and James 1987). At London, egg laying extended from the beginning of May until mid-July (Darley 1982). Also at London, the onset of laying was 3 or 4 May but was not until 13 May in the coldest year. The average laying rate was 0.73 egg per day. Fifty percent of birds were still laying in the last week of June. Scott and Ankney (1980) concluded that the average laying period was 4 May until 28 June, a total of 56 days. In Algonquin Park, eggs were present from early June to mid-July, nestlings were present mid-June to late July, and dependent fledglings were recorded from late June to late August (Tozer 2012). Other studies found that the egg-laying period lasts for 11-12 weeks. The initiation date may vary depending upon weather conditions but the end of the laying season is fairly constant. Egg-laying rates of 0.77-0.79

egg per day have been reported elsewhere (Fleischer et al. 1987; Igl and Johnson 2007; Norris 1947; Rivers et al. 2010). Incubation periods of 9-14 days have been reported in Ontario, and these varied by host species: 9-12 days in Eastern Phoebe nests, 9-10 days in Red-winged Blackbird nests, 14 days in a Northern Cardinal nest, 12 days in an Indigo Bunting nest, at least 10 days in a Purple Finch nest, and 9 days in an American Goldfinch nest. The incubation period was considered to be the time between the laying of the last host egg until the cowbird egg hatched. Incubation periods of less than 10 days probably indicated that the host began incubation before the clutch was complete (Peck and James 1987). In British Columbia, the incubation period was 10-13 days (Campbell et al. 2001). In Ohio, Nice (1939b) reported incubation periods of 11-14 days. In Pennsylvania, the average nestling period was 8.7 days (range 8-10 days). Friedmann (1929) stated that the incubation period was usually 10 days but that it could be as long as 12 days. Young may leave the nest at age 9 days if disturbed. Woodward (1983) reported nestling periods of 8-13 days (mean 10.9 days); 10-11 days was typical.

The cowbird is capable of laying approximately 40 eggs during a breeding season. In London, females laid an average of 40 eggs per season. An average of 4.0-4.6 eggs was laid on consecutive days, usually separated by 2 days without laying or occasionally only a single day. Twenty-eight percent of birds laid only 1 or 2 eggs before a day of not laying. The number of consecutive eggs has been termed a clutch by many authors. In late May and early June, the London clutch size averaged 4.5 eggs but declined to 3.5 eggs in late June and early July (Scott and Ankney 1980, 1983). In Illinois, laying patterns varied. One female laid an egg every day for 32 days and a total of 40 eggs in 48 days. Laying patterns were not significantly different from random and gave no indication that eggs were laid in clutches or sets. One female never laid on consecutive days and 18 had laying runs of 5 consecutive eggs with a mean of 9.0 days of uninterrupted laying. Many nonlaying runs lasted only a single day but some were as long as 17 days. These females were all yearlings that were capable of producing 30 eggs per year. These studies were done on wild birds confined in aviaries. Birds in pens may potentially lay more eggs than wild birds because they are fed ad libitum and do not expend energy by flying long distances (Jackson and Roby 1992). Chace et al. (2005) reported that females commuting 12 km between breeding and feeding areas laid 50% fewer eggs in a 5-day period than those commuting 2 km. In California, Fleischer et al. (1987) estimated that females laid an average of 30.5 eggs per season. Yearlings laid only 70.7% of the number of eggs as adults did, probably because they begin laying later in the season. Yearling laying rates were significantly lower than those of adults in May but similar later. In California, Oklahoma, and Michigan, Payne (1965, 1973, 1976) reported the same patterns as in London, with females laying a series of eggs on consecutive days with intervals of a few days to a few weeks between laying periods. The number of consecutive eggs averaged 3.1-3.8 (range 1-6 eggs), and the number of consecutive eggs laid was significantly higher at the start of the breeding season. Each female laid about 30 eggs, 200% of her body weight. The breaks between days of consecutive laying may be a result of the female not have enough stored protein or fat to produce an egg. In Michigan, a female laid 25 eggs in host nests over a period of 66 days (Walkinshaw 1949). Norris (1947) concluded that females laid at least 14 eggs per season in Pennsylvania. These 2 studies may have underestimated the actual number of eggs laid. The researchers may not have found all nests that the female parasitized. Eggs lost due to being dumped outside a nest, ejection by the host, or predation may not have been accounted

for. In New York, Hahn et al. (1999) calculated the effective fecundity of the cowbird to be 8.16 eggs per female per season. The effective fecundity included only those eggs that were laid in appropriate host nests and were not subsequently rejected by hosts. When a female does not find an appropriate host nest, she may dump an egg in an inappropriate host's nest or elsewhere, reabsorb the egg in the oviduct, or eat it after laying it to regain the nutrients. Although the cowbird lays a large number of eggs within a breeding season, only about 20% of them have an opportunity to develop into nestlings.

The cowbird greatly prefers to lay a single egg in each host nest and avoids laying more unless host nests are limited and it has no alternative. If more than 1 egg is laid in a host's nest, the cowbird nestlings have to compete with each other for food. Many smaller hosts are incapable of raising more than a single cowbird (Darley 1983; Goguen et al. 2011). In New York, only 1 of 92 nests (1.1%) was multiply parasitized by the same female. Approximately a third of nests were multiply parasitized and 73.3% were where home ranges overlapped. Home ranges, especially where they are defended, are important in reducing the incidence of multiple parasitism. Much multiple parasitism may be due to opportunistic laying by yearling females who may not be mature enough to hold a home range (Hahn et al. 1999). In Pennsylvania, 61.6% of parasitized nests contained a single cowbird egg and most (but not all) multiply parasitized nests were parasitized by more than 1 female. In Kansas, all nests were multiply parasitized, probably due to the high densities of cowbirds and broadly overlapping home ranges. About 40% of nestlings were full siblings, indicating that a single cowbird had laid multiple eggs in the nest; 19.6% of nests were parasitized by 3 or more females (Rivers et al. 2010, 2012). Friedmann (1929) reviewed approximately 9,000 records of parasitized nests of 195 host species and found that 66% contained a single cowbird egg. Ontario parasitized nests (n = 2,504) contained 1-7 cowbird eggs, with single records of 10 and 12 eggs. Of these, 65.3% contained a single cowbird egg and an additional 24.6% contained 2 eggs (Peck and James 1987). In British Columbia, parasitized nests contained 1-8 cowbird eggs, with 69% containing a single egg (Campbell et al. 2001).

Both sexes are capable of breeding when they are 1 year old. Payne (1973) concluded that it was unlikely that yearling males bred, or at least not in proportion to their numbers in the population. Yearling males have significantly smaller testes than adults but some are large enough to allow breeding. At London, there was no significant difference in the ability of yearlings and adults to procure mates and a similar proportion of each age class became paired. To acquire a mate, a male has to defend only the female and not an entire territory. The sex ratio of this population was 1.5 males to 1 female, so competition for mates was intense. Since yearlings succeed despite this extra competition suggests that male experience is not a critical factor in attracting a mate (Darley 1978). The Brown-headed Cowbird appears to be the only species in which adult males dominate yearlings at food resources but not at mate acquisition (Weatherhead and Teather 1987). In New York, 41.6% of paired males were yearlings, similar to their proportion in the population (Dufty 1982). Near London, yearling males were more likely to be paired or in groups of males; adult males were much more likely to be single. Because of the highly skewed sex ratio, many males were unsuccessful in acquiring a mate (Ankney and Scott 1982). At London, 113 of 154 males (73.4%) were unmated. Previous experience and age were not factors in whether a male became mated. Of 10 returning males that were mated the previous year, only 5 (50%) acquired a mate in the current year

(Darley 1982). It is typically assumed that all females breed, but this was not the case at London. Of 102 females, 44 (43.1%) were breeding residents, 2 (2.0%) were nonbreeding residents, and 56 (54.9%) were nonresidents. The 2 nonbreeding residents were yearlings (Darley 1983). In California, some males did not breed. Their behaviour differed from those of mated males. They did not have a consistent morning range, were equally likely to occur in feeding as breeding areas in the morning, were silent and sedentary on the breeding range, and used a communal roost rather than roosting individually similar to mated birds (Rothstein et al. 1984).

The mating system of the Brown-headed Cowbird has been described as monogamous, polygynous, polyandrous, and promiscuous. Most early studies concluded that the differing conclusions were because some researchers studied only associations of males and females; others based their conclusions on observed copulations. It is now recognized that the cowbird uses all these mating strategies. Although mating strategies often vary geographically, they are mostly determined by the density of cowbirds. Even within a given area, individuals may use differing mating strategies. In London, monogamy prevailed. Most females copulated with a single male and the pair remained mated for the entire season. Darley (1982) temporarily removed some females. Some replacement males were mated neighbours, resulting in them becoming bigamists. Bigamy occurred despite the presence of unmated males indicating that females preferred to mate with dominant males. Near Kingston, Teather and Robertson (1986) reported 4 cases of monogamy and 3 of polygynous matings, including 1 male that was trigynous. There were also 2 possible cases of polyandry, but data were insufficient to confirm this. Some males exhibited simultaneous polygyny, being associated with more than 1 female at the same time. They usually alternated days with their mates, spending 1 day with one and the next day with the other. When a male was removed, the number of times his female was courted by other males increased significantly, suggesting that mate guarding was effective. Forty-five percent of males were unmated. Observed copulations suggested that there were opportunities for them to obtain extra-pair copulations. Both the spatial distribution of host nests and the sex ratio of the cowbird population may influence the mating system. If host nest density is high, females may defend their home ranges. Mate guarding would result in monogamy in this scenario. If the distribution of host nests is such that it is not advantageous for the female to defend the home range, the effectiveness of mate guarding declines and promiscuity results. Pair bonds may also break down as the sex ratio approaches unity, thus reducing the advantage to males of mate guarding. In Tennessee, Laskey (1950b) concluded that the cowbirds around her house were monogamously mated. Females displayed against males other than their mates who attempted to court them. In the London area, the mating system was a combination of monogamy and promiscuity. Males use 2 tactics to obtain copulations. The first is to obtain a mate and vigorously defend her from other males, resulting in a monogamous relationship. The second tactic is to not attempt to mate but to steal copulations from mated females (Ankney and Scott 1982). Friedmann (1929) concluded that most birds near Ithaca, New York, were monogamous. Dufty (1982) also concluded that the population he studied in New York was predominantly monogamous. In Kansas, the mating system was promiscuous. Males regularly courted and chased several females daily and females were observed copulating with different males. In this area, cowbirds were abundant but hosts were less abundant, so females did not defend their home ranges. Long-term pair bonds appeared to be nonexistent (Elliott 1980). In

California, the mating system was monogamous. Males attempted to be bigamous but few (5%) were successful. Mated females refused advances from males other than their mate; 0 of 73 observed copulations were extra-pair. Monogamy appears to be the dominant mating system where cowbird densities are low and where females establish well-defined home ranges (Yokel 1986, 1989; Yokel and Rothstein 1991). At another California site, there was little monogamy in the population (Rothstein et al. 1984). In Illinois, Strausberger and Ashley (2003) used DNA analysis of eggs and nestlings to determine mating strategies. Results indicated frequent repeat matings among pairs (monogamy) and frequent polygyny. Both sexes sometimes reproduced with multiple partners (promiscuity) and 5 females mated polyandrously with 2-3 males. Polygynous males typically mated with females that parasitized nests in the zone of overlap of home ranges. The mating system did not fall neatly into any of the 4 mating system categories and exhibited varying degrees of each category. The cowbird reproduced most frequently with a primary partner and less often with additional individuals. The incidence of monogamy may decline as cowbird density increases and extensive overlap of home ranges may contribute to the frequency of promiscuous behaviour. Most pair bonds persisted throughout the breeding season in Iowa and New York (Dufty 1982; Lowther 1987). In New York, both members of some pairs returned the following year. Some reunited and occupied much the same home ranges as in the previous year. One female settled with a new mate in an area adjacent to her former mate, who also had a new mate (Dufty 1982).

Feeding home ranges differ from breeding areas by having areas of short grass or other low vegetation. Breeding areas are rarely used for foraging, but the cowbird may feed opportunistically on cicadas or on oak flowers (Curson et al. 2000; Schweitzer et al. 1998). Nonbreeding birds may forage within breeding areas (Rothstein et al. 1984). Feeding rarely occurs during the first 5 hours after sunrise. This may cause stress to birds, particularly females due to the energetic costs of reproduction. Females spend more time at feeding areas and less time travelling between feeding and breeding areas than males. Only females exhibit a peak in feeding just before dark (Rothstein et al. 1984). Almost all feeding occurs on the ground, usually by hopping, pecking, or scratching, and it preferentially forages with cattle, horses, or other large ungulates. When foraging with cattle, it groups around foraging and moving cattle rather than those that are stationary. They remain within 1 m of the cow, behind its feet and mouth, and dart after insects flushed by the cow's feet. It eats seeds exposed in grazed vegetation, in bare soil, and in dried lakebeds. At horse corrals, it commonly hawks slow-flying insects and pecks insects from livestock manure. It eats dandelion seeds from seed heads by pinning the stem to the ground with 1 foot. It follows tractors working up the land in flocks mixed with Red-winged and Brewer's blackbirds. These flocks feed in a rolling-block formation, with birds at the back of the flock continuously flying to the front just behind the tractor. Early in spring, it may feed on leaf buds (Beasley and Carothers 1974; Bent 1958; Fitch 1958; Friedmann 1929; Gates and Evans 1998; Goguen and Mathews 1999; Goguen et al. 2005; Laskey 1950b; Lowther 2020c; Morris and Thompson 1998; Rothstein et al. 1980; Schweitzer et al. 1998). Weatherhead and Teather (1987) provided food for cowbirds and determined that adult males were dominant to yearling males in 81.8% of cases. Bent (1958) reported a female cowbird feeding young in a Rose-breasted Grosbeak nest. It fed only the cowbird nestling and pecked the young grosbeaks on their heads when they begged. There is a record of a female cowbird feeding a cowbird nestling in a Yellow Warbler nest. In both cases, it was unknown if the female cowbird was the parent.

Nestlings are fed the same food that hosts provide to their own nestlings. This entails little adaptation by cowbird nestlings. Although adults of the host species may eat a wide variety of food items, most feed their young an insectivorous diet. Those that feed their young seeds, such as the finches, are poor hosts because the diet they provide is deficient in the protein that young cowbirds require. The diet of 14 nestlings included march flies, caterpillars, spiders and their eggs and cocoons, foxtail seeds, short-horned grasshoppers, weevils, burrowing mayflies, dock seeds, snail shells, stink bugs, click beetles, leaf beetles, ground beetles, hymenopterans, smartweed seeds, wolf spiders, grubs, buds, cicadas, dragonflies, moths, treehoppers, ants, dodder seeds, and sedge seeds. Most stomachs contained 99-100% animal matter but one was half full of vegetation fibres. Cowbird nestlings have been observed being fed cutworms, small insects, caterpillars, and small moths by Red-eyed Vireos and Chipping Sparrows; neuropterans, cutworms, caterpillars, mayflies, wasps, and moths by Chestnut-sided Warblers; and earthworms by American Robins. One Common Yellowthroat fed a small garter snake to a young cowbird. Many species feed it eggshells (Friedmann 1929).

Early in spring, the adult diet is predominantly vegetarian through the prelaying period, becomes insectivorous during laying, and switches back to mostly plant foods postlaying. Animal food comprises 10-15% of the spring diet, mostly weevils and caterpillars. The plant food is mostly foxtail seeds but the cowbird also eats seeds of barnyard grass and ragweed. During laying, the consumption of insects is much more pronounced in females. Both sexes eat snail shells at this time, especially females during the laying period. By mid-July or earlier, the diet once again becomes mostly vegetarian (Friedmann 1929; Payne 1965; Scott and Ankney 1980). Overall, the diet consists mostly of weed seeds: 94% by volume in winter and 48% in summer. Foxtail seeds are favoured in most areas and ragweed seeds are important in some regions. Other seeds it commonly consumes include those of oats, corn, crabgrass, wheat, smartweeds, panic grasses, croton, timothy, and barnyard grass. Less frequently, it consumes smooth sumac, blackberries, blueberries, mulberries, thistle seeds, amaranths, chickweeds, mustard seeds, blackberries, huckleberries, wild cherries, and wild grapes. Grasshoppers and locusts are favoured insect foods and these are the species most frequently flushed by foraging ungulates. It commonly eats beetles and lesser numbers of caterpillars, spiders, and millipedes are eaten. Other animal foods include house fly pupae, ants, plant bugs, scarab beetles, harvestmen, thread-waisted wasps, true bugs, weevils, long-horned grasshoppers, and leafhoppers. In Ohio, the diet consisted of 28.0% wheat, 26.7% corn, 10.6% flatsedges, 6.6% bulrushes, 6.3% smartweeds, and 3.4% animal matter, including dragonflies, beetles, and flies (Bent 1958; Friedmann 1929; Lowther 2020c). In Quebec by volume, the diet 10-19 May consisted of 40.7% vegetable matter, 31.8% animal matter, and 27.5% unidentified material. The vegetation consisted of 34.4% barley, 3.4% corn, 2.2% prostrate knotweed, 0.7% timothy, and less than 0.1% curly dock. The animal food consisted entirely of beetles: 15.8% scarab beetles, 6.4% weevils, and 3.2% each for bark, ground, and click beetles. The diet 14-29 July was comprised of 44.5% vegetable matter, 38.0% animal matter, and 17.5% unidentified material. The vegetation consisted of 23.4% barley, 5.8% prostrate knotweed, 5.5% curly dock, 3.9% corn, and 3.9% foxtails. The animal matter consisted of 9.5% spiders, 4.8% ants, 4.8% millipedes, and 18.9% beetles (9.5% scarab beetles, 4.7% click beetles, and 4.7% weevils). The diet 12 August to 16 September was comprised of 64.1% vegetable matter, 7.5% animal matter, and 28.4% unidentified material. The

plant food consisted of 27.0% barley, 10.9% prostrate knotweed, 9.7% corn, 5.3% panic grass, 4.5% foxtails, 3.7% timothy, and 3.0% curly dock. The animal food consisted of 1.9% crickets, 1.9% scarab beetles, 1.9% rove beetles, and 1.8% true bugs (Potvin et al. 1976). Beal (1900) examined the contents of 544 stomachs. The birds had consumed 22.3% animal matter and 77.7% vegetable matter. The animal food was almost entirely insects and spiders with a few snails. Insects included wasps and ants, bugs, a few flies, beetles, grasshoppers, caterpillars, and bugs. The bugs were mostly stink bugs and leafhoppers but it consumed a few cicadas. It ate many leafhoppers, especially in June and July when they constituted 60% of the contents of some stomachs, but they represented only 1.5% of the annual diet. Wasps and ants constituted 3% of the annual diet and beetles represented 5.3% of the diet. These were mostly weevils that were consumed April through June. Grasshoppers were the favourite animal food, comprising about half the animal food and 11% of the annual diet; in August, they represented 45.1% of the diet. Caterpillars were eaten every month but constituted only 2% of the entire diet, peaking at 10% in May. Grain constituted 16.5% of the diet (8.6% oats, 1.4% wheat, and 6.5% corn) with about half being waste grain. Fruit was insignificant in the diet with only a few raspberry and blueberry seeds in stomachs; they may have been eaten as seeds rather than fruits. Weed seeds were the most important component of the diet and were consumed year-round. It ate weed seeds almost exclusively in winter and they comprised 60% of the total annual diet. The most abundantly eaten seeds in decreasing order were barnyard grass, ragweed, panic grass (with these 3 dominating the diet), smartweeds, sorrel, paspalum, and amaranths, with small amounts of thistles, black mustard, chickweed, plantains, sunflowers, gromwells, and blue-eyed grass.

Habitat loss is a significant limiting factor for the Brown-headed Cowbird, although limited mention has been made of this in the literature. The eastern population has declined in the United States due to an increase in forest cover and planting grasslands to trees. Natural forest regeneration reduces habitat and has made more areas unsuitable for it in the Canadian Shield of Ontario (Chace et al. 2005; Houle and Choiniere in Gauthier and Aubry 1996; Tozer 2012). Loss of grasslands and pastures are more significant than an increase in forest cover, particularly south of the Shield in Ontario and Quebec. A high proportion of these have been converted to row crops which provide no breeding habitat and foraging habitat that is inferior to grasslands. Pastures that support livestock are optimum for foraging, but the number of cattle in the province has declined significantly and continues to decline (Statistics Canada 2018). In addition, cattle are now often confined to barns or other enclosures where their feeding activities do not stir up insects for cowbirds to prey upon. Its decline in Quebec between their 2 atlases was attributed in part to new farming practices and habitat loss. In the St. Lawrence Lowlands approximately 75% of perennial crops were replaced by annual crops from 1993 to 2004, accompanied by livestock confinement (Houle and Choiniere in Gauthier and Aubry 1996; McCracken 2003b; Michaud in Robert et al. 2019). In Illinois, the decline in area of pastures in the first half of the 20th century was considered an important loss of both breeding and feeding habitat (Graber and Graber 1963). Another form of habitat loss is the decline in populations of several host species. As the number of potential hosts declines, there are fewer nests to parasitize and fewer cowbirds will be raised. A scarcity of host nests can lead to multiply parasitized nests, further lessening the likelihood of cowbirds fledging (Friedmann 1929). Grassland birds are generally in decline and these are the cowbird's traditional hosts.

Another significant limiting factor for the Brown-headed Cowbird is its low nesting success. It rarely lays eggs in nests of completely inappropriate hosts in which the egg has no chance of survival (Sealy 2015), but egg dumping outside a nest may be common. It frequently lays eggs in nests of species that eject eggs and these eggs have limited potential for success. These include the kingbirds, meadowlarks, orioles, American Robin, Gray Catbird, Brown Thrasher, and Cedar Waxwing. At London, 43.8% of catbird nests were parasitized but these produced few cowbirds. There is evidence that some of the larger species that were formerly acceptor species are beginning to eject eggs at a higher rate and are evolving into rejecter species, particularly the meadowlarks and Baltimore Oriole. Laying eggs in nests of rejecters is a significant source of mortality for the cowbird (Chace et al. 2005; Friedmann et al. 1977; Grzybowski and Pease 1999; Lowther 2020c; Peer et al. 2000, 2005; Rivers et al. 2010; Scott 1977). Hosts that feed their nestlings a granivorous diet may be frequently parasitized, but cowbird eggs laid in their nests have little chance of survival. These include the House Finch, Purple Finch, Pine Siskin, and American Goldfinch. Aerial insectivores such as swallows and wood-pewees may cease feeding their nestlings for extended periods during inclement weather. These species typically raise few or no cowbirds (Campbell et al. 2001; Grzybowski and Pease 1999; Kilpatrick 2002). The nest success rate of the cowbird is much lower than that of its host species. This is because many hosts abandon parasitized nests, bury cowbird eggs, or have other defences. It has been estimated that the average survival of a cowbird egg to adulthood is only 3%. When a host deserts a parasitized nest, the cowbird egg dies but the host has an opportunity to raise a replacement brood. In Pennsylvania, 26.8% of cowbird eggs laid in a variety of host nests produced fledglings compared with 37.7% for hosts. In Michigan, 1 female laid 25 eggs and 0 produced a fledgling. Most parasitized nests were deserted and a few were depredated. Yellow Warblers tend to either bury the cowbird egg or abandon parasitized nests. Cowbird success rate has been determined to be very low in Yellow Warbler nests in Manitoba, Michigan, and Ontario, with only 5.4% of Ontario eggs producing a fledgling. Nonetheless, parasitism rates on the Yellow Warbler tend to be high. In Kansas, only 13 of 157 cowbird eggs (8.3%) were successful. This was attributed in part to the high density of cowbirds and a high rate of multiple parasitism. In Prairie Warbler nests, only 9 of 102 cowbird eggs (8.8%) hatched and only 5 produced fledglings. At London, 80% of Northern Cardinal nests were parasitized. Cowbird egg mortality was 85% in cardinal nests as a result of egg removal or nest desertion. Only 5.4% of cowbird eggs produced fledglings and this occurred only in broods with a single or no cardinal nest mates. The cardinal is another commonly parasitized species that produces few cowbirds. South of the Shield in Ontario, parasitized nests of the Red-eyed Vireo, Yellow Warbler, cardinal, Chipping Sparrow, and Song Sparrow were all abandoned significantly more than unparasitized nests (Campbell et al. 2001; Elliott 1977; Friedmann 1963; Graham 1988; McGeen 1972; Nolan 1978; Norris 1947; Peer et al. 2005; Scott and Lemon 1996; Walkinshaw 1949; Weatherhead 1989). Species that have been in long contact with the Brown-headed Cowbird have learned to recognize it as a threat and are extremely aggressive toward it. These include some of the superior hosts such as Red-winged Blackbird and Song Sparrow as well as the Eastern Kingbird, Willow Flycatcher, Eastern Phoebe, and Red-eyed Vireo. Aggression appears to be effective only where the host occurs at high densities relative to the cowbird. The Red-winged Blackbird's mobbing behaviour is the most effective at preventing or reducing the incidence of parasitism. It is one of the best hosts for the cowbird, along with the Song Sparrow, but is parasitized significantly less than its availability because of its aggressive nature

(Chace et al. 2005; Friedmann 1963; McGeen 1972; McLaren et al. 2006; Nice 1937; Peer et al. 2005; Robertson and Norman 1976, 1977). Most hosts continue to evolve behaviours to avoid or reduce parasitism and these are likely to lead to further declines in cowbird productivity unless it can evolve new strategies such as laying highly mimetic eggs. In this event, egg patterns may have to be distinct in different areas to reflect local host populations (Peer et al. 2005). Another factor that may lower cowbird productivity is the constant begging of its nestlings. This has the potential to attract predators.

Humans often directly affect cowbird nesting success by removing eggs from hosts' nests and killing adults to reduce parasitism rates. Many individuals believe that they are doing a good deed by removing a cowbird egg from a nest, but the cowbird is a native species whose population is declining significantly. No targeted cowbird control programs have been implemented in Ontario, but several occur in the United States in efforts to conserve species-at-risk songbird populations. The most common method is to trap and kill cowbirds in the local area and remove parasitic eggs from nests. This may be effective in reducing parasitism rates and improving nest success rates of the target species, but in no case has this resulted in an increase in the host population. Other techniques have been used to attempt to reduce parasitism rates. These include moving grazing cattle to extend the distance between breeding and feeding areas, controlling cowbirds on feeding ranges that serve as a network of breeding areas, and massive kills of birds at winter roosts. These other techniques have generally failed because of the prevalence of feeding areas other than grazed pastures; many birds, especially females, do not exhibit a consistent commuting pattern between breeding and feeding ranges; and birds from winter roosts disperse to disparate geographical areas so a large kill at 1 site has minimal effect on breeding populations at a given area. The only effective control method is local removal within the area of a population of an endangered species. Control methods should be considered temporary stopgap measures until the real limiting factors affecting the endangered host can be rectified. Long-term control programs have the potential to have 2 adverse effects. The first is the perception that appropriate management is being undertaken. Control programs may divert funds that would be better invested in creating habitat for the species at risk. The second is that host communities that experience long-term periods of parasitism control may not evolve their own antiparasitic behaviours that could protect them in future from parasitism (Bent 1958; Chace et al. 2005; Hahn et al. 1999; Laymon 1987; Lowther 2020c; Ortega et al. 2005; Rothstein et al. 1987).

The cowbird responds favourably to forest management. In the Boreal Forest Region, it increased by 60% when 80% of trees were removed. It was almost 100% more abundant when 0% of trees were retained compared with where 100% of trees were retained (Vanderwel et al. 2007). In Ontario south of the Shield, it was significantly more abundant in heavy diameter-limit cuts than in selective cuts and uncut forests. It was not significantly more abundant in woodlots selectively cut than in those that were not cut. It was negatively correlated with basal area (Holmes et al. 2004). In Minnesota, it increased in abundance in response to tree removal (Hanowski et al. 2003, 2005). In Pennsylvania, it was more than 2 times as abundant in forest stand improvement plots where snags were retained than where snags were removed. Areas with snag retention had a more patchy and open growth and greater abundance of low plant growth (Stribling et al. 1990). In New York, the

cowbird occurred regularly in clear-cuts in low numbers. Its density was low 2-5 years after cutting, moderate 6-10 years after cutting, and low 14-120 years after cutting (Keller et al. 2003).

The cowbird responds favourably to all types of forest fragmentation (Lowther 2020c). In West Virginia, it increased significantly closer to well pads, access roads, and pipelines and was attracted to them. Its probability of occurrence increased to 40% from almost 0% (Farwell et al. 2019). In Alberta, it was more abundant near seismic lines than in adjacent forest interior, but not significantly. It was significantly more abundant at well pads than in adjacent forest interior (Bayne et al. 2016). In New Jersey and Pennsylvania over a 15-year period, hemlock declined from 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The cowbird increased and exhibited one of the strongest positive associations with hemlock decline (Toenies et al. 2018).

Two studies concluded that fires in grasslands elicit no significant responses by the cowbird (Madden et al. 1999; Roberts et al. 2012). Rose and Simons (2016) studied its response to fire in a pine-oak forest. It occurred more frequently in burned than unburned areas, but only after high severity burns that caused almost complete removal of the understorey and more than 60% mortality of the canopy. Peak occupancy occurred 0-5 years after fire and declined thereafter.

Status

It is unlikely that the cowbird occurred in Ontario prior to European settlement. At that time, it was endemic to the short- and mixed-grass prairies of the Midwest where it was associated with bison. Widespread destruction and fragmentation of forests by Europeans created much more habitat and allowed it to expand its range eastward and, to a lesser extent, westward. It was widespread in the eastern United States by the early 1800s and reached the far west by the 1920s. It moved into Ohio and Michigan just before 1840. Other factors that contributed to its range expansion included widespread draining of swamps and marshes to create croplands, irrigation of arid lands in the southeast, and the proliferation of cattle (Chace et al. 2005; de Vos 1964; Friedmann 1929; Lowther 2020c; Rothstein and Peer 2005; Schweitzer et al. 1998).

The cowbird was first recorded in Ontario in the 1870s according to McLaren et al. (2006), but Weir (2008) reported that it was common in the Kingston area in the 1850s. It appeared to decline starting in the 1970s. In Elgin County, it was extremely common in 1891 (Lancaster et al. 2004). It occurred in the southern counties of Ontario by 1886 and first appeared in Muskoka and Parry Sound districts in 1889 (de Vos 1964; Mills 1981). de Vos (1964) reported that it was frequent at North Bay in the late 1930s and that there had been significant increases west of Lake Superior. In the 20th century prior to his publication, its range expanded northward approximately 320 km. Fleming (1907) considered it an abundant summer resident in Toronto. Friedmann (1929) considered the Ontario range of the cowbird to extend from the southern Great Lakes to the north shore of Lake Superior and Lake Huron. It was absent in the Boreal Forest Region. Baillie and Harrington (1936) reported that it occurred north to Moose Factory and west to Lake of the Woods. It had been found breeding throughout this range, but was not common in the northern parts of its range except in the extreme west. The first atlas determined that its range included all of Ontario south of the Boreal Forest Region, with occasional records within this area in the northwest, east of Lake Nipigon, and in the Clay Belt. Breeding was confirmed in the Moosonee area. It was most abundant in the

agricultural south. It associated mostly with agriculture in the north, but also occurred along highways through densely forested landscapes (Graham in Cadman et al. 1987). James (1991) considered the cowbird a common summer resident north to Kenora, Lake Nipissing, and Cochrane and rare to Pickle Lake and Moosonee.

The second atlas revealed only minor changes in the distribution of the cowbird since the first atlas. It was not recorded in many of the blocks in the Boreal Forest Region where it was previously documented. It continued to breed in the Moosonee area. Its probability of observation declined significantly province-wide and in all regions except the Carolinian Forest Region. The declines were attributed to agricultural intensification, loss of pastureland, disappearance of small dairy farms in the south, and increased forest cover in the north. Highest densities occurred in the intensively farmed areas of southwestern Ontario. The entire area south and east of the Canadian Shield supported moderate to high densities. Low densities were reported in the Shield portion of the Great Lakes–St. Lawrence Forest Region and around the northern shore of Lake Superior (Falk in Cadman et al. 2007).

BBS data indicate that the Brown-headed Cowbird has been decreasing at a significant rate continent-wide and in Canada since the survey was initiated in 1966. Declines are most pronounced in eastern Canada and the eastern United States, but it is still increasing in the far west where it is a more recent arrival (Chace et al. 2005). McCracken (2003b) stated that it had been declining at a rate of 2.3% per year since the BBS started. This resulted in a continent-wide cumulative loss of 33% of its population. Losses were higher in Canada at 57%. Cadman et al. (2016) reported that it declined in Ontario at a rate of 3.7% per year from 1983 to 2013. It was tied for 15th for the greatest decline rate of all Ontario breeding birds. BBS data indicate that it decreased at annual rates of 0.958% in Canada and 4.16% in Ontario 1970-2021. Trends 2011-21 were annual decreases of 0.58% in Canada and 4.17% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

There are 5 stages of fledgling development: leaving the nest, inactive, active, superactive, and independence. At fledging, young are capable of very weak flight and tend to move 3 m or less from the nest. Height above the ground after fledging was 0-5 m in Virginia and Maryland (average 2 m). Nine fledglings perched in a tree or shrub and one remained on the ground. Shortly after fledging, they tend to move higher in the vegetation, usually by short flights or climbing through trees. The inactive period lasts for the first 2-3 days out of the nest. They perch quietly during this stage except when the foster parents arrive with food or they have not been fed in a while. They occasionally fly short distances, usually less than twice an hour. Most mortality of fledglings occurs in the inactive stage. The active stage occurs 3-13 days out of the nest and is characterized by 2-9 flights an hour, increasing with age. Flights are usually independent of the hosts' activities but they occasionally fly toward an adult to be fed. Fledglings start pecking 1-6 days out of the nest and first feed themselves at age 20-22 days. As they mature, they spend more time on the ground, 5-13 days after fledging at age 14-23 days. The superactive stage begins 12-23 days out of the nest at age 21-32 days and 3-11 days before independence. This stage is characterized by constantly flying after their hosts and actively begging. They forage for themselves when the hosts are absent, but stop feeding and beg when they return. They become independent 16-28 days after leaving the nest at age 25-39 days

(mean 31.5 days). The final step in achieving independence occurs when the host stops feeding. Fledglings do not become imprinted on their hosts. They appear to recognize them as a species but not as individuals. They are occasionally fed by host-conspecific birds that had not raised them. Birds of other species are usually ignored but they regularly beg from their host. Occasionally they beg from other species and may even be fed by them. Fledglings raised by different host species behaved in the same manners except for their perch heights. They typically perched near the heights where hosts obtained their food and this varied by species: 0-3 m for Carolina Wren, Song Sparrow, and Eastern Bluebird; 6.1-9 m for White-eyed Vireo, 9.1-12 m for Eastern Phoebe, and 12.1-15 m for Acadian Flycatcher and Blue-gray Gnatcatcher. The difference in height preferences often occurred in the same habitat patches, so the variability was due to host preferences. Home ranges of fledglings were 0.3-5.6 ha and highly correlated with the hosts' home range size. Only perch height and home range size were modified in a host-specific manner. Their primary adaptation was their loud and persistent begging resulting in them being fed more than the hosts' fledglings (Friedmann 1929, 1963; Woodward 1983; Woodward and Woodward 1979b).

Fledglings develop the typical cowbird foraging behaviour regardless of which host species raise them. This increases their chances of survival during the period that they depend upon the host. By the time they are 20-25 days old, they have developed all behaviours required to maintain them. The feeding rate for fledglings varied from host to host but was always significantly greater than for the hosts' young. They are fed different foods depending upon the host. Phoebes fed larger items such as dragonflies, adult and larval lepidopterans, flies, crickets, plant bugs, and mulberries. Carolina Wrens fed smaller items that were mainly isopods and harvestmen with some adult lepidopterans and caterpillars. The Eastern Bluebird provided caterpillars, moths, grasshoppers, flies, and blueberries. Common Yellowthroats provided grasshoppers and caterpillars. The Acadian Flycatcher, Blue-gray Gnatcatcher, and Song Sparrow provided food items that were too small to identify. When 2 fledglings leave the same nest, they separate until late in the fledging period but are aware of the other being fed (Woodward 1983).

There is some evidence that adults may associate with their own young and possibly feed them on occasion. In New York, Hahn and Fleischer (1995) used DNA analysis to determine that 4 of 11 pairs of adult females and juveniles trapped together were related; 0 of 18 randomly paired trapped birds were related. This suggested that the female may follow the progress of her eggs and associate with her offspring once they become independent, or nestlings could become visually and vocally familiar with the female if she is frequently in the area. Lorenzana and Sealy (1998) reported 5 cases of both adult males and females feeding cowbird nestlings and fledglings. In Saskatchewan, 2 independent fledglings were observed soliciting food from a pair of adults. Bent (1958) reported a cowbird feeding an individual cowbird fledgling but ignoring others. In Hamilton, 2 males used vocalizations to wean a fledgling away from its Northern Cardinal host (Curry 2006).

Once they become independent, juveniles form large flocks that do not contain any adults. These flocks wander widely in open habitats. Flocks may form as early as the end of July and are most prevalent toward the end of August (Campbell et al. 2001; Friedmann 1929). Once the egg-laying period is over, adults vacate the breeding areas. They may completely disappear from a site around mid-July and not be observed again until autumn migration in September or October. In

some areas, adults disappear by the end of June, with females leaving later than males. The reason for the disappearance of the adults is uncertain, but may be related to the moult which starts in late July or early August and extends to mid-September. It has been stated that adults spend the moult in marshes but no study has been done on this (Campbell et al. 2001; Friedmann 1929; Norris 1947; Payne 1973; Rothstein et al. 1980).

During the postfledging period, cowbirds leave the treed and shrubby habitats where most breeding occurs and concentrate in feeding areas. These often are in different locations than the breeding season feeding areas. Birds wander considerably at this time and their habitat preferences may change. In the Hamilton area, flocks initially concentrate around grazing cattle and move to harvested cornfields later in the season. The early part of the postfledging period may be when it concentrates most around livestock, but the switch to agricultural lands prior to migration is typical throughout its range. Historically, it inhabited patches of wild rice at edges of marshes in Ontario. It may occur in a variety of habitats in both urban and rural areas. In British Columbia, it heavily uses farmlands, especially pastures and feedlots with horses and cattle as well as agricultural crops. It also occurs in nurseries, urban parks, backyard feeders and gardens, utility rights-of-way, clear-cuts, garbage dumps, marshes, reservoirs, ponds, and estuaries. Similar habitats are used in Ontario and other locations. It usually occurs in flocks, with flocks as large as 10,000 reported elsewhere. Once it moves to agricultural croplands, it may occur in mixed flocks with other blackbird species (Campbell et al. 2001; Curry 2006; Friedmann 1929; McIlwraith 1894; Porneluzi et al. 2014).

Roosts are an important habitat component during the postfledging period. Cowbirds roost communally and often with other species such as the Purple Martin, American Robin, European Starling, House Sparrow, Red-winged Blackbird, and Common Grackle. In mixed roosts, the dominant species are usually starlings, Red-winged Blackbirds, and grackles, with cowbirds representing a small proportion of roost mates (Friedmann 1929; Joyner et al. 1980; Lyon and Caccamise 1981; Weatherhead et al. 1980). In New York, 20 roosts were in hardwood stands and 2 were in common reed. The cowbird avoided contiguous forests avoided as roost sites and selected smaller wooded patches. Roost sites were 0.13-10.4 ha, with larger areas supporting more birds. Tree density was typically high at roosts (average 1,741 trees per ha). No sites with fewer than 720 trees per ha were used. The most consistent characteristics of roost sites were related to canopy structure. The canopy at roosts was closed with a compact vertical arrangement of twigs of uniform size. These features were typical of young stands in early successional stages. The mean age of stands supporting roosts was 25 years (range 18-34 years); 68% of roosts were in stands 21-26 years old. The mean age of stands supporting roosts was significantly less than stands without roosts (41 years). These roosts were dominated by starlings and grackles, so their habitat preferences may have affected roost-site selection by the cowbird (Lyon and Caccamise 1981). In late August and September, it often selects marshes for roosting along with other blackbird species (Friedmann 1929; Joyner et al. 1980; Sheppard et al. 1936).

The diet of the cowbird changes during the postfledging period. Early in the period, it continues to feed on animal foods, particularly beetles, caterpillars, grasshoppers, and leafhoppers and later switches to vegetable matter. In Oklahoma, the percent occurrence of food items in 35 stomachs was 71% sorghum, 63% ragweeds, 63% insects, 49% sunflowers, 49% Johnson grass, 46% foxtails,

26% lamb's-quarters, 20% croton, 14% amaranths, 14% sand dropseed, 14% paspalum, 6% panic grasses, 3% bush-clovers, 3% bluestems, 3% wheat, and 3% miscellaneous and unidentified matter (Goddard 1969).

Unlike some blackbird species, the cowbird inflicts minimal damage on agricultural crops. Bernhardt et al. (1987) determined that it was least likely to attack ripening corn compared with the Red-winged Blackbird, Common Grackle, and European Starling. It was ineffective at opening husks, could open only a small area in the ear, and ate only the kernels within this area. It often fell off corn ears attempting to open the husk. It damaged 19% of ears with a mean of 1.8% damage to each ear, the least of all species. It may do some damage to ripening corn, but probably only after the ears have been opened by another species. In Oklahoma, it did not do significant damage to sorghum crops unless the harvest was delayed by late autumn rains (Goddard 1969). In Louisiana, it did not cause measurable damage to rice crops (Brugger 1988).

MIGRATION

The Brown-headed Cowbird is a diurnal migrant that travels early in the morning and late in the afternoon. During the remainder of the day, it wanders considerably, often in large mixed flocks with the Red-winged Blackbird and Common Grackle, and also Brewer's and Rusty blackbirds where their ranges overlap. Cowbirds typically comprise only 1-3% of the birds in these flocks (Friedmann 1929; Lowther 2020c). Birds banded in Ontario were recovered December through February in Ontario (17%), states just south of the Great Lakes (31%), the Gulf Coast states (32%), and states in between. Only a few were found in New England coastal states. One Ontario bird was recovered at sea south of Nova Scotia 1,461 km away. Others wintered in Texas, Florida, and Arizona as far as 2,169 km from the banding location. There was no differential migration between sex and age classes (Brewer et al. 2018). Movements from Ontario were southwestward to the northern tip of Lake Michigan and the southern portion of that lake, through Essex County, and through the Kingston area at the eastern end of Lake Ontario (Burtt and Glitz 1977). Birds from the Great Lakes area averaged 1,225 km away in January and 1,137 km in February. There were no significant differences in migration distances for the sexes (Dolbeer 1982).

During spring migration, adult males arrive first followed by adult females then yearlings. In New York, Friedmann (1929) broke migration into 6 phases: arrivals of vagrants, migrant males, resident males, migrant females, resident females, and yearling males and females. Vagrants arrived before true migration began. These were likely birds that wintered not far away and their movements may have been wandering rather than migration. They were mostly single males but some females occurred. No vagrants arrived in some years. Migrant males arrived about 1 week after vagrants and continued to move northward. They occurred as scattered individuals within flocks of Red-winged Blackbirds. The interval between the arrival of migrant and resident males was about 3 days. Residents immediately established themselves at their singing posts in their home ranges. Female migrants simply passed through and arrived simultaneously with the resident males. They initially arrived as individuals within flocks of other blackbirds but later formed their own flocks; males paid little attention to these females. Resident females arrived within another week and these were courted by the males. Yearlings may not arrive until a month later. By this time, some adults that initiated nesting early had already completed breeding. In Pennsylvania, males arrived about 9 days

before females (Norris 1947). The interval between arrival of the sexes was 10 days in Tennessee (Laskey 1950b).

Cowbirds returned to London at the end of March or in the first week of April. Adults of both sexes arrived first, followed 2 weeks later by yearling males. Yearling females arrived another week later. Sixty percent of adults were present by the time the first yearlings arrived (Darley 1982, 1983). In Elgin County, the first arrivals are males who appear in late February or early March. Numbers increase through March and it is common and widespread by April (Lancaster et al. 2004). At Long Point, the mean capture date was 25.1 April for adult males, 28.5 April for yearling males, and 2.6 May for males of undetermined age (Stewart et al. 2002). In southern Ontario, it regularly arrives in mid-March with earliest arrivals in late February and peak numbers occurring in late April and early May (Curry 2006; LaForest 1993; Weir 2008). In the St. Lawrence River valley in southeastern Ontario and southwestern Quebec, some birds are present by 31 March, but most arrive in the first half of April (Weatherhead et al. 1980). In the southern Shield, it arrives in late March or early April (Mills 1981; Tozer 2012).

At Delta Marsh in Manitoba over a 63-year period, it exhibited no significant change in arrival times in response to warmer temperatures (Murphy-Klassen et al. 2005).

In Algonquin Park, most leave by late August with a few recorded in September and October and single birds occur at feeders in early November and December (Tozer 2012). In early autumn in the St. Lawrence River valley, most birds present are those that have bred locally. More than 20% leave by the end of September (Weatherhead et al. 1980). In the Kingston area, autumn migration is obvious during late September and October; birds may tarry until late November (LaForest 1993; Weir 2008).

Different habitat is used by the Brown-headed Cowbird during spring and autumn migration. Migrants occur in typical breeding habitat in spring mornings and in feeding areas in the afternoon. At night, migrants roost communally in marshes with other blackbird species. Resident birds that intend to breed in the area roost solitarily in their home ranges (Friedmann 1929). Early migrants often visit bird feeders. During spring migration in Minnesota and Wisconsin, it was equally abundant in mature upland and floodplain forests (Kirsch et al. 2013). During spring migration in Pennsylvania, it was significantly more abundant in shrublands than in forests (Smith and Hatch 2008). During autumn, it occurs in the same habitats as in the late postfledging period. These are predominantly agricultural lands where it continues to occur within flocks of mixed species of blackbirds. Communal roosts with other blackbirds continue to be an important habitat feature during autumn migration (Friedmann 1929; Lowther 2020c).

Spring migrants that continue to move northward feed predominantly on weed seeds and also visit bird feeders. In early spring, resident males tend to eat caterpillars and other animal foods (Friedmann 1929). Many birds landed on a ship off the coast of Massachusetts during an autumn storm. Two cowbirds had killed a wren which was reduced to a partially eaten mass of feathers and entrails. This appears to be the only documentation of it killing and eating vertebrate prey, but it may have been an act of desperation (Backus 1954). Fitch (1958) observed cowbirds eating fruits of rough-leaved dogwoods during autumn migration in Kansas. In autumn, the diet consists of weed seeds and grain. In Elgin County, flocks consisting only of cowbirds or flocks with mixed blackbird

species frequently feed on waste grain in fields along the Lake Ontario shoreline (Lancaster et al. 2004).

Blackbirds cause significant damage to corn and small grain crops in the St. Lawrence River valley. The possibility of killing blackbirds at their spring and autumn roosts was considered, with roosts supporting Red-winged Blackbirds, Common Grackles, and starlings in addition to cowbirds. Based on the migration timing of the roosting species, Weatherhead et al. (1980) concluded that the cowbird would be affected by control procedures implemented in early spring and early autumn, but not in late autumn. Control when the cowbird was present would affect mostly the local breeding population.

James (1991) considered the Brown-headed Cowbird a common to locally abundant migrant. Flocks as large as 5,000-6,000 have occurred (Curry 2006).

WINTER

The Brown-headed Cowbird continues to be gregarious in winter and to associate with other blackbird species. Migrants from many disparate breeding populations merge together in unstructured flocks where the composition changes day to day. In winter, it occurs mostly in the southeast with a range extension northward along the Mississippi and Ohio rivers. The densest population is in Georgia, but there are disjunct wintering populations in California, Arizona, and New Mexico (Dunn and Tessaglia-Hymes 1999; Root 1988). Friedmann (1929) reported that the winter range extended northward to Massachusetts, New York, and Michigan. By the 1950s, its range included southern Ontario and southern Illinois, where it was absent 1907-09 (Graber and Graber 1963; Lowther 2020c). The northward range extension may have been due to the increase in cereal crops and bird feeders.

In winter, the cowbird usually inhabits bird feeders and feedlots with concentrations of cattle. In snow-free areas, it continues to visit grain stubble fields to forage on waste grain. In Ontario, most wintering birds occur near feeders, but some are found at feedlots (Bent 1958; Fitch 1958; LaForest 1993; Lancaster et al. 2004; McIlwraith 1894; Tozer 2012; Weir 2008).

Roosts continue to be important in winter. In Niagara Region, it associated and roosted with House Sparrows (Sheppard et al. 1936). Bent (1958) stated that solitary birds often roosted with House Sparrows. In Hamilton, McIlwraith (1894) reported birds roosting on beams of barns above cattle. In 1976, there was a large roost in a cedar swamp in Guelph (Curry 2006). Elsewhere, communal roosts that usually supported other species were in oak trees on university campuses, in deciduous trees at margins of pine plantations, in shrubby marshes, in cattail marshes, in a woodlot of second-growth maples, and in ornamental elms around an urban courthouse. In this roost, starlings roosted in the uppermost branches and the cowbirds roosted beneath them. Some roosts that support multiple species of blackbirds and starlings are quite large. In the southeastern states, there are at least 125 known roosts that support more than 1,000,000 birds. Cowbirds represent a small proportion of birds in these flocks. It was estimated that 2-5% of birds in 1 roost of 5,000,000 birds were cowbirds. As many as 300,000 cowbirds have been reported at a single roost (Arnold and Johnson 1983; Bent 1958; Dolbeer 1982; Dolbeer and Smith 1985; Dunn and Tessaglia-Hymes 1999; Johnson et al. 1980; Lowther 2020c).

Based upon continent-wide banding returns, there was extensive replacement of cowbirds from 1 wintering area to another in subsequent years. Birds at a given wintering area represent populations from a wide breeding area (Dolbeer 1982). Brewer et al. (2018) concluded that it exhibited little site fidelity to wintering areas. At a roost in Texas, there was limited turnover in the cowbirds present within a given year; recaptures suggested reasonable site fidelity (Arnold and Johnson 1983; Johnson et al. 1980).

In winter, the cowbird feeds mostly on seeds and other plant material but also eats small quantities of insects when they are available. The diet of 57 birds collected at an Ohio roost was dominated by corn, comprising 65.5% of the total stomach contents by weight. Grass seeds constituted 20.6% of the diet and 67% of these were foxtails. Ragweed seeds were next in abundance at 2.6%. Insect parts, amaranths, pokeweed, and miscellaneous seeds (common St. John's-wort, stitchwort, nightshade, rushes, and smartweeds) all contributed less than 1% to the diet. Significantly more corn was eaten by males than females. Females ate significantly more weed seeds. The sexes exploited slightly different food niches in winter, thereby reducing competition for food (Dolbeer and Smith 1985). Birds at a Kentucky roost consumed 74% weed seeds, including those of sorghum, smartweeds, and goosegrass, plus corn (Lowther 2020c).

The cowbird frequently visits bird feeders. It is more abundant at eastern than western feeders and at rural than suburban or urban feeders. It is most common at feeders during migration, particularly in spring in Ontario. Males are dominant to females and are frequently found at the best food resources. It prefers mixed seeds, millet, cracked corn, and probably pet food. It infrequently selects sunflowers, safflower, hulled peanuts, suet, bird puddings, water, canary seed, milo, dried fruit, and oats (Dunn and Tessaglia-Hymes 1999). A total of 40,108 cowbird feeding observations demonstrated that it preferred white proso millet and platform feeders over tube and hopper feeders (Horn et al. 2014).

Blackbirds cause significant damage to rice and other crops in the southeastern United States. Extensive efforts are undertaken to control their populations, and this is typically done at winter roosts. All birds in roosts are indiscriminately targeted, including the cowbird. From 1974 to 1992, a detergent that eliminates the waterproofing ability of feathers was sprayed on roosts followed by spraying of cold water. This resulted in the birds dying of exposure. Hundreds of millions of blackbirds were killed in this manner. In Kentucky and Tennessee, an estimated 28,000,000 were killed 1974-82. This method of control is no longer allowed. Subsequently, DRC-1339 was applied as bait on the ground or spread on rice grains. This chemical kills birds by shutting down liver and kidney functions. Millions of birds were killed by this organochlorine pesticide. The proportion of birds that are killed that are cowbirds is unknown, but may be in the order of 2-5% of the total kill. Nonetheless, the number of cowbirds killed by these control methods is substantial (Dolbeer 1982; McCracken 2003b).

Mortality may occur at winter roosts due to natural causes. Some mortality occurred annually at a Texas roost and the cowbird was the species affected most. Over a 2-year period, 9,500 cowbirds died. One mortality event was caused by a violent rainstorm. Males experienced higher rates of mortality than females, and adult males were more likely to succumb than juvenile males. The mortality appeared to be related to depletion of winter food supplies (Arnold and Johnson 1983;

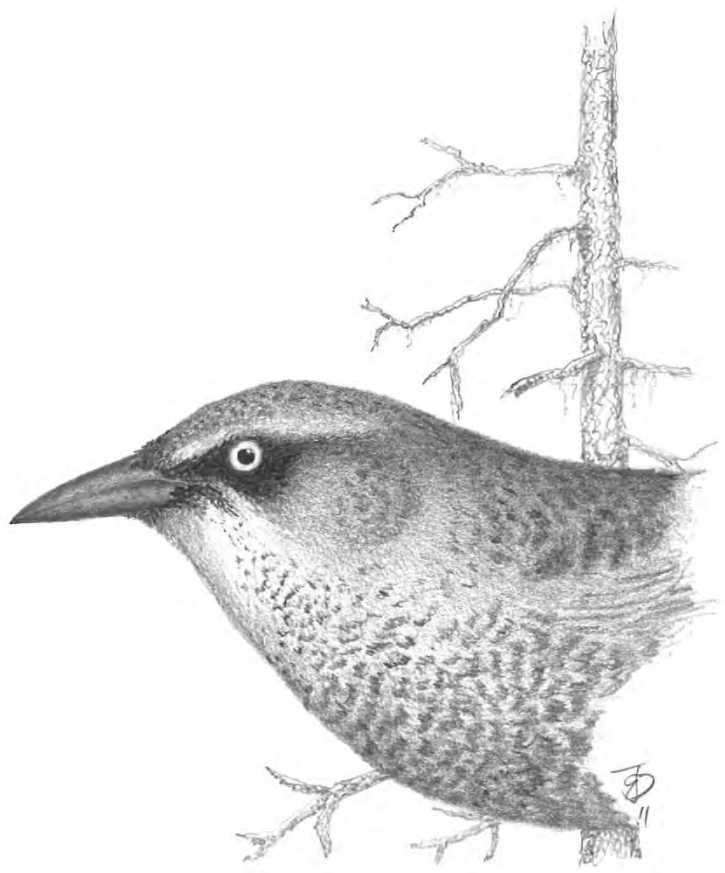
Johnson et al. 1980). At a Kentucky winter roost supporting 45,000 starlings, Red-winged Blackbirds, cowbirds, and grackles, a snowstorm resulted in 0.8% of birds dying. No dead cowbirds were found (Stewart 1978).

James (1991) considered the cowbird a rare to uncommon winter resident in the south north to Ottawa, and occasional and rare at Thunder Bay. At Hamilton, McIlwraith (1894) had only 2 records of cowbirds overwintering, both flocks of 10-12 birds. Curry (2006) reported that a few usually overwintered each year in the Hamilton area. He reported a roost of 85,000 in Guelph in January 1978, 1,500 near Cayuga on 15 January, and 120 on 20 February in Brantford. Winter flocks consisted primarily of males. Lancaster et al. (2004) considered it uncommon in Elgin County in winter and Mills (1981) considered it rare in Muskoka and Parry Sound districts.

Freedman and Riley (1980) summarized CBC results for southern Ontario for 1929-77. The cowbird increased both in abundance and frequency, especially since 1960, but it still occurred in low numbers. CBC results indicate that it decreased in Ontario at annual rates of 2.8% 1970-2021 and 0.79% 2009-21 (National Audubon Society 2022).

Rusty Blackbird

Euphagus carolinus



BREEDING SEASON

Habitat Requirements

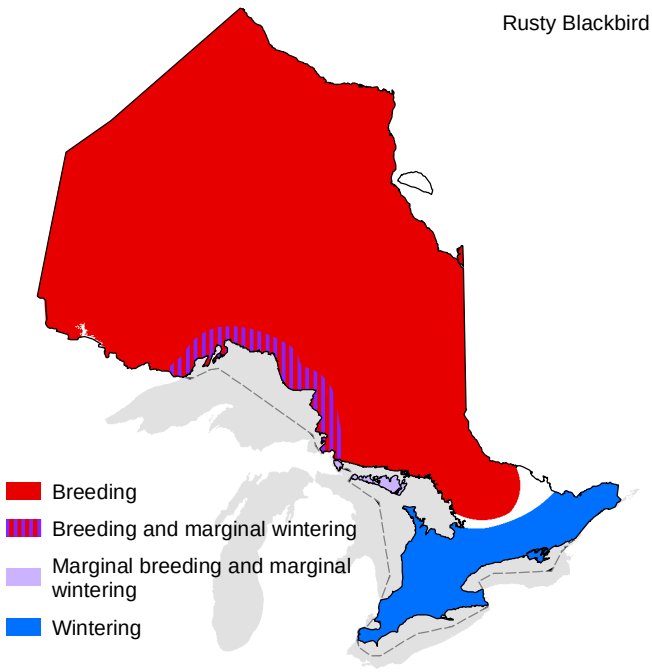
In Ontario, Rusty Blackbird nests were near forest edges or openings (52.8% of nests) and in open areas (30.6% of nests). They were almost always near water, including lakes, rivers and streams, swamps, bogs, fens, and beaver ponds. Occupied wooded areas were mostly coniferous (57.9%), with 36.8% of nests in deciduous woods and 5.3% in unspecified woods. Open areas included bogs and fens (50% of nests in open areas), lake and stream shorelines (25%), old beaver meadows (12.5%), and fields near highways (12.5%; Peck and James 1987).

Through the Hudson Bay Lowland of Ontario and Manitoba, the Rusty Blackbird was most abundant in coniferous scrub followed by mixed scrub, heath, deciduous scrub, coniferous forest with an understorey, and mixed forest. It was absent in deciduous forest, coniferous forest without an understorey, and tundra (McLaren and McLaren 1981). Along the northern Ontario coasts, it nests mostly in willow shrub thickets at edges of rivers and in wetlands (Manning 1952; Manning and

MacPherson 1952). It probably breeds at most forested areas, if there is water nearby (Wilson and McRae 1993).

In the Clay Belt, Welsh and Lougheed (1996) found it in 3 forest stands: 2 dominated by black spruce and 1 by balsam poplar–white cedar. All stands were on wet sites. The spruce stands were nutrient-poor; the other was nutrient-rich. In the Ontario portion of the Boreal Forest Region, Erskine (1977) reported it nesting in peat with low conifers.

In Algonquin Park, the Rusty Blackbird nested along swampy and marshy creeks (MacLulich 1938).



Throughout its range, the Rusty Blackbird is closely associated with water, especially wetlands. Occasionally it nests in drier habitats such as recent clear-cuts. On Cape Breton Island, it nests in drier pasture edges and plantations. In Nova Scotia it breeds in young clear-cuts in northern hardwood stands (Campbell in Stewart et al. 2015; Erskine 1992; Freedman et al. 1981; Morgan and Freedman 1986). The most common nesting habitat includes margins of wetlands, watercourses, and lakes imbedded in boreal forest and taiga. It nests mostly in dense stands of young conifers, particularly spruce and balsam fir, and in shrub thicket swamps dominated by willow and alder. It may use stands of dead conifers and deciduous shrubs for nesting. Black spruce and balsam fir near emergent vegetation, ponds, and particularly lakes, may be favoured habitat. Where conifers are scarce or form contiguous stands, it selects deciduous shrubs along watercourses, water bodies, and wetlands. Breeding occurs in swamps, bogs and fens with coniferous tree growth, alder and willow swales, beaver ponds and meadows, wetlands adjacent to mature coniferous forests and young clear-cuts, wetlands associated with recent burns, open moss- and lichen-spruce woodlands, sedge marshes, islands and floating bogs, and areas of windthrow within coniferous forests. In addition to willow and alder, it may nest in shrub thicket swamps dominated by sweet gale and buttonbush (Avery 2020; Bent 1958; Buidin in Robert et al. 2019; Campbell et al. 2001; Erskine 1977; Gillespie and Kendeigh 1982; Greenberg and Droege 1999; Imbeau et al. 1999; Jehl and Smith 1970; Kennard 1920; LaRue et al. 1994; Machtans et al. 2007; Matsuoka et al. 2010b; Nadeau in Gauthier and Aubry 1996; Powell et al. 2010a, 2010c, 2014; Savignac 2006; Sinclair et al. 2003; Whitaker and Montevecchi 1997, 1999).

Some studies examined the habitat of the Rusty Blackbird at the landscape scale. Savignac (2006) reported that its breeding range was closely associated with the Boreal Forest Region and the taiga ecozone, where it was associated with coniferous forest wetlands. The 2 Quebec atlases found that it was most common in black spruce and spruce-moss ecoregions and slightly less common in areas dominated by balsam fir and white birch. Within these ecoregions, it preferred

wetlands interspersed with small patches of forest (Buidin in Robert et al. 2019; Nadeau in Gauthier and Aubry 1996). In Alaska, it was positively correlated with the area of lakes, ponds, and emergent vegetation. Areas with nesting pairs had 10 times the mean surface area of lakes and ponds and 1.5 times the mean area of emergent vegetation than areas without nesting pairs. The number of nesting pairs increased with the area of lakes and ponds and decreased with the area of upland habitat. At another site, it decreased as the area of low shrub wetland increased. Areas with nesting pairs had 41% of the mean area of low shrub wetlands found in areas without Rusty Blackbirds. It was associated with open water, but where water was rare it nested in riparian woody wetlands. At Anchorage, it selected shrub-scrub wetlands, with lesser numbers of nests in emergent wetlands, forested swamps, and uplands. It was 7.4 times more likely to nest in forested wetlands than in uplands, which it tended to avoid. On the Tanana Flats of Alaska, it nested mostly in sedge meadows and forested wetlands, with intermediate use of tall shrub wetlands. It avoided low shrub wetlands and areas with tall canopies and selected areas with dense growths of balsam fir 1-3 m tall (Matsuoka et al. 2010a). In Maine, Powell et al. (2010a, 2010c) concluded that optimum landscapes contained combinations of wetlands with patches of shallow water rich in aquatic prey, and undisturbed wetlands with small confers for nesting. In Maine and Vermont, wetlands surrounded by more than 70% conifers were 2 times more likely to be occupied, those with shallow (less than 6 cm) water that was not connected to flowing or other open water were more than 4 times likely to be occupied, wetlands with beaver activity were 2 times more likely to be occupied, and wetlands that were previously occupied were more than 2 times likely to be occupied than wetlands without these features. It selected wetlands surrounded by conifers regardless of their age. It appeared to select habitat at multiple scales, targeting wetlands surrounded by at least some short coniferous growth and also good foraging habitat such as shallow water supporting high invertebrate biomass. These areas of shallow water were an important component of habitat selection. Beavers probably create both nesting and foraging habitat. They selectively remove hardwoods and promote growth of conifers, and their ponds result in increased biomass of important aquatic prey such as dragonflies, damselflies, caddisflies, and snails (Powell et al. 2014). In Maine and New Hampshire, habitat selection was affected by the basal area (BA) of small conifers with a diameter at breast height (DBH) of 4 cm or less, and canopy closure. For each 5 m^2 per ha increase in BA of small conifers, the odds of occupancy for nesting increased by 65%. With each 10% increase in canopy closure, occupancy decreased by 39%. The home-range scale consisted of a 500-m radius around the nest. Nests in Maine had 20% wetland cover at this scale compared with only 6% in New Hampshire. The conifers in Maine were young and pole-sized. Occupied areas in New Hampshire contained significantly more mature conifers and hardwoods. Luepold et al. (2015) found evidence for an effect of young conifers on habitat selection at the home-range scale and of an interaction between site and wetlands. With each 10% increase in wetland cover, the odds of occupancy increased by a factor of 5.47 in Maine and 2.46 in New Hampshire. For both areas, each 10% increase in young conifer cover resulted in a 46% increase in the probability of occupation. There was a preference for young conifers even when they were the result of timber harvesting. Overall, high BA of small conifers and a lack of overhead canopy closure were important predictors of site occupation, but the amount of wetland area was more important.

Other studies examined microhabitat preferences of the Rusty Blackbird and the effects they have on nest success. At Anchorage, it nested in black spruce and white spruce in proportion to their availability and avoided nesting in alders and white birch. In interior Alaska, it selectively nested in black spruce and white spruce, used willow and alder in proportion to their availability, and avoided white birch and balsam poplar. In Anchorage, it nested in areas with a higher density of black spruce than random sites. In the interior, there were no differences between nest sites and random areas. At Anchorage, nest sites were characterized by a preponderance of black spruce and a scarcity of willow but the opposite was true in the interior. In both areas, canopy closure was sparse at 20.5% and 25.2%. Nesting in wetlands may be advantageous because densities of red squirrels and other predators were low (Matsuoka et al. 2010b). In Maine and New Hampshire, 88% of nests were in harvested stands. Total BA within a 5-m radius of nests was significantly higher in New Hampshire (57.5 m^2 per ha) than in Maine (36.9 m^2 per ha). BA of conifers was also significantly different: 41.6 m^2 per ha in New Hampshire and 24.7 m^2 per ha in Maine. Alder density was significantly higher in Maine (9.5 stems) than in New Hampshire (2.8 stems). Mean nest-tree DBH was 4.4 cm in Maine and 4.1 cm in New Hampshire. BA was the most important variable influencing nest success with nest success higher in denser conifers. Mean BA was 57.6 m^2 per ha around successful nests and 35.3 m^2 per ha around unsuccessful nests. This was because young dense stands of spruce or balsam fir do not produce cones and therefore support few red squirrels, thereby enhancing nest success (Luepold et al. 2015). In British Columbia, fallen trees and flooded snags around wetland shorelines provided important foraging habitat (Campbell et al. 2001). In Nova Scotia, its presence was positively correlated with canopy height heterogeneity and negatively correlated with depth to water table, canopy height, and distance to a coniferous stand. Presence of a high water table was the most important factor (Bale et al. 2020).

The Rusty Blackbird is predominantly an edge species, frequently nesting at the transition between wetland and forest habitats. In balsam fir and balsam fir–white cedar forests in Newfoundland and Quebec, it occurred only in deciduous wetlands along streams and was absent in adjacent coniferous forests (LaRue et al. 1995; Whitaker and Montevecchi 1997, 1999). Kennard (1920) reported a nest that was 90 m from a stream within a swamp.

This blackbird does not appear to be area sensitive. In Maine and Vermont, Powell et al. (2014) detected it in 1 of 78 wetlands (1.3%) smaller than 0.1 ha. Wetlands less than 0.5 ha were less likely to be occupied than larger wetlands.

Ontario nests were near or over water, with 72.7% in living and 18.2% in dead trees and shrubs. One nest was on the ground, one was in a fallen dead spruce over water, and one was in a hollow trunk standing in water. Coniferous trees (22 nests in 3 species) were preferred to deciduous trees and shrubs (6 nests in 4 species). Preferred species included spruces (19 nests), willows (3 nests), and balsam fir (2 nests). Nests were most often against the trunk on horizontal branches and in forks. Two nests were near the base of a tree and another was on branches between the trunks of 2 small spruces. Elevated nests were 0.3-2.7 m from the ground, with most 0.8-1.8 m up (Peck and James 1987).

Most nests are in small trees or shrubs. Powell et al. (2010c) found 43 nests in Maine and Vermont: 23 in black or red spruce, 16 in balsam fir, 2 in white spruce, 1 in white cedar, and 1 in a

viburnum shrub. The mean age of nest trees was 17.9 years (median 14 years, range 8-50 years). All nests were within 75 m of water (range 0-71 m); 29 were in wetlands and the 14 nests in uplands averaged 7.3 m from the wetland-upland interface (range 0.3-95 m). Matsuoka et al. (2014) found 184 nests in Alaska and summarized results across Canada for an additional 230 nests. Nest substrates included 59.8% conifers, 34.2% deciduous shrubs, and 6.0% deciduous trees or other substrates. It was most likely to nest in conifers in all areas except the interior of Alaska where 15% of nests were in conifers and 78% were in shrubs, including living and dead willows and alders. Of nests in conifers, 75% in Alaska and 80% in Canada were in spruce with small numbers of Canadian nests in balsam fir and white cedar. Most nests in spruce were in black spruce with small numbers in white spruce. In Alaska, 39% of spruces used for nesting were dead. Eleven nests were in deciduous trees: white birch, balsam poplar, red maple, and pin cherry. Two nests were in grasses, 6 were in emergent sedges or cattails, and 1 was on the ground on a beaver dam. The average height of 321 nests was 1.6 m but it varied by nesting substrate: 0.23 m for ground, grass, sedge, and cattail nests (range 0-0.5 m); 1.0 m for shrubs (range 0-4.1 m); 1.3 m for deciduous trees (range 0.3-5.0 m); and 2.0 m for conifers (range 0-16.2 m). Kennard (1920) found several nests in Vermont and Maine, almost all in dense growths of young conifers but also in other sites. Nests were in spruce (both dead and living), balsam fir, dead branches of a broken-off spruce top, a dead spruce top in a stream, sweet gale, buttonbush, and at the top of a large stump standing in water. Some nests were in intermingling branches of 2 conifers but most were near the trunk of a tree. Nests in dead trees were well concealed by dense growths of beard lichen. Fifteen nests were 0.3-6.1 m from the ground or water (average 1.83 m). In Maine, nests averaged 1.8 m from the ground in trees 3.4 m tall. In New Hampshire, nests averaged 1.7 m from the ground in trees 2.5 m tall (Luepold et al. 2015). At Churchill, Manitoba, nests were 0.3-1.5 m from the ground in willows (Jehl 2004). In British Columbia, 59% of nests were in small or medium-sized conifers, usually black spruce, followed by deciduous shrubs (31%) and small deciduous trees. Fifty-six percent of nests were over standing water, usually among flooded woody vegetation, or in trees or shrubs overhanging water; 34% were in dead or dying trees and shrubs; 6% were on islands in lakes; and one was in a natural cavity in a pine tree. Nests were in thick clumps of woody vegetation or among horizontal branches, usually near the trunk but occasionally as far as 60 cm from it. Nests were 0.2-6.1 m from the ground, with most 0.6-1.5 m up. The lowest nests were usually in dead flooded trees or shrubs. Higher nests were on drier ground, well concealed in live conifers (Campbell et al. 2001). Bent (1958) reported a nest 3 m up in the top of a broken-off spruce in a damp pasture thickly overgrown with spruce. New nests are built for replacement clutches and in subsequent years. They may be placed close to the previous year's nest (Avery 2020; Bent 1958; Campbell et al. 2001; Kennard 1920; Matsuoka et al. 2010b).

It is unknown whether the Rusty Blackbird defends a territory. In most cases, only a single pair nests at a wetland, but occasionally groups of 2-6 pairs nest at a wetland. Grouped pairs are reported mostly in Newfoundland, Labrador, and Alaska, with 1 report in Maine. In Alaska, only 4 pairs of nests have been found within 50 m of each other (Bent 1958; Campbell et al. 2001; Kennard 1920; Matsuoka et al. 2010b; Powell et al. 2010a, 2010b). Avery (2020) reported that it nested both solitarily and colonially in Nova Scotia. Colonial groups occurred where water levels fluctuated and isolated pairs occupied areas where water levels were stable. Powell et al. (2010b) reported a colony of 6 nests within 6.9 ha in Maine; 2 other nests were 869 and 1,481 m from the colony. It is uncertain if

this was a true colony, with nests averaging 283 m apart (range 67-531 m). On 3 occasions, they observed males aggressively chasing each other and males cooperatively mobbed field crews. Birds that nested in groups had larger home ranges than those that nested singly. Group nesting was rare. The authors surveyed 561 wetlands in Maine and Vermont and found 43 nests but only 1 colony. No birds returned to nest in the colony in the following year. The Rusty Blackbird is known to fly long distances during the breeding season (Matsuoka et al. 2010a). In Maine, the mean size of 13 home ranges was 37.5 ha (range 3.8-172.8 ha). The mean core area was 11.1 ha (range 1.5-34.8 ha). Birds included an average of 2.8 wetlands within their home range and 1.4 in their core areas. They often visited wetlands and wet patches that were not connected to the wetland that was used for nesting. There was no significant difference in the mean home range sizes of males (48.0 ha) and females (28.4 ha) or home range sizes of males (23.1 ha) and females (22.0 ha) paired to each other. Core area sizes did not differ by sex: 12.0 ha for males and 10.3 ha for females for all birds and 7.4 ha for males and 8.2 ha for females within pairs. Home ranges of birds nesting in the colony were significantly larger (51.8 ha) than for those nesting solitarily (14.6 ha). Eleven of 13 birds had home ranges larger than 10 ha. Two birds that were presumably nonbreeders had home ranges of 72 ha and 173 ha. Wetlands encompassed only 12% of home ranges and 19% of core areas, but their significance may have been underestimated due to the scale of their mapping. It was often observed foraging in very small wetlands such as seeps, depressions resulting from logging and road construction, skidder ruts, roadside ditches with alders, and borrow pits. Many were less than 16 m^2 and too small to be delineated as wetlands (Powell et al. 2010a).

No information is available on natal philopatry. Limited information is available on adult site fidelity rates. In Vermont and Maine, Kennard (1920) found several nests close to where he had observed nests in previous years. He assumed that the same birds had returned but they were not banded. In Alaska, 60% of Rusty Blackbirds banded in 2008 returned the following year, but only 18% of those fitted with geolocators returned. The body mass of these birds was lower than in the previous year, suggesting that geolocators may affect survival rates (Johnson et al. 2012). Zero of 6 nesting pairs returned to a nesting colony in Maine (Powell et al. 2010c).

Limiting Factors

Eggs have been reported in Ontario nests from the beginning of May until the last week of June, with most present from the last week of May until mid-June (Peck and James 1987). In Algonquin Park, eggs are present from early May to early June, nestlings are present from late May to early July, and dependent fledglings have been observed from early June to late July (Tozer 2012).

No information is available on how long it takes to build the nest. Eggs were laid in 1 nest before the lining was complete suggesting that intervals between nest completion and initiation of egg laying are brief. Incubation appears to begin with the laying of the first egg, particularly during cold weather. Later in the season, incubation may be initiated with the laying of the penultimate or last egg. The incubation period in Alaska averaged 11.8 days (range 10-13 days). The eggs hatch over a 1-2 day period. The nestling period in Alaska averaged 11.5 days (range 10-13 days; Avery 2020; Bent 1958; Kennard 1920; Matsuoka et al. 2010b).

The Rusty Blackbird raises a single brood in a season but may renest if the first nest is lost. In Nova Scotia, 2 nests were collected and the females began building new nests the next day. Two

Alaska females renested 57 m and 196 m from their first nests after they failed. In Vermont and Maine, most females vacated the home range when their nest was collected. One female built 4 nests and laid 4 clutches after the researcher collected the first 3 nests (Bent 1958; Kennard 1920; Johnson et al. 2012; Matsuoka et al. 2010b). Clutches of 3-5 eggs were reported in Ontario, with 4-egg clutches most common (mean 4.00 eggs; Peck and James 1987). Clutches of 3-6 eggs have been reported, with most containing 5 eggs, but 4-egg clutches are also common. Only a single complete 3-egg clutch has been reported; 1 nest contained 7 nestlings. Mean clutch sizes include 5.3 eggs in Alaska (mode 5 eggs), 4.6 eggs in Canada (mode 4 eggs), 4.4 eggs in unharvested and 4.5 eggs in recently harvested forests in Maine and Vermont, and 4.47 eggs for clutches reported to the Western Foundation of Vertebrate Zoology. Clutch size declines as the season advances (Avery 2020; Bent 1958; Campbell et al. 2001; Matsuoka et al. 2010b; Powell et al. 2010c).

The age at first breeding is presumed to be 1 year, but this has yet to be confirmed. It is unknown if all adult and yearling birds breed. In Maine, 2 adult birds appeared to be unmated (Powell et al. 2010a). The mating system appears to be monogamous particularly since most pairs nest solitarily. Those nesting in groups may have opportunities to engage in extra-pair copulations, but this has never been documented (Avery 2020).

The diet of the Rusty Blackbird may be the main reason for its preference for wetlands. During the breeding season, it feeds predominantly on aquatic insects and other invertebrates and small vertebrates associated with water. It often feeds on moist soils and in shallow water where it wades, often ducking its bill or entire head underwater to obtain prey. It feeds on floating logs and mats of vegetation, among emergent wetland plants, and in seasonally flooded meadows. It may flip dead leaves at the edge of a wetland or lake in the manner of a waterthrush. In addition to margins of larger water bodies, it forages in puddles and very small wetlands and may visit landfills and forage with gulls. It picks caddisfly cases from the substrate of water bodies and opens them to obtain the larvae or pupae inside. It inspects rotten wood at ends of logs and excavates it to obtain insects and gleans prey from moss and litter and from under twigs and other debris. It exposes prey in soft mud and loose soil by inserting its bill and opening it to loosen the substrate. It may make nearly vertical flights to about 4.6 m above the ground to hawk mosquitoes and caddisflies, then glide to the ground and repeat the process. During severe cold or snowy weather in late winter or early spring on the breeding grounds, it may attack and kill other birds. It has killed Wilson's Snipes, American Robins, American Goldfinches, Lapland Longspurs, Snow Buntings, White-throated Sparrows, White-crowned Sparrows, American Tree Sparrows, Dark-eyed Juncos, and Brown-headed Cowbirds. It does not always eat its victims but when it does, it eats mostly the brain and tissue from the head. This appears to occur only when there is a food shortage during adverse weather (Avery 2020; Beal 1900; Bent 1958; Cade 1953; Campbell 1974; Greenberg and Droege 1999; Matsuoka et al. 2010a; McRae 1992; Powell et al. 2010a, 2014).

Nestlings are fed aquatic insects, particularly dragonfly nymphs. Limited information is available on the breeding season diet of adults. It feeds mostly on aquatic invertebrates and small vertebrates such as dragonfly nymphs, beetles, mayfly nymphs, caddisfly larvae and pupae, snails, crayfish, tadpoles, salamanders, and small fish (Avery 2020; Beal 1900; Kennard 1920; Matsuoka et al. 2010a, 2010b; Powell et al. 2010a).

The ranges of the Brown-headed Cowbird and Rusty Blackbird barely overlap, so parasitism is rare. There are 2 old reports of parasitism from Alberta (Avery 2020), and Campbell et al. (2001) reported that 1 of 27 British Columbia nests (3.7%) was parasitized.

The most significant limiting factors for the Rusty Blackbird occur within its wintering range, but habitat loss on the breeding grounds is also occurring. The most extensive habitat losses occur outside Ontario but some losses are occurring within the province. The largest habitat losses have been in the southern Boreal Forest Region in the Prairie Provinces, where forest has been converted to agricultural uses. In northern Quebec and Labrador, more than 10,000 km^2 of boreal forest were flooded by hydroelectric dams. Habitat loss is also occurring due to mining, oil and gas exploration and development, and a number of other industrial activities. It has been estimated that about 5% of Canada's boreal forest is no longer suitable habitat and another 4% loss is projected to occur within the next 50 years. Indirect habitat loss is occurring due to rising temperatures caused by climate change. Satellite imagery indicates that the total area of shallow ponds and boreal lakes decreased by 6,700 km^2 during 2000-09. Climate modelling predicts a 64-90% reduction in core habitat for the Rusty Blackbird by 2100. In Alaska, the area of lakes and ponds has been declining since 1950. There has been a decrease in the amount of surface area of ponds of 4-31% and in the number of water bodies by 5-54%. Large volumes of groundwater and surface water may be displaced during oil and gas extraction, and this may lead to habitat loss or alteration (Greenberg and Droege 1999; Greenberg and Matsuoka 2010; Greenberg et al. 2011; Matsuoka et al. 2010a; Savignac 2006, 2017).

Some authors stated that timber harvesting is the greatest threat to its breeding habitat. Others have reported effects to be negligible. A massive spruce budworm outbreak from 1968 to 1985 defoliated balsam fir and spruce across 550,000 km^2 of forest from Lake Superior to the Atlantic coast. This and related salvage logging may have caused widespread changes to its habitat. More than 60% of the commercially viable southern boreal forest has already been allocated to timber companies for harvesting. Tree harvest rates in Canada are highest in British Columbia, Ontario, and Quebec. From 2000 to 2012, 110,412 km^2 of forest were harvested in Canada. Clear-cutting opens areas to colonization by the Red-winged Blackbird and Common Grackle, species that are dominant to the Rusty Blackbird. Clear-cutting has the potential to create habitat for the Brown-headed Cowbird, although this is not preferred habitat for it (Avery 2020; Baker and Thomas 2015; Greenberg et al. 2011). In Maine and Vermont, Powell et al. (2010a) concluded that clear-cuts constituted an ecological trap for the Rusty Blackbird. Clear-cuts provided dense growth of young conifers which attracted the blackbirds but nest survival rates were significantly lower in clear-cuts (33%) than in areas with no history of recent logging (76%). They suggested that buffers at least 75 m wide around occupied wetlands would improve success rates. A large-scale reduction in nest survival in logged forests may have contributed to its population decline and range contraction. In Maine and New Hampshire, Luepold et al. (2015) found no evidence that harvested stands acted as ecological traps. Nest survival rates were similar to those reported elsewhere in undisturbed stands. They recommended that the practice of precommercial thinning not be done in regenerating stands, particularly in those near wetlands. This reduces stocking densities and enhances growth of select crop trees and is an increasingly common practice. Precommercial thinning may eliminate the dense patches of conifers that it prefers for nesting, make nests more vulnerable to predators and

decrease nest survival rates, and accelerate the development of mature forest that is unsuitable nesting habitat.

Acid precipitation is an issue for the Rusty Blackbird, particularly in the eastern portion of its range in New England and the Maritime Provinces. It does not appear to have had much effect in Quebec. Acid precipitation affects it in 2 manners. The resulting lower pH in wetlands and water bodies may reduce food availability and abundance. Snails and other molluscs are among the first to disappear when water becomes acidified, and these are important components of its diet. Many other aquatic invertebrates are intolerant of acidic waters. The second effect of acid precipitation is that it results in the release of natural mercury from sediments. Acidification promotes the formation of methylmercury, which is the most toxicologically significant form of mercury in birds because of its high bioavailability. The Rusty Blackbird is vulnerable because its diet focuses on prey higher up in the food chain such as predatory aquatic invertebrates (dragonflies) and small fish. Mercury has negative effects on reproduction through decreased egg volume and embryo weight, eggshell thinning, abnormalities and deformities, and deleterious changes in adults' behaviour. Birds were sampled for mercury in New England, the Maritimes, and Alaska during the breeding season, and in the wintering range. Concentrations were significantly higher on the breeding range than the wintering range, with highest concentrations in Vermont and Nova Scotia. Mercury concentrations in Rusty Blackbirds were 13-17 times greater than for Red-winged Blackbirds from the same areas. In addition, mercury may be released by flooding areas or through direct discharges (Edmonds et al. 2010; Greenberg and Droege 1999; Greenberg and Matsuoka 2010; Greenberg et al. 2011; Nadeau in Gauthier and Aubry 1996).

The Rusty Blackbird may have been adversely affected by DDT and carbofurans before the usage of these chemicals was banned (Savignac 2017).

Rusty Blackbird populations appear to fluctuate in complex cycles associated with climate and weather conditions and population cycles of other wildlife species. Savard et al. (2011) monitored the number of Rusty Blackbirds during autumn migration at Tadoussac, Quebec over a 15-year period. Numbers fluctuated greatly between years, with peak movements occurring at 5-year intervals. Numbers ranged from 54 to 2,156 per year with daily averages per year on days observed of 3-80. In peak years, 84% of birds were juveniles. Only 25% were juveniles in low years, indicating high reproductive success in years of abundance. They correlated blackbird abundance with Boreal Owl numbers and climate. The 3 largest movements occurred in years when few Boreal Owls were captured and 1-3 years after peaks in owl abundance. This owl feeds predominantly on the red-backed vole, which has a 4-5 year cycle of abundance. When voles are abundant, the Boreal Owl remains on the breeding grounds in winter but migrates in years of vole scarcity. Rusty Blackbird numbers were highest in peak years of vole abundance, suggesting that the Boreal Owl may seek alternative prey, such as blackbirds, in years when voles are scarce. Autumn abundance of the Rusty Blackbird was positively correlated with the North Atlantic Oscillation (NAO), a large-scale climatic phenomenon that influences winter temperatures and moisture budgets for much of eastern North America. A positive correlation means that it was cooler in the Boreal Forest Region during the breeding season and wet in the southeastern United States during winter. It was negatively correlated with precipitation amounts in June, July, and August. Summers with low amounts of

precipitation may increase the amount of suitable foraging habitat and reduce nestling mortality due to heavy rain. Its current decline may be exacerbated by patterns in the NAO. More frequent negative indices may result in lower reproductive success and possibly reduced winter survival. Reproductive success of the Rusty Blackbird is also tied to the conifer cone abundance cycle and populations of red squirrels. The red squirrel is the primary predator of blackbird nests. Luepold et al. (2015) determined that the red squirrel population increased significantly the year after abundant cone production. All recorded nest predation events by red squirrels occurred in the year that they were most abundant. The abundance of the Rusty Blackbird may be affected by beaver abundance. By creating ponds, beaver activity provides good foraging habitat. Beavers preferentially down deciduous trees, thus favouring growth of conifers that may provide nesting habitat. The beaver was brought to the brink of extinction by excessive trapping by 1930. It is probable that low numbers of beavers had an adverse effect on the Rusty Blackbird population. As a result of trapping restrictions, the beaver population has rebounded and this was beneficial for the blackbird. It is probable that beaver populations will remain high due to anti-fur trade sentiments and low prices of pelts (Avery 2020; Powell et al. 2010c, 2014; Savignac 2017).

Baker and Thomas (2015) cited 1 study that stated nest survival of the Rusty Blackbird was lower nearer roads in New England. The effects of roads may be site specific or may vary annually. Powell et al. (2014) concluded that there was no evidence that major roads had a negative impact on occupancy of sites. Luepold et al. (2015) found that nest survival was highest distant from roads in 1 year and close to roads in the following year.

The Rusty Blackbird does not appear to be adversely affected by fire or be suffering from chronically low nesting success that might explain its drastic population decline (Matsuoka et al. 2010b).

Status

Baillie and Harrington (1936) considered the Rusty Blackbird a fairly common breeder from Grey County and Algonquin Park north through the remainder of the province. MacLulich (1938) reported that it was an uncommon but regular breeder in Algonquin Park. Baillie and Hope (1943) found that it was rare along the north shore of Lake Superior. The first atlas demonstrated that the range of the Rusty Blackbird included northern Ontario to slightly south of Algonquin Park, with scattered records south of the Canadian Shield in eastern Ontario, on the southeastern shore of Georgian Bay, and on the Bruce Peninsula and Manitoulin Island. None of the southern records were of confirmed breeding. It was not reported in a large area of northwestern Ontario. Flood (in Cadman et al. 1987) concluded that the distribution map in the north was conservative and that it probably bred in all blocks. James (1991) considered it an uncommon breeder in the north and in the Algonquin Highlands and rare south to the Bruce Peninsula, Haliburton County, and Ottawa.

The second atlas revealed that there had been little change in the distribution of the Rusty Blackbird. It was essentially absent south of the Shield, but was confirmed to breed in northwestern Ontario where it was overlooked during the first atlas. There was no change in its overall probability of observation, but it declined significantly in the Boreal Forest Region and the Shield portion of the Great Lakes-St. Lawrence Forest Region. It increased significantly in the Hudson Bay Lowland. It was possible that it had not declined province-wide but shifted its range northward. Highest densities

occurred in the Hudson Bay Lowland. In this area, it was detected on 45% of point counts; 39% of squares where it was reported were within this region despite relatively low effort. It was 24 times more abundant in the Hudson Bay Lowland than in the Boreal Forest Region and 120 times more abundant than in the Shield portion of the Great Lakes-St. Lawrence Forest Region. The high densities in the taiga portion of northern Ontario were not previously documented. It is uncertain whether this high density has always been present or whether the dramatic decline in this blackbird's population has affected it differently in different areas of the province. There has not been a significant decline or change in habitat in the Canadian Shield of Ontario, suggesting that declines in the Rusty Blackbird may be related to issues on the wintering range (Francis in Cadman et al. 2007). Mills (1981) stated that the Rusty Blackbird was extremely local in Muskoka and Parry Sound districts. In Algonquin Park, it was formerly a common breeder, but sightings of nests and fledglings became very infrequent after the early 1980s (Tozer 2012).

The Breeding Bird Survey (BBS) indicates that the Rusty Blackbird has declined at a significant rate throughout its range and in Canada and Ontario. The BBS is not well suited for estimating its abundance because of its patchy distribution, solitary breeding habits, and use of boreal wetlands that are frequently remote and inaccessible (Matsuoka et al. 2010b). Coverage by the BBS is limited to less than 30% of its range and is concentrated in the southern portion of the Boreal Forest Region. It may not be representative of trends in more northern areas where its density may be higher and there are fewer threats to its habitat. It is also detected on few routes, many of which have been surveyed sporadically and have frequent observer turnover, resulting in poor precision with wide confidence limits (Greenberg et al. 2011). In the Mackenzie Valley of the Northwest Territories, Machtans et al. (2007) compared its occurrence and relative abundance in 1970 and 2006 and found no significant differences. Although there are deficiencies in the BBS, results from most other studies corroborate that the Rusty Blackbird has experienced a significant decline, and that this decline probably began long before the BBS was initiated in 1966. Greenberg and Droege (1999) reviewed historical accounts that referred mainly to its abundance during migration and winter. It was described as very common to abundant in 56% of accounts published prior to 1920, in 19% of those published 1920-50, and in 6.7% of those published after 1950. It was described as uncommon in 0% of pre-1950 publications, 18% of those published 1951-80, and 53% of those published after 1980. This historical information suggests a decline over the last century with the rate of decline accelerating. The Rusty Blackbird winters in the southeastern United States where it is well surveyed by the Christmas Bird Count (CBC). CBC results indicate that it is declining at a significant rate. Trends at some migration monitoring stations also indicate declines. In Quebec, its probability of observation declined by 60% between the 2 atlases; the Quebec checklist program also indicates a significant decline (Buidin in Robert et al. 2019).

Since 1966 when the BBS was initiated, results of that survey suggest that the Rusty Blackbird population declined by approximately 95%. This is one of the steepest declines recorded by the BBS for any species. The trend in Ontario was −14.9% per year, greater than for the population as a whole (Greenberg and Droege 1999; Greenberg and Matsuoka 2010; Greenberg et al. 2011). Savignac (2006) reported a significant decline on the BBS of 9.97% per year rangewide 1966-2003 and 10.3% in Canada 1968-2003. Machtans et al. (2007) reported a decline in Canada of 12.8% 1966-2005. Baker and Thomas (2015) reported a decline of 6.3% per year 1970-2012 in Canada, with declines most

severe in southern and eastern regions. These were the areas where estimated trends are most reliable but are also on the periphery of the core range where habitat disturbances and changes due to climate are likely to be more prevalent. The rate of decline appears to be levelling off. Savignac (2017) reported a decline rate for Canada of 3.5% per year 1970-2014 and 2.6% per year 2004-14. In Ontario, there was a significant decline of 4.61% per year 1970-2014 and a nonsignificant decline of 2.68% 2004-14. The Canadian results translate into an approximately 80% decline in population 1970-2014. Cadman et al. (2016) reported that the Rusty Blackbird declined at a rate of 5.9% per year 1983-2013, the seventh greatest decline of all Ontario birds. BBS data for 1970-2021 indicate that it decreased at annual rates of 3.31% in Canada and 3.73% in Ontario. The trends 2011-21 were annual decreases of 0.0632% in Canada and 0.0842% in Ontario. The long-term trends were of medium reliability; the short-term trends were of low reliability (A.C. Smith 2023).

As a result of its significant decline and the ongoing threats to the Rusty Blackbird, it has been designated special concern in Canada and Ontario. Baker and Thomas (2015) prepared a management plan with a 2-fold objective: to stop the decline and maintain the population at its 2014 level, and to increase the population, resulting in a 10-year sustained increase in its Canadian population. The current significance of many potential threats is poorly understood, so the short-term objective is to stop the decline and maintain the population. Once threats are better understood and potential mitigation measures are identified, the objective is to create a sustained 10-year increase in population.

POSTFLEDGING PERIOD

Fledglings remain in the immediate vicinity of the nest for the first 2 days after leaving the nest, climbing and hopping among shrubs and low trees. By about the third day out of the nest, they are capable of flight. Later on, they tend to be closer to the adults' foraging areas than the nest. In Vermont, vegetation used by fledglings differed from that at the nest site by having more alder and spruce, although total vegetation density remained high. A pair with fledglings was observed in spruce and willow scrub on a dry ridge on the west James Bay coast. Fledglings have been observed with the adults 4 weeks after leaving the nest. Both adults feed the fledglings (Avery 2020; Kennard 1920; Manning 1952).

Beginning in about mid-July and continuing into August, groups of adults accompany fledglings from multiple nests and form small flocks. Later, flocks merge with other blackbird species such as Red-winged Blackbirds and Common Grackles. It also associates with European Starlings prior to initiation of autumn migration. The Rusty Blackbird may move considerable distances during the postfledging period in preparation for migration. In Alaska, birds were last seen in the breeding areas in mid-July. Distances travelled from the breeding areas during the postfledging period averaged 145 km (range 128-175 km; Avery 2020; Campbell et al. 2001; Johnson et al. 2012; Kennard 1920; MacLulich 1938; Powell et al. 2010a; Tozer 2012).

Once conspecific and multispecies flocks form, the Rusty Blackbird occurs in a variety of habitats. These are often anthropogenic areas such as stubble fields, pastures, and plowed fields. It occasionally visits cornfields where it eats ripening corn (Avery 2020; Campbell et al. 2001).

MIGRATION

Avery (2020) stated that the Rusty Blackbird was a diurnal migrant, but it appears as though most migration occurs at night. In northern Ohio near Lake Erie, 82% of spring departures and 95% of autumn departures occurred at night (Wright et al. 2018a). In late autumn, it may rest in stopover areas for approximately 1 month before proceeding to the wintering areas. Although it is considered a short-distance migrant, those breeding in the northwest may travel in excess of 5,000 km to reach the wintering area (Wright et al. 2018b).

Wright et al. (2018a) radiotracked migrating Rusty Blackbirds captured in Ohio on the southeastern shore of Lake Erie. Wright et al. (2018b) determined that 97.6% of spring migrants were undergoing a prealternate moult of body and/or head feathers. For both sexes, moult peaked during the middle of the migration period. This moult occurs commonly in waterfowl and shorebirds but has not previously been described for other passerines. Four Motus towers within the study area, a 28-km^2 wetland complex, were classified as the local array and the remainder (mostly in Ontario) were called regional arrays. Mean stopover duration for all birds was 25.3 days in spring and 25.7 days in autumn, with ranges of 3-62 days in spring and 2-58 days in autumn. Stopover periods were shorter for birds that arrived or were captured later. Males had longer stopover periods than females in 1 year, but shorter stopovers in the next year. Higher moult scores resulted in longer stopover periods when birds were in poor condition, but had no effect for birds in good condition. Of 39 spring migrants, 28 (71.8%) crossed Lake Erie and the remainder went around the lake. Spring departures were associated with later capture dates, increasing tailwind, and lower body condition. Autumn departures were associated with tailwinds. Nineteen of 58 (32.8%) spring and 35 of 49 (71.4%) autumn migrants made confirmed or probable stopover relocations. Stopover relocations ranged from 10 to 35 km from the local array, often in directions opposite to the predominant migratory direction. The mean capture day of birds that relocated was significantly earlier than for birds that did not relocate. In spring, males were much more likely to relocate than females (58% compared with 15%). Unlike most passerines, the Rusty Blackbird does not undertake rapid migrations punctuated with short refuelling stops. It spent 5 times longer on stopovers than warblers at the same location. Its migration pattern is more analogous to that of shorebirds, with longer stopovers required in spring to moult.

During migration, the Rusty Blackbird travels in flocks. In autumn, these are mostly mixed flocks that contain Red-winged Blackbirds and Common Grackles and possibly Brown-headed Cowbirds and European Starlings. Spring flocks may consist solely of Rusty Blackbirds but may contain these other species (Avery 2020; Lancaster et al. 2004).

At a stopover site in Ohio, there was no difference in the arrival times of the age classes, but males arrived significantly earlier than females by 13.1 days (Wright et al. 2018a). It is probable that males arrive on the breeding grounds before females, but the interval between their arrival may not be as great as at staging areas. In southern and central Ontario, it passes through in late March and early April. Most leave by mid-May, but some remain until late May (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). Manning (1981) observed flocks and single birds 20-25 May on the Twin Islands in James Bay.

Wright et al. (2018a) reported that there were no differences in autumn arrival dates in Ohio among age and sex classes. Manning (1952) reported 35 at Moose Factory on 27 September and singles on the Twin Islands on 2 and 30 September (Manning 1981). In the southern Shield, migration extends from late August until late November or even until late December, with peak movements in October (Mills 1981; Tozer 2012). In the south, it usually arrives in late September and leaves in mid-November; it may arrive as early as late August (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

During migration in Ontario, the Rusty Blackbird has been documented in wet woods, recently plowed and harvested fields, and at cattle feedlots. In Algonquin Park in autumn, it feeds on exposed mud along edges of rivers and inhabits riparian alder thickets, road margins, and campgrounds (Lancaster et al. 2004; McIlwraith 1894; Tozer 2012; Weir 2008).

Two studies characterized Rusty Blackbird migration habitat at the landscape level. In northern Ohio, a major stopover location was comprised of a 28-km^2 complex of wetlands near the Lake Erie shoreline (Wright et al. 2018a). The mean composition of core stopover areas of birds migrating between Alaska and the wintering grounds consisted of 60% croplands, 36% grasslands, 2% water, 1% wetlands, and 1% other habitats (Johnson et al. 2012).

The Rusty Blackbird has been documented in herbaceous-dominated wetlands, small water bodies, grasslands, agricultural crops, pastures, edges of swamps, bogs, swampy lake shorelines, beaver ponds, shrubby or treed margins of rivers and streams, landfills, sewage lagoons, and grassy edges and shrub areas of large wetlands. It is most frequently seen in wet areas or areas with damp soils (Avery 2020; Bent 1958; Campbell et al. 2001; Nadeau in Gauthier and Aubry 1996; Savignac 2017; Sinclair et al. 2003). During spring migration in Ohio, dogwood-willow swamp was the most strongly selected habitat, followed by forest and prairie. These were the least available habitats within the landscape. As spring progressed, dogwood and marsh patches were used less and forests and prairies were used more. Compared with random points, spring foraging areas were closer to habitat edges and in areas with less grass cover, more wet leaf litter, and more shallow water. In autumn, it selected dogwood-willow swamps, followed by forests, open water, and emergent marshes. Marshes were more likely to be used later in the season and forests earlier in the season. Compared with random sites, autumn foraging areas were in areas with more shallow water and dry leaf litter, and less grass, forbs, and herbaceous shrub cover (Wright et al. 2020).

Roosts are important for the Rusty Blackbird during migration. In spring, it often roosts in conspecific flocks but tends to join large multispecies roosts during autumn migration. During spring migration, flocks may roost on the ground in dense ground cover. Most frequently, it roosts in wooded areas, particularly swamps. It also roosts in cattail marshes and buttonbush and willow swamp thickets. In Niagara Region, autumn migrants and overwintering birds roost in a common reed marsh (Avery 2020; Bent 1958; Black and Roy 2010; Fitch 1958). In Ohio, roosting habitat in both seasons occurred in monotypic common reed or cattail marshes with emergents a mean of 2.3 m tall (Wright et al. 2020).

At a stopover site in Ohio, between-season site fidelity was 29% spring 2015 to autumn 2016 and 36% autumn 2016 to spring 2017. Migratory route fidelity was 43% for spring 2017 and 71% for autumn 2016. Site fidelity was high during migration, but several birds migrated past the site

without stopping. This suggests that migratory site fidelity is better measured at larger scales. The Rusty Blackbirds spends about 25% of its life cycle at staging areas, often repeatedly using the same sites and flyways (Wright et al. 2018a).

In early autumn in Ohio, the Rusty Blackbird consumed dogwood berries, with 68% of autumn foraging observations occurring in dogwood thickets (Wright et al. 2018a). Beal (1900) analyzed the contents of 132 stomachs, predominantly from migrating and wintering birds. The diet included 53% animal material, more than any other blackbird except the Bobolink. Beetles represented 13.8% of the annual diet, including 1.7% ground beetles, 2% scarab beetles (11.7% of the April diet), and 10.1% other beetles, which were mostly aquatic beetles and their larvae plus leaf beetles. Grasshoppers constituted 12% of the annual diet, peaking at 44.3% in August and almost as high in October. Caterpillars constituted 2.5% of the diet, peaking at 11.7% in May. A variety of insects, including ants, bugs, flies, dragonflies, caddisflies, and mayflies, constituted 13.7% of the diet. The diet included 4% spiders and millipedes, peaking at 23% in August. Crustaceans, snails, salamanders, and small fish constituted 7% of the diet. The 47% vegetable food consisted of grain, weed seeds, and small amounts of fruit and mast. Corn was the favourite grain and comprised 17.6% of the annual diet. Wheat and oats collectively comprised 6.8% of the diet, with oats preferred and representing 15.4% of the March diet. Most grain was waste grain or taken from corn cribs. Weed seeds did not appear to be preferred, representing 6% of the annual diet with a maximum of 23.3% in May. Fruit was unimportant in the diet but included buffalo-berry, hackberries, and raspberries. Mast was found in a few stomachs. Animal food was preferred, and the proportion that it represents in the diet would have been higher if samples were available from the breeding season. It was not considered a threat to agricultural crops. Other studies reported that it eats grasshoppers, earthworms, rye, foxtails, panic grasses, ragweeds, grapes, elderberries, acorns, beechnuts, pine seeds, white ash seeds, and fruits of American holly, Hercules' club, flowering dogwood, and black gum (Avery 2020; Bent 1958).

The Rusty Blackbird may use traditional stopover sites during migration where it remains for extended periods. These sites may be as critical to it as similar areas are to certain shorebirds during their migration. Few critical stopover areas have been identified for the Rusty Blackbird. Most stopover areas are within agricultural landscapes where they are threatened by fragmentation and isolation due to agricultural intensification (Johnson et al. 2012; Wright et al. 2018a).

The Rusty Blackbird is not protected in Canada. This means that it can legally be killed at any time and its nests destroyed (Savignac 2006). Although it is not protected, it is unlikely that many are killed in Canada. In the United States, it is protected under the *Migratory Bird Treaty Act* but there is a clause in this act that allows it to be killed if it causes property damage. It is legally subjected to blackbird control programs in the United States.

Although the Rusty Blackbird is a nocturnal migrant, it rarely strikes communication towers. At a Florida tower, only 8 were killed out of more than 35,000 birds (Avery 2020).

James (1991) considered the Rusty Blackbird a common migrant in Ontario.

All indications are that the Rusty Blackbird has declined significantly as a migrant throughout its range. In Elgin County, it was a common migrant in 1891 but it was uncommon by 2000 (Lancaster

et al. 2004). It was formerly fairly common as a migrant but is now uncommon in the Hamilton area (Curry 2006). Fleming (1907) considered it an abundant migrant at Toronto. Results from Ontario banding stations are inconclusive, probably because few are captured and the time period is recent (2004-14) and short: +11.4% at Prince Edward Point in autumn (nonsignificant), +6.5% at Innis Point in spring (nonsignificant), −17.5% at Pelee Island in autumn (significant), and −7.7% in autumn at Thunder Cape (nonsignificant). These figures represent the rate of annual decline (Savignac 2017). Autumn banding results in Tadoussac indicated an ongoing decline (Savard et al. 2011). It is probable that a large decline in the numbers of the Rusty Blackbird occurred before any modern surveys were implemented. Beal (1900) stated that it was one of the most familiar sights in spring in New England, with flocks around every farmhouse. It was seen in immense numbers, particularly in the Mississippi Valley. Bent (1958) reported that flocks of 10,000 were seen in Manitoba in 1882 and 100,000 were reported in New York on 1 May in 1880. In October 1937 in Massachusetts, a flock was reported to be 1.6 km long. The spring migration was spectacular, with Rusty Blackbirds ubiquitous. Birds could be seen in enormous numbers almost everywhere in cultivated fields, stubble fields, and treed swamps.

WINTER

The Rusty Blackbird is associated with snow. It is least likely to occur where there are frequent changes between snow cover and bare ground (Keyser et al. 2023).

In northern areas outside the normal wintering range, such as Ontario and British Columbia, the Rusty Blackbird inhabits agricultural fields and livestock feedlots, and visits bird feeders. It avoids very open areas in winter and during cold spells early in spring. It is associated with anthropogenic habitats (Campbell et al. 2001; LaForest 1993; Lancaster et al. 2004; Weir 2008).

Johnson et al. (2012) characterized the winter habitat of 3 individuals at the landscape scale. Core wintering areas of a male and female consisted of 99% cropland and grassland. The winter range of another female consisted of 51% coniferous forest, 17% deciduous woodland, 18% wetlands, 10% croplands and grasslands, and 4% other habitats.

The most important wintering habitat in the southeastern United States is bottomland hardwoods, but the Rusty Blackbird uses other forested habitats that produce mast, such as pecan orchards. Flooded woodlands, wooded vegetation along streams, and forested river floodplains are its main habitats. It is commonly associated with livestock feedlots and manured fields. It prefers contiguous semi-flooded forests but in drier areas is associated with smaller wetlands such as beaver ponds. It prefers forests with mature oaks, small creeks, and patchy inundated areas of shallow water and exposed substrate. It may use red cedar thickets bordering on open marsh. It frequents cornfields and rice patches and may occur on race courses, golf courses, and lawns. Two resources appear to be important for suitable winter habitat. Semi-flooded wetlands where the water is unfrozen is required for foraging, and it also requires small-seeded oaks and pecans (Avery 2020; Baker and Thomas 2015; Bent 1958; Greenberg and Droege 1999; Greenberg and Matsuoka 2010; Greenberg et al. 2011; Hobson et al. 2010; Savignac 2017).

Luscier et al. (2010) surveyed 219 sites in Arkansas, Louisiana, and Mississippi over 3 winters to determine the habitat preferences of the Rusty Blackbird. Habitats they examined included swamp forests with water deeper than 50 cm, wet bottomland forests with water 5-20 cm deep, moist

bottomlands with water 2-10 cm deep, and dry bottomlands with water 0-2 cm deep. Water in dry bottomlands was predominantly due to precipitation. Water in the other habitat types was due to flooding from agricultural lands and watercourses. Swamp forest was the only habitat where they did not detect flocks of 100 or more birds in any year. All habitats except dry bottomlands had detections of 20 or more blackbirds in every year. Habitat type was not a consistent predictor of its occupancy rates: canopy cover, tree density, and water cover were not consistently good predictors. It was not as specialized in its winter habitat use as previously reported. It appeared to have flexibility in its choice of winter habitat and possibly diet that allowed it to respond to variable conditions. It was equally likely to occupy agricultural fields adjacent to wetlands and bottomland forests but avoided large open fields distant from these features. It may move to different areas depending upon water levels. Water depth is important because it requires shallow water for foraging.

During winter, the Rusty Blackbird may segregate by age and sex classes, with females and juveniles wintering further south than adult males. Male foraging areas may be of higher quality and have greater food availability than areas used by females and juveniles (Baker and Thomas 2015).

Roosts are an important component of winter habitat. In Niagara Region, the Rusty Blackbird roosts in a wetland dominated by common reed (Black and Roy 2010). In British Columbia, it prefers to roost in wooded areas (Campbell et al. 2001). In the core of its winter range, roosts occur in fields, scrub, and forests. Preferred roosts were often in afforestation areas with dense vegetation near the ground, but were also in fields with short vegetation or in trees and shrubs in residential yards. These often supported 20-400 Rusty Blackbirds, with urban roosts also containing large numbers of other blackbird species. As winter progresses, it occurs more frequently in large mixed-species blackbird roosts. These may support millions of birds, with Rusty Blackbirds typically representing less than 1% of the total number of birds. In South Carolina, most roosts are in cattail marshes adjacent to salt marshes (Avery 2020; Greenberg et al. 2011; Savignac 2017).

The most significant limiting factors for the Rusty Blackbird appear to occur in the wintering range, and are related to habitat loss and blackbird control programs. Habitat loss is the most significant factor. Since European settlement, there has been a continuous decline in its winter habitat, with 75-80% of bottomland forests converted to agricultural uses. Conversion of forest to agriculture has progressed from drier to wetter areas over time. Habitat conversion in the last half of the 20th century may have been more deleterious because it winters in wetter areas. Some low-lying areas remained uncultivated until the 1970s when high soybean prices resulted in their being cleared and farmed, and this may have been some of the best habitat. Subsequent declines in soybean prices led to afforestation, but shifting markets could result in these lands being converted back to agricultural uses. The direct loss of habitat has been significant and has caused indirect effects. Much of the remaining wooded wetlands and bottomland forests are small patches. Fragmentation may degrade habitat by exposing the Rusty Blackbird to increased predation and increased competition from Common Grackles and other blackbirds. Draining and diversion of water may change soil moisture regimes and affect the quality of foraging habitat. The effects of the numerous water control projects on the Mississippi River and its major tributaries on the Rusty Blackbird are potentially quite large but have not been evaluated (Greenberg and Droege 1999; Greenberg and Matsuoka 2010; Greenberg et al. 2011).

The Rusty Blackbird is not an agricultural pest, but many are killed on the wintering grounds because it associates with other blackbird species that are significant depredators of crops. From 1974 to 1992, 83 roosts were sprayed with a surfactant that killed 38 million birds. These were mostly grackles, starlings, Red-winged Blackbirds, and cowbirds. It was estimated that 120,000 Rusty Blackbirds were killed, but this was a crude estimate based on the fact that less than 1% of the birds at mixed-species roosts are typically Rusty Blackbirds. The use of this surfactant was banned in 1992. The toxicant DCR-1339 was used in the rice production areas of Texas and Louisiana. These poison baits were placed in staging areas and at feedlots and dairy farms. No estimates on the number of Rusty Blackbirds that were killed by this compound are available. Some researchers have trivialized the effects of blackbird control programs on the Rusty Blackbird because the number of birds killed is low relative to other species and none of the other species have declined significantly as a result. The latter point is not true because significant declines in the eastern populations of the Common Grackle have been attributed to blackbird control programs. Other studies acknowledge that the number killed and the effect on the Rusty Blackbird population is unknown (Greenberg and Droege 1999; Greenberg and Matsuoka 2010; Greenberg et al. 2011). Winter populations fluctuate considerably year to year (Greenberg and Matsuoka 2010) and this may be consistent with the cyclic pattern observed during autumn migration in Quebec. Savignac et al. (2011) concluded that a cyclic pattern in its abundance and reproductive success could make it more vulnerable to blackbird control programs than other blackbird species.

In Illinois, Graber and Graber (1979) observed a 75% decline in the abundance of the Rusty Blackbird after a severe winter storm. It was unknown whether the birds suffered mortality or emigrated.

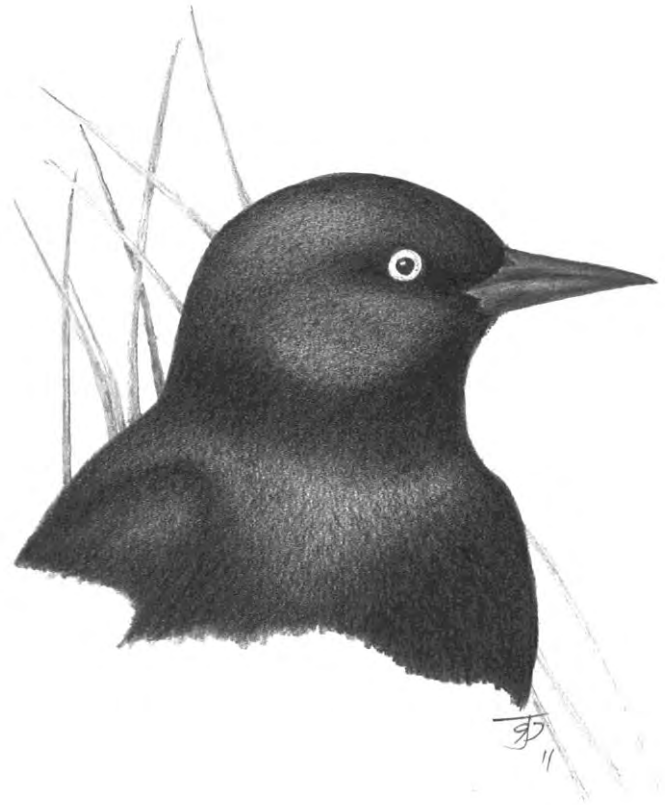
James (1991) considered the Rusty Blackbird rare to common in winter in the south north to Manitoulin Island and Ottawa, and occasional and rare north to Thunder Bay, Wawa, and Moosonee.

The number of wintering Rusty Blackbirds in Ontario appeared to increase in the first half of the 20th century before declining. McIlwraith (1894) had no winter records for it. Freedman and Riley (1980) analyzed CBC data for southern Ontario for 1929-77. They found a recent trend to greater abundance and frequency of occurrence, but at low total numbers. In the Hamilton area, it overwintered regularly singly or in small numbers in the last half of the 20th century, but it is now rare (Curry 2006). In the Kingston area, it appears to have become more common since 1991 (Weir 2008).

CBC data indicate a significant long-term decline in the Rusty Blackbird. Data for 1966-2005 indicate a decline of 4.5% per year, which equates to an 85% population decline. High numbers were detected in the 1950s and early 1960s, although it had probably declined previously, and there was a marked decline around 1965 continuing into the 1970s. During 1994-2003, the rate of decline levelled off at 2.1% per year (Greenberg et al. 2011; Savignac 2017).

Brewer's Blackbird

Euphagus cyanocephalus

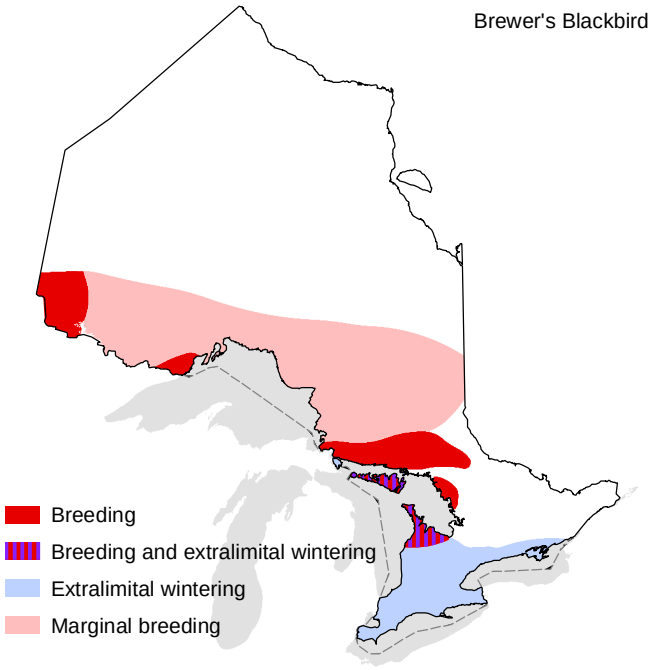


BREEDING SEASON

Habitat Requirements

Ontario Brewer's Blackbird nests were along road and railway rights-of-way on edges, ditches, and embankments (71.3% of nests); in fields and pastures (17.1%); in open bogs (6.7%); in open clear-cuts or burns (3.0%); on dry ridges and dunes (1.2%); and in a black ash swamp (0.6%). Nesting areas were usually open and occurred in both wet and dry sites (Peck and James 1987).

Most nesting habitat described for Ontario was in the Canadian Shield portion of the Great Lakes-St. Lawrence Forest Region, although the Brewer's Blackbird occasionally nests in the southern Boreal Forest Region and south of the Shield. At Fort Francis, it nested in peatlands with willow shrubs, but vacated the area after it burned. The first colony reported for Ontario was at Thunder Bay in a 3.2-ha clearing between 2 roads. The site supported a few dead trembling aspens that it used as perches. In the highway corridor between Sault Ste. Marie and Sudbury, most nesting



occurred along the highway, often between the road and railway in planted conifers or on the ground. A small colony occurred in a 4-ha marsh dominated by woolgrass with a few narrow-leaved cattails, red-osier dogwoods, and meadowsweet. There was a dense growth of alders and willows around 2 sides of the marsh. Another colony was in wet grassy fields at the junction of 2 highways. In Parry Sound District, colonies were found at Magnetewan, Powassan, South River, Trout Creek, Sundridge, and Verner. At the first 3 sites, the colonies were in peatlands, one of which had been logged a few years previously. These supported typical bog and fen species such as leatherleaf, cottongrass, bog laurel, sedges, sphagnum moss, and scattered black spruce and tamarack. Where it nested in peatlands, open fields, roadsides, golf courses, and other open habitats were usually present in the immediate vicinity. The Trout Creek colony was in a clear-cut with windrows, the Sundridge colony was in hayfields, and the Verner colony was in rows of conifers. A nest in Muskoka District was in open farmland near a road (Allin and Dear 1947; Baillie 1961; Crins and O'Donnell 1993; Devitt 1964; Walton 2000; Wood 1955).

Throughout its range, the Brewer's Blackbird nests in many open habitats. These include patches of shrubs, particularly sagebrush in the west; highway, railway, and utility rights-of-way; villages and suburban areas; bogs and fens; marshes with emergent vegetation; dry marshes that have been burned; damp meadows and fields; riparian habitats along wetlands, streams, and lakes; grazed pastures; on banks of streams and ditches; in stubble agricultural fields; in fields planted to vegetables; urban parks and yards; shrubby prairies; clear-cuts and burns; conifer plantations; pine and oak barrens; windbreaks; hayfields; and university campuses. Although most nesting habitat is anthropogenic, it nests at higher altitudes in mountain meadows and along shrub-lined watercourses. In heavily forested landscapes, it is restricted to nesting in wetlands and along human-created rights-of-way. Highest numbers tend to occur in rural and agricultural settings (Campbell et al. 2001; Finch 1991a; Furrer 1975; Horn 1968; Leighton et al. 2002; Martin 2020; Mossman et al. 1991; Niemi and Hanowski 1984a; Orians and Horn 1969; Pitelka 1942; Stepney 1979; Walkinshaw and Zimmerman 1961; Williams in Bent 1958). In British Columbia, 59% of nests were associated with human-modified habitats, 14% with forested lands, 10% with shrublands, 7% with wetlands, and 6% with grasslands. Modified habitats included 41% farmland, 28% rural land, 23% suburban areas, 4% urban areas, 3% orchards and vineyards, and 1% clear-cuts. Natural nesting habitats were comprised of 45% shrublands, 28% wetlands including marshes, and 20% forest edges. Nesting areas were often close to wetlands or low-lying areas that it used for foraging. In farmlands and rural areas,

nesting habitats usually included hedgerows, tangles of vegetation, or ditches with sloped banks. In grasslands and shrubby areas, nests were in copses of shrubs, dense ground cover, or at edges of clumps of trees. In wetlands, it nested in willow thickets, emergents such as cattails, or on hummocky ground. In suburban areas, it nested in large gardens with ornamental trees, especially conifers. It also nested in riparian thickets and open pine woodlands. In boreal areas, it often nests in open burns (Campbell et al. 2001).

In Washington, nesting colonies typically had 3 habitat features: the nesting habitat, a nearby foraging area, and high perches from which the nest sites were visible. All sites with all 3 features had either active colonies or a number of nests remaining from previous years. Single nests were occasionally found where there were no extensive areas of densely foliated sagebrush, the predominant nesting substrate. No colonies were found in the absence of water bordered by short grasses or sedges, the primary foraging habitat, and no nesting occurred where elevated perches were absent. Males spend much of their time on perches when females are laying and incubating where they guard against predators. Perches tend to be 3-7 m high and may consist of trees, cliffs, and telephone and hydro poles and wires. These latter features are greatly preferred as roosts by birds nesting near roads (Horn 1968, 1970; Williams 1952).

On an elevational gradient in Wyoming, the Brewer's Blackbird nested mostly in mid-elevational areas in dense shrubs. It was associated with drier areas with increased ground cover and occupied a variety of upland habitats far from streams. It occurred in areas with more than 65% coverage by herbaceous species and grasses that were densely foliated by shrubs in the mid-canopy layer; many sites were moist. It used an intermediate range of habitats and its habitat preferences most closely approximated those of the Song Sparrow (Finch 1989b, 1991a).

Most Ontario nests were well concealed; 88.0% were on the ground and the others were elevated. Ground nests were often in depressions, sometimes excavated by the females, or were in vegetation such as moss. They were in or under clumps of grasses and forbs (40.4% of nests); in or under shrubs (39.4%); at the base of saplings, stumps, and trees (8.5%); under dead branches (3.2%); in moss (3.2%); fairly exposed on bare ground (2.1%); under an overhanging bank (1.1%); in the open end of a fallen stump (1.1%); and in a pail lying on its side (1.1%). Most elevated nests were over dry land, but 18.2% were over water. Of 22 elevated nests, 18 were in living trees or shrubs, one was in a cavity in a dead tree, one was on top of a sawed-off stump, one was in an open Tree Swallow nest, and one was in rushes. Both coniferous (2 species, 10 nests) and deciduous (4 species, 8 nests) trees and shrubs were used, with the most frequently used species being pines (8 nests), spruces (3 nests), blueberries (3 nests), Labrador tea (2 nests), and Manitoba maple (2 nests). Elevated nests were 0.2-2.7 m from the ground, mostly 1.2-1.8 m up (Peck and James 1987). At Sault Ste. Marie, 2 nests were on the ground in sparse woody cover and 3 were in tops of solitary spruce 3 m tall (Wood 1955). Near Sudbury, 8 nests were 1.2-1.8 m (average 1.5 m) from the ground in conifers. All were in extremely dense vegetation that had developed around the flattened tops where the crowns had been cut off (Stepney 1975a). Nests at Sault Ste. Marie were also in dense foliage resulting from pruning. Conifers without human disturbance apparently were not dense enough to be attractive to nesting birds. Four colonies that had been under observation for a few years all contained conifers that were not used for nesting, although nests were often placed under them. A nest at Luther Marsh

and several at a colony at Sault Ste. Marie were less than 30 cm above water. Nests in the Sudbury area were on dry knolls in low vegetation, sunken into the ground so that their tops were flush with it. One was partially hidden beneath dead bracken fern and a small spirea. In addition to these species, vegetation around the nests consisted of strawberries, raspberries, blueberries, asters, goldenrods, fringed false milkwort, Canada mayflower, willow, yarrow, sweet fern, and flat-branched tree-clubmoss. Another nest was in the centre of a clump of dried rushes in a marsh, 15 cm above water (Devitt 1964). A nest at Thunder Bay was on the ground and covered with 15-cm tall grasses, mostly redtop. Sedges, violets, and early leaves of other herbaceous species occurred in the immediate vicinity of the nest (Allin and Dear 1947, 1955).

Furrer (1975) described 4 nest types in Washington: those in shrubs, nests in emergent vegetation, ground nests, and nests in crevices and on ledges of cliffs. No nests were found in trees and those on cliffs were rare. Overall, 66.7% of nests were in shrubs, 16.2% were on the ground, and 17.1% were over water. There were seasonal differences in the frequency of nest types. During the peak of nest building in early spring, almost all nests were in shrubs, with other nest types becoming more frequent later in the breeding season. Ground nests occurred in both dry and wet areas. Upland ground nests disappeared before the end of the season and wet ground nests did not appear until later. It took longer for vegetation to become sufficiently established in wet areas to provide cover. Most nests on dry ground relied on shrubs for cover. There was no optimal nest type that was suitable for all conditions. There was no correlation between the type of a bird's natal nest and the type of nest that it built, and individuals did not always build the same type of nest. Nests are commonly placed in trees and dead stubs standing in water. Several nests were in anthropogenic or unusual features. These included a bird box in Manitoba, in a Tree Swallow nest box, on building support beams, on ledges, in fence posts, on telephone poles, in haystacks, on a road grader, under a walkway, in an abandoned car, among the roots of a fallen tree, in a burned-out woodpecker cavity, and in an abandoned mine shaft in a tunnel under a rock (Baily 1950; Bancroft 1986b; Butler 1981; Campbell et al. 2001; Wiggins 1990). In British Columbia, 38% of nests were in deciduous and coniferous shrubs, 29% were in trees, 17% were on the ground, 2.2% were on beams or sides of buildings, 1.9% were on posts or poles, 1.7% were in snags or stumps, 1.6% were in vines, and 1.3% were in reeds or cattails. Sixty-five percent of nests in live trees were in conifers. The Brewer's Blackbird appeared to have regional preferences for nest types. There were equal numbers of nests in trees and shrubs in 1 area. In other areas, nests were mostly in shrubs, in trees, or on the ground (Campbell et al. 2001). A variety of trees, shrubs, and emergents have been used for elevated nests. These include sagebrush (which is highly preferred in the western United States), pines, oaks, firs, cypress, junipers, willows, apple, wild roses, juneberries, gooseberries, poplars, cattails, eucalyptus, and snowberry. Nests in trees are usually saddled on a horizontal branch or often near the top of the tree in dense foliage. They are rarely at the end of a limb in dense tufts of needles. Nests in shrubs are in those with the densest foliage, and the nest is in the densest portion of the shrub. There is 1 report of a colony nesting in cavities at tops of tall fir trees with none lower than 45.7 m above ground. This is exceptional and most elevated nests are much lower than this. At the same colony the previous year, all nests were 1.2 m or less above ground in shrubs. Tree nests in California were 2.1-13.1 m from the ground with most 6.1-9.1 m up. In British Columbia, nests were 0-10.0 m from the ground, with most 0.5-2.2 m up. In Nevada, elevated nests were 0.15-

6 m from the ground (average 1.55 m). Average height above ground in Colorado was 17.7 cm (Campbell et al. 2001; Furrer 1975; Horn 1968, 1970; Leighton et al. 2002; Martin 2020; Pitelka 1942; Walkinshaw and Zimmerman 1961; Williams 1952; Williams in Bent 1958). Nests on the ground are often associated with an abrupt change in relief such as the slope of a railway grade, a ditch bank, the base of a perpendicular bank bordering a stream, or at the top of a small bank or rise. They may also be placed at distinctive changes in vegetation or at the base of a plant that differs in height or colour from the rest of the habitat, including beneath features that are taller than the general cover. Ground nests are under or next to a clump of vegetation, among thick ground cover, or at the base of a sapling (Campbell et al. 2001; Martin 2020). In Nevada, all 75 nests were in shaded areas protected from the sun but across its range and between years, nest placement varies from bright sun to deep shade. Nests are placed in all directional orientations. There are 2 records from British Columbia of nests being reused (Campbell et al. 2001; Martin 2020; Walkinshaw and Zimmerman 1961).

The Brewer's Blackbird is colonial and defends only a small area around the nest. Solitary nesting occurs, but most birds nest in loose colonies. In Ontario, 14 isolated nestings were reported compared with 56 colonies with an average of 4-5 nests (Peck and James 1998b). In California, Williams (1952) reported 10 colonies in about 300 km^2 and found no singly nesting pairs. The female begins to aggressively defend the nest site against other females as soon as she selects it. The area around the nest may or may not be defended by the male. Males may be aggressive at the nest site and adjacent guard perches, but only after pair formation has taken place, with the peak of aggression during nest building and egg laying. Nests tend to be more widely spaced than those of many other blackbird species. At a Sudbury colony, nests were 4.6-109.7 m apart. At a California colony, nests were 2.7-11.3 m apart. Most colonies are small, supporting 10-30 nests, with a maximum of 12 nests in Ontario. Maximum colony size in British Columbia is 22 nests (average 8 nests). Colonies larger than 100 pairs have been reported in Nevada (Campbell et al. 2001; Horn 1968; Martin 2020; Stepney 1975a; Walkinshaw and Zimmerman 1961; Williams 1952; Williams in Bent 1955).

In Washington, Horn (1968, 1970) examined whether aggregations of nests were true colonies and if nesting in groups was beneficial. Nests were always near water and therefore the clumped distribution of nests might be due in part to the patchy distribution of water. Other factors pointed toward coloniality. Males give alarm calls from their perches in response to predators and fly out to harass those that approach the colony too closely. Predators were attacked 100 m from the nest, approximately 4 times the mean distance between nests. This resulted in mobbing that was effective in deterring flying birds but did not drive away snakes, mammals, or perched birds. The mobbing effectively prevented Ring-billed Gulls from flying over colonies and eliminated predation due to this species. Birds that lost their own nest due to predation left the colony and did not stay to help defend other nests. In colonies in nonlinear patches, nests that were further apart than the median distance were depredated more frequently than those closer together. In linear-shaped colonies, nests that were closer together were depredated more frequently. The predation pattern conferred a slight advantage to nest clumping in nonlinear colonies. Dispersed nests were more advantageous in linear colonies. In both types of colonies, predation by Ring-billed Gulls was prevented by nest grouping. Displays of nesting birds resulted in high nest synchrony in colonies.

Those nesting on the periphery of the colony or distant from it may not be synchronized. Nest synchrony may be advantageous in predator mobbing if all birds are on the same schedule. If extra-pair copulations are an important mating strategy, synchronized nesting could be beneficial. Feeding may be the main reason for coloniality. Suitable feeding areas are often patchily distributed and the suitability of each site changes frequently. Whenever there was a steady wind of 8 km or greater, Brewer's Blackbirds foraged on the lee shores of lakes because emerging damselflies were more abundant there. All birds tend to forage in the same location and follow those that were successful at foraging. In this manner, the colony usually exploits the best food source at all times. Occasionally, colonies shift because of human disturbance or habitat degradation. When this occurs, all birds move together to a new site, including individuals who could have still used portions of the old site.

The only information on natal philopatry rates is from Washington where Furrer (1975) banded 555 nestlings in 1 year and 679 in the next year. Of the 555, 46 (8.3%) were resighted and 45 of the 679 (6.6%) were resighted, for an overall return rate of 7.4%. Results were higher for those banded in the first year because of the extra year for recovery. Four (0.7%) nestlings banded in the second year were not seen as adults until 3 years later. A nestling banded in Michigan was recovered in Ontario the next breeding season (Martin 2020).

Colony sites tend to be stable and used year after year. Brewer's Blackbirds are flexible enough to move entire colonies if the habitat becomes unsuitable or the colony is disturbed. One colony was apparently deserted because a Loggerhead Shrike nested near it. When colonies shifted in Washington, the birds continued to use the same foraging areas (Campbell et al. 2001; Horn 1970; Martin 2020). No information is available on the rate of adult site fidelity, but it may be high. In California, some birds were mated together in as many as 5 consecutive years (Williams 1952). In Washington, some birds shifted among colonies. Each bird made only a single change. After moving from another colony, they remained at their new colony until they disappeared (Williams 1952). An adult female that nested in Washington nested in British Columbia 3 years later (Martin 2020). One banded in June in Michigan was recovered the next June in Ontario 340 km from the banding location (Brewer et al. 2018).

Limiting Factors

Eggs have been found in Ontario nests from early May to early July, with most present in the last week of May and first week of June (Peck and James 1998b). Resident birds form pairs while they are still in winter and early spring flocks. New pairs are established shortly after arrival at the colony. In resident populations, pair formation may last 12 weeks but it is likely much less in migratory populations and may be very brief in polygynous matings. Females took 9-10 days to build nests in Ontario but only 5-9 days in California. Egg laying usually starts 1 day after the nest is complete and 1 egg is laid per day. Incubation typically begins with the laying of the penultimate egg. In some cases, hatching may take place over a 3-day period suggesting that incubation may begin earlier. In Ontario, the incubation period is 12 to 13 days. Elsewhere, incubation periods of 11-17 days have been reported with 12-13 days typical. The nestling period is 12-16 days but mostly 13-13.5 days. If nests are disturbed, young may leave the nest when they are as young as 9 days (Campbell et al. 2001; Furrer 1975; Horn 1970; Martin 2020; Peck and James 1987; Williams 1952).

The nesting season is very short in Ontario and only a single brood is raised. In most areas, the Brewer's Blackbird raises a single brood but double broods are fairly common in coastal California, Washington, and Oregon and in much of British Columbia. Only 1 brood is raised in northern British Columbia. Replacement clutches are common if the first nest is lost, with the new nest built close to the original one. As many as 3 attempts may be made to raise a brood (Campbell et al. 2001; Martin 2020; Peck and James 1998b; Williams 1952). Peck and James (1987) reported clutches of 2-6 eggs in Ontario (average 4.93 eggs, mode 5 eggs). Mean clutch size in the Sudbury area was 4.72 eggs. Elsewhere, clutches of 3-7 eggs have been reported with rare records of 8 eggs or nestlings. In British Columbia, clutches of 1-7 eggs were reported and 1 nest contained 8 nestlings. Most nests contained 4 or 5 eggs with May clutches tending to have 5 eggs and June clutches having 4 eggs. Overall mean clutch size has been estimated at 4.98 eggs (mode 5 eggs). Mean clutch sizes in other areas include 5.00 in Colorado, 4.87 in Nevada, and 4.9 and 5.6 in Washington (Campbell et al. 2001; Martin 2020; Stepney 1975a; Williams in Bent 1958).

Both sexes are capable of breeding when they are 1 year old and they breed annually thereafter. In California, an older male evicted a yearling mate and took his mate as his secondary female. This suggests that yearlings may not be able to compete successfully with older males. Unmated birds have been observed in some populations but their age and sex were not determined (Martin 2020; Pitelka 1942; Williams 1952).

The Brewer's Blackbird is monogamous in Ontario, Colorado, Nevada, and Washington, but polygyny has been reported in California (Martin 2020; Orians 1980). At a California site, there were 80 cases (69.6% of matings) of monogamy and 35 (30.4%) of polygyny. Polygyny was most frequent in the year that there were 2 times as many females present as males. Polygyny also occurred when mated males mated with a neighbouring female after her mate died or her nest was destroyed. Most polygynous males (82.9%) were bigamous but 14.3% were trigynous and 1 (2.9%) had 4 mates. Of 29 males that were present for 2 or more years, 6 (20.7%) were constantly monogamous, 1 (3.4%) was constantly polygynous, and 22 (75.9%) switched status. Nests of females mated to a polygynous male were occasionally in the same tree, but also in different trees, sometimes with the nest of another pair in between. Of 69 females, 34 (49.3%) were always primary, 20 (29.0%) were always secondary, and 15 (21.7%) changed status. Some changed from primary to secondary status for their second nest. Only 2 females became primary to females that they had been secondary to previously. Males guarded secondary females as assiduously as primary females. Usually the eggs of the primary female are hatching when the secondary female begins to incubate. Of 29 males with 2 mates, 20 (69.0%) fed nestlings at both nests, 2 of 4 (50.0%) with 3 mates fed nestlings at all nests, and the male with 4 mates did not feed at all nests. Males may feed fledglings from the primary nest and nestlings in the secondary nest on the same day. Polygyny is advantageous to males because they produce more offspring. Feeding rates by polygynous males were lower than for monogamous males with a resulting higher death rate of nestlings. Mating with a polygynous male may be disadvantageous for females (Williams 1952). The pair bond lasts for a single season but birds frequently remate if both return in a subsequent year. Some California pairs bred together in as many as 5 consecutive years. In 45 cases, both members of a primary pair returned; 42 (93.3%) remated and 3 (6.6%) divorced. Of 45 secondary pairs, both members returned in only 6 cases and they all divorced (Williams 1952).

It is probable that extra-pair copulations are an important component of the mating system, but this has not been tested genetically. During the nest-building phase, females frequently display for copulation. All males in the vicinity respond even if they are already mated. Males are usually successful in guarding their females from the advances of rivals but promiscuous copulations have been observed. Males do not guard the female constantly during the incubation period and this may provide him opportunities to seek extra-pair copulations or another mate (Howell and Bartholomew 1952; Martin 2020; Williams 1952). Intraspecific parasitism is a rare mating strategy. Five of 162 nests (3.1%) in Washington were parasitized by another Brewer's Blackbird (Martin 2020).

The Brewer's Blackbird regularly forages in both aquatic and terrestrial habitats. In wetlands and water bodies, it prefers to forage in short grasses and sedges along margins of lakes and wetlands. It has longer legs than Yellow-headed and Red-winged blackbirds and is much better adapted to exploiting resources in this zone. The other blackbirds are adept at clinging to vertical stems of emergent wetland plants but the Brewer's Blackbird is very clumsy when attempting this. When it forages in marshes, it prefers areas of blown-down cattails and bulrushes where it can walk over a more or less flat surface. The other 2 blackbird species expel the Brewer's Blackbird from their territories. Within marshes, the foraging areas of these 3 blackbirds are spatially distinct. They all forage in short grasses and sedges, but the Brewer's Blackbird is much more efficient in this habitat. Where newly emerged damselflies are the primary aquatic prey, both the Brewer's and Red-winged blackbirds shift their foraging areas during the day. They feed in aquatic habitat during peak periods of damselfly emergence in mid- to late morning and in terrestrial habitat in the afternoon. Most foraging by Brewer's Blackbirds occurs near the colony but birds may make foraging flights as far as 1.6 km. It responds quickly to changes in food availability and feeds on the lee shore of lakes whenever the wind exceeds 8 km per hour because emerging damselflies are more abundant in calm areas (Horn 1968, 1970; Orians 1980; Orians and Horn 1969). It commonly wades in water as deep as its belly to obtain aquatic prey, occasionally in the company of shorebirds. It also forages on exposed sandbars covered in flotsam (Campbell et al. 2001; Williams in Bent 1958). In Nevada, it foraged on extensive growths of Canada waterweed in a lake. It landed on the plants with the water coming up to the middle or upper parts of its tarsometatarsi. It also walked and fed on water-lily pads. It was once seen on a river hovering near open water and snapping food from the surface. It has been observed dipping bread and popped corn into water before eating it (Richardson 1947; Williams in Bent 1958). In terrestrial habitat, the Brewer's Blackbird forages mostly on the ground. A foraging sequence consists of a period of walking in a zigzag fashion followed by a brief pause. In Ontario, foraging-site suitability was determined by vegetation height and ease of walking. Areas of short (2.5 cm) grass were preferred to taller grass or shrubs by adults foraging for themselves. Grasses taller than 15 cm were preferred by adults capturing food for nestlings. When foraging in taller grasses, it preferred areas lacking litter and other features that impeded movement, with areas supporting fresh growth after burning particularly favoured. Areas of taller grass that were used usually abutted borders of low vegetation or road margins with birds penetrating only short distances into the tall vegetation. While foraging, it mostly gleans from the ground or low vegetation. It flips over cattle dung, stones, and small branches and rarely probes in the soil with its bill. It forages in shrubs by walking underneath them and capturing insects on the branches above, or in tops of denser shrubs. It does not forage among the branches of shrubs as does the Red-

winged Blackbird. The Brewer's Blackbird rarely feeds while perched on fairly rigid vegetation such as sunflowers. It has been observed gleaning insects from sheep. It may sally from the ground or an elevated perch to capture insects, with males hawking more than females and closer to the ground. In early spring, it may feed in manure piles. It occasionally feeds in trees, taking spittle bugs from among pine needles and cherries from trees in orchards. It may glean bread, popped corn, and other human foods while foraging in parking lots. It frequently feeds in flocks in fields by following tractors plowing or disking the soil where it captures insects and other invertebrates and young leopard frogs and voles. It has fed on other birds, including Barn Swallows, young Ring-necked Pheasants, and fledgling Lesser Goldfinches and Brewer's Sparrows. The Barn Swallow was carrion. It was uncertain if the other species were carrion or killed by the blackbirds. The Brewer's Blackbird uses a variety of terrestrial habitats for foraging including shrubby prairies, pastures, barnyards, roads, streets in villages and towns, lawns, agricultural fields, parking lots, golf courses, cemeteries, mowed urban parks, university campuses, overgrown fields, schoolyards, and railways. It is a highly opportunistic forager that readily abandons a traditional foraging area to exploit an insect outbreak or an abundant source of food elsewhere (Beal 1900; Beasley and Carothers 1974; Campbell et al. 2001; Martin 2020; Orians 1980; Orians and Horn 1967; Powers and Wheeler 1987; Verbeek 1964; Walkinshaw and Zimmerman 1961; Williams 1952; Williams in Bent 1958).

In most areas, the Brewer's Blackbird does not defend a foraging area. Feeding areas may be used by all or most birds in a colony, and the foraging site may change daily or even within a day. It is not profitable for a bird to attempt to defend a feeding area when the best foraging areas are transient and constantly changing. An exception was near Sudbury where suitable foraging sites were limited. Pairs vigorously defended feeding territories with high-intensity pursuits and threat displays. The size of 7 foraging territories ranged from 0.05 to 0.2 ha with no overlap in areas where adjacent pairs foraged for their young. Where feeding territories were defended, most food was collected within 50 m of the nest (Horn 1968; Martin 2020; Orians 1980).

Females are capable of fledging young without male assistance. Some birds may fly several kilometres to obtain food for nestlings. Birds foraging within 50 m tend to bring a maximum of 7 food items per trip but those returning from longer distances bring very large loads of food (Martin 2020; Orians 1980; Walkinshaw and Zimmerman 1961; Williams 1952). In Washington, the nestling diet consisted of 34% odonates (predominantly damselflies), 21% flies, 7% orthopterans, 7% other insects, 5% spiders, 1% cicadas, and 1% miscellaneous items. Orthopterans and cicadas were numerically unimportant yet provided 24% and 11% of the calories delivered to nestlings respectively. Odonates were important at 34% of the diet both numerically and from a caloric perspective. The prey items delivered to nestlings varied during the day because adults foraged in upland areas in early morning and mid- to late afternoon and in wetland areas from mid-morning to early afternoon. In the morning, the diet consisted predominantly of small amounts of flies (mostly midges and mosquitoes), lepidopterans (small caterpillars and adults of a plume moth), plus other items that have no diurnal variations in abundance such as small snails, spiders, and other insects. At 1000 hours, the use of odonates peaked at about 98% of the diet. In the afternoon, few odonates were taken, with flies, lepidopterans, and other items constituting much of the diet. In 1 year there was an irruption of cicadas that was not exploited by the Yellow-headed Blackbird but they constituted 10% of the energy delivered to Brewer's Blackbird nestlings and 25% of the energy

for Red-winged Blackbird nestlings. Although the diet of the 3 blackbirds overlapped considerably, competition for food was minimized by their different foraging techniques and microhabitats. The average size of prey delivered to nestlings by Brewer's Blackbirds from near the water (mostly damselflies) was much greater than the average size delivered from upland areas (midges, mosquitoes, and caterpillars). The importance of food taken near water was much greater (Horn 1968; Orians 1980; Orians and Horn 1969). These studies demonstrated the importance of damselflies in the diet of nestlings. In many areas, the Brewer's Blackbird may nest in drier locations where damselflies are scarce or absent in the diet. Martin (2020) reported that 634 food items collected from the gizzards of 78 Ontario nestlings consisted of 4% odonates, 11% orthopterans, 2% true bugs, 14% beetles, 61% lepidopterans, 1% flies, 1% hymenopterans, 3% spiders, 1% snails, and 1% miscellaneous. Of 500 items in Ontario, the diet consisted of 1% odonates, 6.5% orthopterans, 3% true bugs, 6.5% beetles, 1.5% caddisflies, 35% lepidopterans, 14% flies, 1% hymenopterans, 22% spiders, 3% snails, and 6.5% miscellaneous.

In Washington, adults foraging for nestlings usually ate the same foods (Orians 1980). In British Columbia, summer flocks often fed in fields on waste grain, weed seeds, and grasshoppers (Campbell et al. 2001). Beal (1900) analyzed the contents of 146 stomachs collected in every month except April. The diet consisted of 31.8% animal matter and 68.2% vegetable matter. The animal food was almost entirely insects except for a few spiders and snails. The insects were mostly beetles, ants, wasps, and grasshoppers. Beetles constituted 7.8% of the diet. These were mostly weevils which constituted 29% of the May diet but only 3.4% of the annual diet; ground beetles represented 1.7% of the annual diet. Hymenopterans comprised 2.5% of the annual diet but represented 14.8% of the August diet. These were mostly ants and wasps, with a few smaller parasitic species. Grasshoppers were the favourite animal food, constituting 16.1% of the annual diet and 47.5% of the August diet. Miscellaneous insects included flies, bugs, and caterpillars; these were not important in the overall diet. The vegetation consumed included 60.3% grain with all other vegetation representing only 7.9% of the diet. Grains consumed included oats, corn, wheat, and a little barley. The Brewer's Blackbird highly preferred oats which comprised about 75% of the grain consumed and was eaten in every month. It ate both waste and ripening grain and subsisted almost entirely on grain in winter. It has eaten newly sown wheat. The other vegetation consisted of weed seeds. The major prey item of birds foraging on Canada waterweed was recently emerged damselflies (Richardson 1947). Martin (2020) reported that 125 stomachs collected from all months in California contained 38% animal matter and 62% vegetable matter. Animal matter peaked at 100% of the diet in June and was lowest at 3% in December. Of 1,135 animal food items, all were insects except for 1 spider. Beetles, especially weevils, were the dominant insects in the diet. Vegetable matter peaked at 97% in December but was 0% of the June diet. It most frequently consumed grains, followed by weed seeds such as those of red-root amaranth, pale smartweed, duckweed, and barnyard grass. During insect outbreaks, the Brewer's Blackbird gorges on crickets, butterflies, treehoppers, alfalfa weevils, cutworms, termites during their dispersal flights, grasshoppers, corn earworm moths, and forest tent caterpillars. Six birds collected in June in Utah had eaten treehoppers, alfalfa weevils, clover leaf weevils, clown beetles, click beetles, grasshoppers, stink bugs, milkweed bugs, leaf bugs, aphids, leafhoppers, metallic wood-boring beetles, caddisflies,

caterpillars, fly larvae, ants, and spiders. It may feed on shore flies in the company of sandpipers (Williams in Bent 1958).

The Brewer's Blackbird is a host of the Brown-headed Cowbird that readily accepts the parasitic eggs and typically raises fledglings of both species. Despite egg removal by the cowbird, parasitism appears to have no significant effect on the Brewer's Blackbird (Martin 2020). One of 206 Ontario nests (0.5%) was parasitized (Peck and James 1998b). In British Columbia, 24 of 797 nests (3.0%) were parasitized and there were 5 reports of it feeding cowbird fledglings (Campbell et al. 2001). Parasitism rates reported elsewhere include 268 of 837 nests (32.0%) in Washington; 85 of 371 nests (22.9%) in Alberta, Saskatchewan, and Manitoba; 10 of 27 nests (37.0%) in Manitoba; 42 of 217 nests (19.4%) in Colorado and Wyoming; and 0 of 28 nests, 3 of 83 nests (3.6%), and 4 of 13 nests (30.8%) in California (Martin 2020).

Habitat loss and degradation do not appear to be limiting factors for the Brewer's Blackbird in Ontario or throughout its range. It has increased due to habitat modifications by humans. Fragmentation of forests by roads, railways, and utility corridors has allowed it to expand its range into formerly unsuitable or inaccessible habitats. It also benefitted from establishment of cattle feedlots and irrigation in arid areas (Martin 2020).

The Brewer's Blackbird and Common Grackle appear to be interspecifically competitive. In Ontario, the eastward expansion of the Brewer's Blackbird resulted in competitive exclusion of the grackle from long-occupied sites in rural settings dominated by grassy habitats. Grackles formerly nesting in grasslands were forced to move into marshes, but the Brewer's Blackbird was unable to encroach into suburban and urban habitats where the grackle remained dominant (Martin 2020). In the west, the Brewer's Blackbird declined in cities and towns and around farmsteads in apparent response to an increase in grackle populations. The Brewer's Blackbird appears to be dominant to the grackle in grassland habitats but subordinate near rural dwellings and human communities (Jones and Bock 2002; Martin 2020).

Human disturbance early in the breeding season may result in colonies being abandoned. In Washington, a colony was disturbed by large numbers of fishermen. This colony moved but still nested that year and used the same foraging areas (Horn 1970). Other colonies may not be able to successfully relocate if there is no nearby suitable nesting habitat or if foraging areas are too distant.

Some nests are destroyed by flooding in boggy areas and in emergent vegetation in reservoirs (Martin 2020).

In Saskatchewan, Pylypec (1991) examined the effects of fire in native fescue grassland on the Brewer's Blackbird. There were no significant differences in its abundance in burned and unburned plots. In Ontario, burning of grasslands improved conditions for foraging (Martin 2020).

The Brewer's Blackbird may be affected by climate change, particularly by increasing temperatures. Iron (1998) observed Brewer's Blackbirds near Coldwater when the temperature was 27°C. They were all panting but Red-winged Blackbirds and Common Grackles in the same area exhibited no evidence of heat stress. She surmised that the Brewer's Blackbird may not be able to tolerate heat and humidity and that these factors may have inhibited it from spreading throughout

southern Ontario. Price (2004) predicted that it could disappear as a breeding species in southern Ontario if the average summer temperature increased by 2°C.

Status

The Brewer's Blackbird experienced a significant eastward range expansion. Prior to the 1900s, its eastern distributional limit was in the Red River valley in Minnesota. Its occurrence further east was probably restricted by the broad band of forest that paralleled this valley. By 1800, the forest had already been removed from areas that it colonized later in Minnesota and Wisconsin, but range expansion was delayed until the intervening band of forest was removed around 1900. With its removal, range expansion was rapid and appeared to be accomplished by single birds or small groups pioneering to the nearest suitable habitat. Local populations became established at Fort Francis, Thunder Bay, Sault Ste. Marie, and Sudbury, presumably due to the increase in grassland habitat around these population centres. One route of expansion was north from Minnesota, which divided into northern and eastern routes. The northern route further subdivided into western and eastern routes, establishing populations in Fort Francis and Thunder Bay respectively. The eastern route resulted in colonies in the Sault Ste. Marie and Sudbury areas. The routes of expansion followed the main railways and highways linking human activity centres, with the Great Lakes and changes in vegetative cover acting as the main barriers to movement (Stepney and Power 1973). Power (1971) collected birds from Ontario and Manitoba and found no differences in skin and skeletal characteristics. Ontario birds do not represent a closed population and this supports the hypothesis that range expansion was a gradual movement into the nearest suitable habitat rather than long-distance pioneering. Once an area became densely populated, birds started to spread. Baillie (1967) concluded that it was possible that the birds that nested at Luther Marsh entered the province via southern Michigan. It started breeding 80 km west of the Detroit River as early as 1955.

The first record of the Brewer's Blackbird in Ontario was in June 1939 when a male was collected at Lake Attawapiskat, but there was no evidence of breeding. A male was seen at Thunder Bay in 1943 and the first nesting for the province was confirmed there in 1945. By 1955, it was established in 5 areas around the Lakehead and was fairly common in the Thunder Bay area by 1958. It nested near Fort Francis 1951-57 until fire altered the habitat. Nesting was confirmed at Sault Ste. Marie in 1953 and in the Sudbury area in 1962. In 1963, 13 groups as large as 8 birds were observed in a single day in 1963 along Highway 17 between Sault Ste. Marie and Sudbury. The Sudbury records represented an eastern range expansion in excess of 1,100 km. Nesting occurred at Luther Marsh in 1967, in Oshawa in 1968, and at Holland Marsh and near Coldwater in 1969 (Allin and Dean 1947; Baillie 1961, 1967; Devitt 1964; Power 1971; Stepney 1975a; Wood 1955). The first atlas indicated that the Brewer's Blackbird population declined sharply after 1975, but its distribution was still greater than in the late 1960s. In addition to the Sault Ste. Marie–Sudbury corridor, it bred in the south on Manitoulin Island and the Bruce Peninsula, at single locations on Lake St. Clair and near Point Pelee, and 2 sites south of Lake Simcoe. In the north, it continued to nest around the Lakehead and from Thunder Bay to Lake of the Woods and in the southern Boreal Forest Region north to Red Lake, east of Lake Nipigon, and Lake Abitibi. Highest densities occurred in the Sault Ste. Marie–Manitoulin Island area. It was locally common from the Manitoba border to Thunder Bay and from Sault Ste. Marie to the north shore of Lake Nipissing (Gordon in Cadman et al. 1987). James (1991) considered the Brewer's Blackbird locally uncommon Kenora to Thunder Bay, Sault Ste. Marie to North Bay, on

Manitoulin Island, and on the Bruce Peninsula; and rare north to Red Lake, Geraldton, and Timiskaming District, south to Point Pelee, and east to Prince Edward County. New colonies were found in Bruce County and Parry Sound District in 1991 and more than 100 pairs were observed in the southern half of Bruce County in 1993 (Crins and O'Donnell 1993; Peck and James 1998b).

The second atlas revealed that the breeding range of the Brewer's Blackbird had shrunk and become more discontinuous since the first atlas. It was not documented between the city of Thunder Bay and Rainy River District, in most areas of the southern Boreal Forest Region, and around the Lakehead. It was not found in many of the areas near Sudbury and on Manitoulin Island where it previously occurred and was absent in the extreme southwest. Its probability of observation decreased province-wide and in all regions where it occurred, but only the decline in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region was significant. This was primarily due to a decrease in its occurrence between Sault Ste. Marie and Sudbury. There was an increase in detections on the Bruce Peninsula and in scattered areas east of Georgian Bay (Dunn and Gordon in Cadman et al. 2007).

The Brewer's Blackbird has experienced a rangewide decline in population, with a decrease of 35% since the Breeding Bird Survey (BBS) began in 1966 (McCracken 2003b). The rate of decline has levelled off in the United States. During 1966-98, it declined overall 4.0% per year, including declines of 0.7% per year in Canada and 5.3% per year in the United States. During 1980-98, the overall rate of decline was 1.9% per year, including declines of 1.0% per year in Canada and 2.1% per year in the United States (Martin 2020). BBS data indicate that it decreased at annual rates of 2.41% in Canada and 1.51% in Ontario 1970-2021. For 2011-21, it experienced annual decreases of 2.3% in Canada and 3.93% in Ontario. All results were highly reliable except that Ontario short-term trend was of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

When young leave the nest, they can fly distances of 0.9-2.1 m, and crouch low in the vegetation. In Ontario, fledglings have been observed on a wet hummock of small black spruce, leatherleaf, bog laurel, and sphagnum. In the Northwest Territories, they were seen among willow shrubs in a cleared area adjacent to a gravel airstrip (Crins and O'Donnell 1993; Martin 2020; Stepney 1979; Williams 1979).

Both sexes feed the fledglings and may continue to do so for as long as 26 days after they leave the nest. Fledglings join their parents in family groups. One to 2 weeks after fledging, several family groups coalesce into a flock that remains in the vicinity of the breeding area as the young develop independence at age 34-39 days. The fledglings are adept at flying by the time they are 23 days old. At this time, the flock of multiple families becomes more mobile and may either move a moderate distance from the breeding area or completely leave. Larger flocks form in August and congregate in good foraging sites, which are predominantly agricultural areas. Foraging flocks may mix with other blackbird species, including grackles, cowbirds, and Red-winged, Yellow-headed, and Rusty blackbirds (Campbell et al. 2001; Martin 2020; Williams 1952).

The Brewer's Blackbird begins to roost communally during the postfledging period. It roosts both solely with other Brewer's Blackbirds and with the other blackbirds that it forages with. In multispecies roosts, it tends to segregate from the other species and roost at margins of the roost.

Roosts may be in a variety of habitats including urban and suburban areas, marshes, woodlands, savannahs, broom-sedge fields, and on the ground in grain stubble. They are often along edges of open habitat such as on ridges, field edges, along edges of water, or along railway tracks or dykes. Most roosts are in dense upland cover including coniferous hedges, large coniferous trees, and riparian thickets. In wetlands, it roosts in cattails, bulrushes, or willows. One roost was on floating duck blinds. Large flocks assemble late in the day and then move en masse to the roost. Prior to roosting or after leaving the roost, birds often assemble on roadside utility wires (Campbell et al. 2001; Martin 2020; Williams in Bent 1958).

During the postfledging period, the Brewer's Blackbird eats grain and insects in open habitats such as lawns, pastures, feedlots, grain stubble, fallow land, burned fields, freshly plowed or disked fields, beaches, and mudflats (Martin 2020).

MIGRATION

The Brewer's Blackbird is a partial medium-distance migrant. It is a year-round resident in California, coastal Oregon, and southern British Columbia. Populations east of there are migratory. It migrates during the day in conspecific and mixed-species flocks containing cowbirds, grackles, European Starlings, and Red-winged, Yellow-headed, and Rusty blackbirds. When it travels with other species, the Brewer's Blackbird tends to move independently or at the edge of a larger flock, maintaining some segregation. Flocks in the northern part of the winter range are composed mostly of males, indicating that females migrate further south (Martin 2020). A bird banded east of Sault Ste. Marie in June was recovered in winter in Mississippi, a distance of 1,490 km (Brewer et al. 2018).

The winter range of the Brewer's Blackbird has expanded, probably due to the eastward expansion of its breeding range. In 1900, it occurred only sporadically east of the Mississippi River, but it is now established as a regular winter resident in the Gulf Coast states. Banding results suggest a general tendency for birds occupying the eastern portion of the breeding range to winter more to the southeast (Stepney 1975b).

Spring migration is rapid and birds arrive at the breeding grounds on predictable dates. Males tend to arrive several days in advance of females (Martin 2020). In southern Ontario, spring migrants have been observed from mid-March to late May, but mostly from mid-April to mid-May (Black and Roy 2010; Curry 2006; Lancaster et al. 2004; Weir 2008).

Autumn migration is much more protracted. Birds may start wintering in the more northern portion of their range and gradually withdraw southward as winter progresses and conditions deteriorate. The timing of the onset of winter greatly affects the location of the population. In the south, numbers may peak after Christmas Bird Counts (CBC) have been completed (Stepney 1975b). It is probable that some of Ontario's winter records are of late autumn migrants. A flock of 12 was seen at Longlac on 1 September (Devitt 1964). In southern Ontario, most migrants arrive around mid-October, but birds may be present from late August until January (Black and Roy 2010; Curry 2006; Lancaster et al. 2004; Weir 2008).

During autumn migration, habitat of the Brewer's Blackbird is similar to that used during the postfledging period. At this time, it forages with other blackbirds and has a predominantly vegetarian diet consisting of waste grain, weed and grass seeds, and stockyard spillage and waste

(Martin 2020). Habitats described for migrants in British Columbia are typical: pastures, plowed and stubble fields, berry patches, nurseries, barnyards, sewage lagoons, feedlots, garbage dumps, vacant lots, grassy roadsides, dykes, golf courses, railway lines, campgrounds, lawns, backyards with feeders, marshes, beaches, mudflats, lake shorelines, sedge meadows, riparian thickets, and bottomland forests (Campbell et al. 2001).

Communal roosts continue to be an important habitat component during autumn migration, and these are in similar areas as those used during the postfledging period. No migratory roosts have been reported in Ontario.

James (1991) considered the Brewer's Blackbird a rare to locally uncommon migrant. In Elgin County, it had not been observed by 1891; by 1954, there was a single record. By 2000, it was a very rare spring and autumn migrant with a total of 9 records (Lancaster et al. 2004). There are only 6 records of migrants for Niagara Region (Black and Roy 2010). Curry (2006) considered it a vagrant in the Hamilton area with a total of 20 records; it was first observed in 1958. The first record for Kingston was in 1972, where it is a very rare irregular migrant (Weir 2008). For Algonquin Park, there is 1 record for both spring and autumn (Tozer 2012).

WINTER

The winter distribution of the Brewer's Blackbird and its abundance appear to be dictated by snow cover. Most birds winter in areas that receive less than 2.5 cm of snow or that have 10 or fewer days of snow cover. It occurs in lower numbers in areas that receive as much as 63.5 cm of snow and snow cover persisting as long as 40 days (Stepney 1975b). Due in part to the effects of snow cover and snowfall, it has low fidelity to wintering sites. Birds commonly vacate areas used in previous years and move to more favourable locations as they become available (Martin 2020).

In winter, the Brewer's Blackbird uses habitat similar to the postfledging and autumn migration periods, with increased use of feedlots, fields of waste grain and stubble, and bird feeders. Communal roosts continue to be important habitat, with the Brewer's Blackbird representing about 2% of the blackbirds and starlings that roost in the United States in winter (Martin 2020). In California, abundance of the Brewer's Blackbird was positively correlated with grasses and feeders (Kalinowski and Johnson 2010).

In winter, the Brewer's Blackbird forages in flocks that may contain other blackbird species. There is a negative relationship between temperature and the amount of time spent foraging. In British Columbia, it spent 16 and 25% of its time foraging on 2 days when the temperature was +7.8°C, but 53% of its time at –0.6°C, 54% of its time at –1.1°C , and 56% of its time at –2.2°C. Food was unlimited, so temperature was the only variable that affected the amount of time spent foraging (Verbeek 1964). The winter diet is predominantly vegetarian. Although it frequently congregates and forages with the Red-winged Blackbird, there is little overlap in their diets (Martin 2020). The Brewer's Blackbird is a sporadic visitor to feeders and is most likely to visit them during spring migration. Nonetheless, a high proportion of late autumn and winter sightings in Ontario are at feeders. Favourite feeder foods include mixed seeds and cracked corn. Infrequent choices include water, striped and black oil sunflowers, and hulled peanuts (Dunn and Tessaglia-Hymes 1999).

The Brewer's Blackbird plays little role in crop depredation. Because it occurs in mixed winter flocks and roosts, it is subject to the blackbird control programs that are implemented in the southern United States. No information is available on how many Brewer's Blackbirds are killed by these programs (Martin 2020).

James (1991) considered the Brewer's Blackbird occasional and rare in winter in the south, north to Manitoulin Island, and also in the north at Thunder Bay, Schreiber, and Matachewan. It is uncertain how many birds persist throughout the winter, with many occurring early in the winter only. In Elgin County, there are 3 records at feeders spanning the period December through February (Lancaster et al. 2004). CBC data indicate that it decreased in Ontario at annual rates of 3.75% 1970-2021 and 4.53% 2009-21 (National Audubon Society 2022).

Common Grackle

Quiscalus quiscala

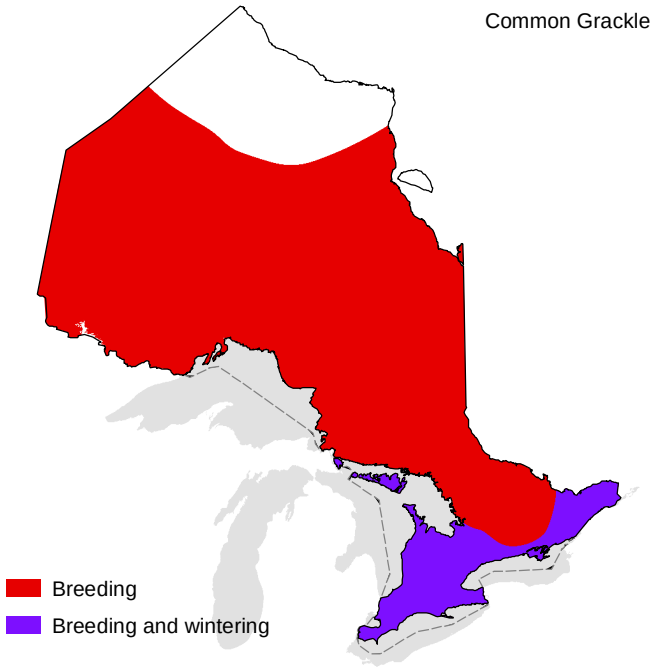
BREEDING SEASON

Habitat Requirements

Ontario Common Grackle nests were in woodlands (29.0% of nests); in urban and rural residential and recreational areas, including gardens, parks, farmyards, and golf courses (27.7%); wetlands, including marshes, beaver ponds, swamps, and bogs (25.4%); lake and river shorelines, islands, ditches, and dykes (9.7%); farmland, including pastures and abandoned fields (6.2%); sand dunes (1.2%); and rock cliffs (0.8%). Coniferous and mixed forests were selected slightly more often than deciduous stands. No noticeable preference was apparent for wet or dry areas. Nest-site availability was probably more important than the moisture regime (Peck and James 1987).

In the Boreal Forest Region, the Common Grackle was scarce near the town of Pickle Lake. It also nested on abandoned mine derricks (James 1980). Erskine (1977) reported that it preferred wetter

areas such as bogs and fens dominated by sedges and low shrubs such as sweet gale and willow. It also nested in farmland and old fields and the inner suburbs of Ottawa.



In the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region in Muskoka and Parry Sound districts, the Common Grackle shunned contiguous forests and bred in rural and residential areas, on small islands, in broken forests, and in bogs and beaver ponds (Mills 1981). In Algonquin Park, it nested along creeks and lakeshores, and in marshes, bogs, swamps, beaver ponds, forest clearings and open areas, and around human structures (MacLulich 1938; Tozer 2012). Martin (1960) reported it in both wet and dry bogs in Algonquin Park where it occurred predominantly from the top of the shrub layer to the tops of dead stubs. It occurred in low density in white birch–poplar–balsam fir–spruce stands.

In the Great Lakes–St. Lawrence Forest Region south of the Shield, Speirs and Orenstein (1975) reported the grackle in a young open forest with standing water, a black spruce bog surrounded by a red maple–poplar swamp, an open-canopy forest, a mature white cedar–elm swamp, a mature sugar maple–oak forest sloping down to a river floodplain, a mature beech–sugar maple forest, a sugar maple forest sloping down to an open white cedar–balsam fir–spruce swamp, and an old beech woodlot with a pond and creek. In Toronto, it nested in residential areas including recent subdivisions with no vegetation, areas with trees taller than 9 m lining the streets, and areas where most vegetation was lower than 9 m and formed an open canopy. Subdivisions had either 1-storey or 2-storey homes in differing densities (Savard and Falls 1981). At Luther Marsh, it originally nested in dead stubs over water, in cavities in flooded timber, in willow shrubs, and rarely in Wood Duck nests (Boyer and Devitt 1961). Once the coniferous plantations around the marsh matured, they became the preferred nesting habitat, although the other habitats were still used sparingly (Sandilands 1984).

In the Carolinian Forest Region, McIlwraith (1894) concluded that the grackle preferred to nest near water. It was very common at that time, breeding close to the banks of the Grand River in Cambridge. He also reported a colony nesting in a Norway spruce at a Hamilton residence.

In Great Lakes coastal wetlands, the Common Grackle was positively correlated with wetland cover and the amount of urban and agricultural land in the watershed. It was not affected by water levels (Tozer et al. 2024).

South of the Shield in southern Ontario, abundance of the grackle was negatively correlated with the amount of forest cover more than 100 m from edge, woodlot size, and the amount of

regional forest cover. It was positively correlated with the amount of forest cover within 2 km. All relationships were nonsignificant (Austen et al. 2001). There was no significant difference in its abundance on organic and conventional farms. It was positively correlated with farmsteads, hayfields, pastures, woods, row crops, and spring grain. It was negatively correlated with the biomass of crops and herbicides (Kirk et al. 2011).

The Common Grackle nests in a variety of habitats. These include urban parks, ornamental trees and shrubs near buildings, red cedar groves and savannahs, dense stands of conifers including plantations, buttonbush and willow thicket swamps, riparian forests along watercourses and lakeshores, roadside trees and shrubs, cattail and common reed marshes, botanical gardens and university campuses, shelterbelts, white cedar groves and plantings, Christmas tree plantations, field borders and hedgerows, open woodlands and forest edges, treed and shrub swamps, pine and oak barrens, brush prairies, oak savannahs, sewage lagoons, shrub carrs, alder thickets, flooded woods, old fields and meadows with some tree or shrub cover, bogs and fens, drainage ditches, orchards, cemeteries, pastures, hayfields, young strip-cuts and clear-cuts, along railway and utility corridors, and in or on buildings and bridges. It most commonly nests near water, agricultural fields, and buildings. In Illinois, it preferred edge shrubs, hedgerows, marshes, and agricultural areas but was found in all habitat types that were surveyed (Bent 1958; Campbell et al. 2001; Conover et al. 2009; Erskine 1977; Falardeau et al. 1999; Graber and Graber 1963; Gross in Bent 1958; Hoffman 1989b; Homan et al. 1996; Howe 1976, 1978; Karr 1968; Lenington and Scola 1982; Maddox and Weatherhead 2012; Maxwell 1970; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991; Peer and Bollinger 2020; Petersen and Young 1950; Snelling 1968; Suthers 1988; Wiens 1965; Yahner 1982).

Several studies described the habitat of the Common Grackle at the landscape level. Peer and Bollinger (2020) reported that it avoided extensive mature woodlands. Taylor and Taylor (1979) concluded that it was restricted to large and small woodland openings and edges. In North Dakota, it nested in areas with 2-22% forest cover. In the mid-Atlantic states, it was significantly negatively correlated with the amount of forest cover within 2 km (Robbins et al. 1989). Its distribution in the Maritime Provinces corresponded well with the distribution of agriculture. It was less abundant in the main agricultural areas of Nova Scotia where the fields were larger, there were fewer hedgerows, and there were fewer abandoned buildings for nesting (Erskine 1971). The Quebec atlases determined that it was most abundant in urban and agricultural landscapes, particularly in the St. Lawrence Lowland. It was associated with areas populated by humans. It was much less abundant in the Boreal Forest Region where it was associated with swamps, beaver ponds, edges of other water bodies, clearings, roads, clear-cuts, resorts, and other human structures (Alvo in Gauthier and Aubry 1996; Denault in Robert et al. 2019). In Ontario, the grackle is most abundant south of the Canadian Shield where the landscape is dominated by agricultural and developed landscapes (Zimmerling in Cadman et al. 2007).

Several studies examined microhabitat preferences of the grackle. In Mississippi, it was equally abundant in fields with no vegetated borders and those with borders 10 m and 30 m or more wide (Conover et al. 2009). In Illinois on reclaimed strip mines, it was common in early shrub habitat where the oldest trees were 10 years old and absent in late shrub habitat where the trees were 37 years

old (Karr 1968). In New Jersey successional fields, it occurred in those that were 10, 20, and 40 years old. It was most abundant in the 20-year-old field which had the greatest diversity of shrubs, saplings, and herbaceous vegetation (Suthers 1988). In South Dakota green ash woodlots, it was 6.5 times more abundant in early than late forest seral stages. Younger stands had less chokecherry coverage in the understorey, more patchy distribution of woody vegetation from less than 1 to 2 m tall, and a more open and patchy canopy (Rumble and Gobeille 1998). In British Columbia, most nests were in wetlands near pastures or farmland (Campbell et al. 2001). In the Prairie Pothole Region of Iowa, its abundance was positively correlated with the percentage of a wetland that was marsh or wet meadow vegetation (Fairbairn and Dinsmore 2001a, 2001b). In Wisconsin, Wiens (1965) compared the nest sites of the Common Grackle and Red-winged Blackbird in a cattail marsh. Nests of both species were usually on edges of cattail clumps bordering on open water. Grackle nests were in denser cattail clumps and slightly lower than Red-winged Blackbird nests. Grackle nests were somewhat hidden and usually shaded. Red-winged Blackbird nests were usually exposed and well lighted. Homan et al. (1996) and Yahner (1982) studied usage of shelterbelts by the Common Grackle in North Dakota and Minnesota. More than 50% of birds nesting in multi-row shelterbelts in these 2 states were grackles. It used single-row windbreaks, but only in proportion to their availability. It highly selected shelterbelts. In North Dakota, shelterbelts of inhabited farmsteads were used more frequently than expected; pothole wetlands, woods, ravines, railway corridors, and lakesides were used less than expected; and abandoned farmstead shelterbelts, pastures, towns, and windbreaks were used in proportion to their availability. Nest sites 100 m or less from a farmstead were used more than expected. Those further away from a farmstead were used less than expected. Colonies were significantly larger in inhabited than abandoned farmsteads. Stands 0-300 m from a residence were used significantly more than those further away. Nest sites 301-500 m from water were used more frequently than expected; those further away were used less than expected. Shelterbelts containing Siberian elm, green ash, Manitoba maple, caragana, hawthorn, blue spruce, lilac, and white elm were more likely to be colonized than those consisting of willow, cottonwood, and trembling aspen. Within colonies, tree species were not used according to their availability. Blue spruce, Siberian elm, and black poplar were used more than expected. Green ash, willow, white elm, trembling aspen, Russian olive, and cottonwood were used less than expected. The preferred trees are profusely branched which aids in nest attachment and concealment and possibly a warmer microclimate. The avoided species had a scarcity of secure nest attachment sites. The grackle also displayed a preference for taller vegetation. Higher nests may be safer from predators and tall vegetation offers good perch sites. In Minnesota, the preferred conifers for nesting were blue spruce and white spruce with white cedar, red pine, and Douglas-fir seldom used. The preferred deciduous species were eastern cottonwood, silver maple, and Manitoba maple. In order of preference, it selected Manitoba maple, blue spruce, white spruce, cottonwood, silver maple, and ponderosa pine. Species that it avoided included green ash, tartarian honeysuckle, white cedar, jack pine, caragana, Amur maple, Norway spruce, white elm, willow, buffalo-berry, flowering crabapple, common lilac, red elderberry, highbush cranberry, river birch, honey locust, and chokecherry. The grackle used 16 of 25 available plant species for nesting and was a generalist. Shelterbelts may provide important habitat where trees are otherwise scarce. In Minnesota, grackle nests represented 54.3% of all nests within shelterbelts. The Mourning Dove, Gray Catbird, American Robin, and Chipping Sparrow were also common. Nests of these 5 species comprised 95.5% of all nests. Yahner (1982) compared the

nest sites of these species. Mean height of grackle nests was 6.27 m, significantly higher than the other species; tree canopy diameter was 2.43 m, significantly lower; height of ground cover was 0.30 m, significantly less; 39.3% closure by vegetation within 1 m of the nest, significantly lower; height of nest tree or shrub 10.07 m, significantly higher; and 0.08 cm diameter of the largest woody stem touching the nest, significantly larger. Grackle nests were 0.23 m from the trunk, significantly less than for the Mourning Dove and Chipping Sparrow; had 44.8% herbaceous vegetation within 1 m, significantly less than for the catbird, robin, and Chipping Sparrow; had 0.36 woody stems less than 2.5 cm within 1 m, significantly less than for the catbird and Chipping Sparrow; and had 0.14 woody stems larger than 2.5 cm within 1 m, significantly lower than for the catbird. Grackle nests were typically high above the ground and exposed, catbird and Chipping Sparrow nests were close to the ground and concealed by herbaceous vegetation, and Mourning Dove and robin nests were intermediate in height and percent herbaceous cover. The shelterbelts were sufficiently heterogeneous to allow these 5 common bird species to select distinct nest sites, resulting in high densities of nests.

In forested habitat, the Common Grackle is an edge species but may penetrate further into the forest if there are gaps in the canopy or flooded areas. In North Dakota shelterbelts, nests were placed randomly with respect to distance from edge (Homan et al. 1996) and the same was true in Wisconsin white cedar stands (Petersen and Young 1950). In Maryland and Delaware riparian forests, there were no significant differences in its probability of detection in forests 50-800 m wide (Keller et al. 1993).

The Common Grackle is not an area-sensitive species, frequently nesting in isolated trees. In Iowa marshes, Brown and Dinsmore (1986) observed it in 67% of wetlands smaller than 1 ha and in 92% of those larger than 20 ha. They considered it area independent. In red maple swamps in Rhode Island, it was more abundant in stands smaller than 1 ha than those 1-5, 6-10, or 11-20 ha (Golet et al. 2001).

Communal roosts are used by the Common Grackle most of the year except during the early stages of the breeding season. It leaves the large multispecies roosts prior to settling on the breeding site. Even during the breeding season, small numbers of grackles may roost together. From late March through May in New Jersey, most birds roosted solitarily but some roosted in scattered groups of less than 12 birds. In mid- to late April, 8-10 roosted in a clump of switch cane in a backyard. Another roost in a backyard white pine supported 2 grackles, 2 robins, 3 starlings, and 2 cowbirds. The grackle appeared at roost sites earlier in the year than the other species (Stewart 1975a). Larger postfledging roosts start to form in early June in New Jersey (Caccamise and Fischl 1985). Roosts may not become well established in southern Ontario and Quebec until mid-July (Alvo in Gauthier and Aubry 1996).

One Ontario nest (0.2% of nests) was on the ground at the base of a stump in a bog and the remainder were elevated. Most (53.5%) were in trees, shrubs, and vines; 21.4% were in or on human-made structures including houses and other buildings, bridges, towers, dams, bird houses, posts, trellises, duck blinds, boards, and a bucket; 13.9% were in cattails, sedges, bulrushes, or grasses; 8.3% were on stumps and logs; 2.2% were in upturned and exposed roots; and 0.5% were in crevices and on ledges of cliffs. Nest trees and shrubs were usually living but sometimes dead. Coniferous species

(7 species, 60.4% of nests) were preferred to deciduous species (23 species, 39.6% of nests). Tree and shrub species most frequently selected included cedars (117 nests), spruces (104 nests), pines (68 nests), willows (65 nests), junipers (36 nests), and hawthorns (33 nests). Many nests in trees and shrubs were in crotches. Fewer were on horizontal branches and some were supported between 2 or 3 adjacent trunks. Most were centrally located at or near the trunk. Others were 0.3-6 m from the trunk, mostly 1.2-3.7 m. Forty-nine tree nests were in old woodpecker and natural cavities. New nests were usually built each year, but old nests were occasionally repaired and reused, one for 4 consecutive years. Three nests were on top of old grackle nests, and old American Robin nests were used on 3 occasions. Two nests were in the base of an Osprey nest and one was in the base of a Great Blue Heron nest. Elevated nests were 0.2-18 m from the ground, with most 1.2-4 m up (Peck and James 1987). Axtell (1955) reported a grackle nest on an occupied beaver lodge in Algonquin Park, among the sticks slightly below the top of the more steeply sloping side. The pond was a flooded black spruce–leatherleaf bog that supported several pairs of grackles. Most had their nests within a few cm of the water and the bottom of one nest was in water. Another nest was 2.1 m up in a hollow stub standing in the water. Nests have been found in Muskoka and Parry Sound districts on buildings and bridges and in bird houses at heights of 0.3-14.3 m (Mills 1981). In residential areas in Toronto, all grackle nests were in conifers although deciduous species were common. They were at heights of 3.66-12.19 m above ground (average 6.55 m). It nested much higher in urban areas than nonurban areas. At 1 site where more than 45% of trees were taller than 9 m, average nest height was significantly higher (8.53 m) than at other sites (6.20 m). Nest height was independent of house density. It appeared to select the most suitable cover available, nesting over a wide range of heights. The exclusive use of conifers probably occurred because deciduous species had not leafed out when nest-site selection occurred. It nested at greater heights in urban areas because suitable low vegetation was less abundant in this habitat (Savard and Falls 1981). Peck and James (1998b) reported 2 nests in a marsh that contained buried Red-winged Blackbird eggs, suggesting that grackles had built their nests on occupied Red-winged Blackbird nests.

Almost all Common Grackle nests reported elsewhere were elevated in trees, shrubs, vines, and aquatic emergent vegetation, or were on or in human-made structures. It is a generalist, nesting in a wide variety of species. Maxwell et al. (1976) summarized 2,601 nests reported to the Cornell Lab of Ornithology. Conifers were highly preferred as a nesting substrate, supporting 62.5% of nests, probably because these provide better cover early in the spring. The remaining nest substrates included 27.4% deciduous trees, 7.8% shrubs, and 6.3% other locations. Red cedar was selected most frequently of the coniferous species, followed by Scotch pine, yew, red pine, juniper, blue spruce, white pine, white cedar, and Norway spruce. Osage orange was the preferred deciduous tree, followed by willow, crabapple, apple, mulberry, oak, and poplar. Honeysuckle was the most frequently used shrub, followed by buttonbush, lilac, bayberry, and dogwood. Other locations included bridges, cattails, nest boxes, buildings, towers, tree cavities, snags, stumps, vines, on a channel marker, under a pail, on a power pole, on a cliff, on a farm implement, and on a railroad bed. In Cape Breton Island, 55.6% of nests were in trees and shrubs less than 4.6 m tall (28.2% in alder, 11.1% in hawthorn, 7.7% in willow, and 8.5% in other), 6.0% were in trees or tree stubs, 11.1% were in abandoned buildings (mostly barns), and 27.4% were on road or railway bridges. Results were biased because fieldwork was conducted only along rivers (Erskine 1971). Other species and

locations where nests have been reported include Siberian elm, Manitoba maple, white elm, cottonwood, sycamore, gooseberry, on top of an active House Sparrow nest, in a roll of fence wire in a marsh, in flooded dead timber or shrubs, in active Osprey nests, in vines on the sides of buildings, and on barn beams with Barn Swallows (Alvo in Gauthier and Aubry 1996; Bent 1958; Campbell et al. 2001; Gross in Bent 1958; Gutzwiller and Anderson 1986b; Hamilton 1951; Homan et al. 1996; Peer and Bollinger 2020; Petersen and Young 1950; Rand and Rand 1952; Yahner 1982). Nests in trees and shrubs may be suspended between 2 or more upright trunks, on lateral branches, in deep crotches, or less frequently, in natural and Pileated Woodpecker cavities. In red cedars in Ohio, most nests were at ends of branches in dense foliage or in a main fork of a horizontal branch. Nests have been reported 0-22 m from the ground or water. Nest height is determined by the available substrate, with the grackle being adaptable enough to adjust its nest height to the vegetation height. In New York, mean nest height was 2.3 m in conifers, 3.3 m in deciduous trees, and 1.8 m in shrubs. Nests were 1.5-8 m (average 3.3 m) from the ground in planted spruce in Michigan and at heights of 1-2 m in a buttonbush swamp. Average nest height was 50.8 cm (range 22.9-68.6 cm) in a Wisconsin cattail marsh. Most British Columbia nests were 0.5-1.2 m up (range 0-16 m). Nests in red cedar averaged 6.1 m from the ground (range 2.1-10.7 m; Bent 1958; Campbell et al. 2001; Gross in Bent 1958; Howe 1976, 1978, 1979; Maxwell 1970; Maxwell et al. 1976; Petersen and Young 1950; Wiens 1965).

The grackle defends only a small area around the nest and may nest singly or in loose colonies. In Ontario, the average size of 310 colonies was 8 nests with most nests at least 4.6 m apart. An exception was a larger leafy structure that resembled a squirrel drey that was used by 2 nesting grackles simultaneously (Peck and James 1987, 1998b). A colony in a coniferous plantation at Luther Marsh supported 40-50 nests (Sandilands 1984). In Michigan, nests were either more than 15 m apart or clumped 1-3 m apart. In North Dakota, 202 colonies contained an average of 18 nests. British Columbia colonies contained 2-13 nests. As many as 10 grackle nests have been reported in a single Osprey nest; 12 nests were in a large Manitoba maple, some within 60 cm of each other; and 28 pairs nested in a Norway spruce (Bent 1958; Campbell et al. 2001; Gross in Bent 1958; Homan et al. 1996; Howe 1978, 1979). As soon as the nest site is selected, the pair defends it against other pairs. Defence is initially intermittent because birds do not remain close to the nest site until nest building begins. Strongest territorialism occurs by the male during nest construction. Later in the nesting season, grackles may visit other nests without encountering aggression even when the other adults are present. There is little to no agonistic behaviour away from the nest site. The entire colony mobs potential predators. Males defend their females from other males and females, even away from the colony. The male keeps in close contact with the female by perching near her, following her, and engaging in mutual displays (R.W. Ficken 1963; Howe 1976, 1979; Lenington and Scola 1982; Maxwell 1970; Wiens 1965). Wiens (1965) studied territorial interactions of Common Grackles and Red-winged Blackbirds nesting together in a Wisconsin cattail marsh. Interactions between the species occurred most frequently during the early part of courtship prior to initiation of nesting. Most were initiated by the Red-winged Blackbird in connection with grackle courtship flights or efforts to feed fledglings in blackbird territories. Seven to 10 days after the beginning of grackle courtship, flights were distinctly oriented to the edges of blackbird territories or areas of poorly defined territories with no penetrations more than 3 m into blackbird territories. Grackles in these

areas were largely ignored or avoided by blackbirds. Blackbirds did not respond to grackle fledglings within their territories, but adults arriving to feed them were displayed to or chased. Courtship, pair formation, and nesting success of the grackle was unaffected by Red-winged Blackbirds although blackbirds may affect the distribution of grackle nests. Grackles were rarely aggressive to blackbirds but dove at them if they approached within 0.6-0.9 m of the nest; blackbirds 1.2 m from the nest were tolerated. Snelling (1968) studied the same wetland and did not observe any spatial segregation of blackbirds and grackles. Home range sizes have not been defined for the Common Grackle, but they may be quite large. It may forage 0.5-1.6 km or further from the nest (Alvo in Gauthier and Aubry 1996; Howe 1979). Birds may also fly considerable distances to their nocturnal roosts.

All information on natal philopatry is from general banding data rather than site-specific return rates. Fankhauser (1971a) reported that 311 of 389 birds (82.1%) banded as young were recovered in the same 10-minute block. Moore and Dolbeer (1989) reported that 76.3% of 955 young were recovered within 20 km of the banding location, with the longest dispersals 2,621-2,640 km from the banding location. Peer and Bollinger (2020) reported that the mean dispersal distance from the natal area was 17.1 km for males and 29.8 km for females. A young banded in Ontario was recovered during the breeding season 6 years later in Nebraska, a distance of 2,084 km (Brewer et al. 2018).

Adult site fidelity appears to be high, with birds probably returning to the same area to breed each year. Ninety-two percent of adults were recovered in the same 10-minute block in which they were banded: 91.1% of males and 94.0% of females (Fankhauser 1971a, 1971b). Moore and Dolbeer (1989) reported that 87.1% of males and 89.3% of females were recovered within 20 km of the banding location. The longest records for dispersal were 2,281-2,308 km for males and 1,221-1,240 km for females. The average dispersal distance for adults was 111.4 km per generation.

Limiting Factors

Eggs have been reported in Ontario nests from the beginning of April until mid-July, with most present in the last 3 weeks of May (Peck and James 1987). In Algonquin Park, nests are under construction from late April to early June, eggs are present from early May to early July, nestlings are present from early June to mid-July, and dependent fledglings have been observed from mid-June to late July (Tozer 2012).

Courtship begins as soon as females arrive. Once pairs are formed, nest-site selection occurs. Of 11 nests that were completed in Ohio, only 4 (36.4%) were used. The time required to build a nest ranges from 4 days to 1.5 months. Nests that take extended periods to build are usually started early in spring and worked at only sporadically. In Wisconsin, it took an average of 11 days to complete a nest in 1 year and 14 days the second year. Egg laying may start the day after the nest is complete but as many as 11 days may elapse before egg laying occurs (average 3 days). In the Maritime Provinces, the initiation of egg laying was 5-7 days after the daily mean temperature reached 6°C. Eggs are laid at the rate of 1 a day, although a day is occasionally skipped. Incubation tends to begin with the laying of the last egg in 3- and 4-egg clutches, and with the fourth egg in 5- and 6-egg clutches. Incubation periods of 11-14 days have been reported in Ontario, mostly 12-13 days. Elsewhere, incubation periods of 11-15 days have been reported (mean 13.5 days). The first 3 eggs usually hatch in close succession within 24 hours, the fourth egg often hatches a day after the first

one, and the fifth egg usually hatches 1-2 days after the first egg. The nestling period is 10-18 days but mostly 12-15 days. Those that leave the nest before age 12 days were probably disturbed and have low survival probability (Erskine 1971; R.W. Ficken 1963; Gross in Bent 1958; Howe 1976, 1978, 1979; Maddox and Weatherhead 2012; Maxwell 1970; Maxwell and Putnam 1972; Maxwell et al. 1976; Peck and James 1987; Peer and Bollinger 2020; Petersen and Young 1950; Wiens 1965).

Although the Common Grackle may raise 2 broods in Illinois, it is single brooded in most areas, including Ontario, Quebec, Michigan, and Wisconsin. Renesting is common if the first nest fails (Alvo in Gauthier and Aubry 1996; Gross in Bent 1958; Howe 1976, 1978; Peck and James 1987; Peer and Bollinger 2020; Wiens 1965). Clutches of 2-6 eggs have been reported in Ontario, with single clutches of 7 and 9 eggs. The 9-egg clutch was probably from more than 1 female. A tenth egg was laying on the ground. Average clutch size was 4.2 eggs; 4-egg clutches were most frequent, followed closely by 5-egg clutches (Peck and James 1987). Overall, clutch sizes of 2-7 eggs have been reported, with clutches of 4 and 5 eggs most frequent. Mean clutch sizes include 5.00 and 4.70 in Nova Scotia, 4.76 and 4.49 in Prince Edward Island, 4.44 and 4.33 in New Brunswick, 4.33 and 5.00 in Saskatchewan, 4.3 and 4.7 in Ohio, 4.9 and 4.26 in Illinois, 4.5 and 4.8 in Michigan, and 4.4 and 4.9 in Wisconsin. Clutch size tends to decrease as the season progresses, but not in every year or location (Bent 1958; Erskine 1977; Gross in Bent 1958; Horsley and Ward 2021; Howe 1976, 1978; Maxwell 1970; Petersen and Young 1950; Wiens 1965). Brood reduction often occurs. Young from the fourth to sixth eggs are frequently one half to two thirds the weight of the first 3 nestlings, due in part to hatching asynchrony. This is despite the fact that later-laid eggs are larger, thereby providing more nutrients and water. The fifth egg in 5-egg clutches is female biased and the sixth egg in 6-egg clutches is male biased. Male nestlings are heavier than female nestlings and require more nutrients for successful fledging. Brood reduction results in differential starvation of males that hatch 1-2 days later than siblings, resulting in a female-biased sex ratio at fledging. Of 20 young that died in Michigan nests, 60% were from the last egg and an additional 15% were from the penultimate egg. No adults that started with a clutch of 6 fledged more than 5 young and broods of 4 and 5 typically lost 1 young before fledging. In 63 nests, 65 of 292 young (22.3%) starved: 0 of 15 from broods of 3, 19 of 88 (21.6%) from broods of 4, 34 of 165 (20.6%) from broods of 5, and 6 of 18 (33.3%) from broods of 6. Only 30% of adults with broods of 5 fledged all young. The grackle has 2 adaptations to rear as many young as possible: increased egg size with the laying sequence and hatching asynchrony. This allows it to maintain the brood for as long as possible, but to allow later-hatching and smaller young to starve if food supplies are inadequate. These young often die by the time they are 4 days old, ensuring an adequate food supply for the remainder of the brood (Howe 1976, 1978; Maddox and Weatherhead 2012).

The age at first breeding has not been determined (Peer and Bollinger 2020), but is probably 1 year. The male is predominantly monogamous, but polygyny occurs. About 50% of males abandon the female while she is incubating and some interact with other females. In Michigan, 2 of 12 males (16.7%) were polygynous in 1 year and one may have had 3 subsequent mates. In the second year, 0 of 15 males were polygynous for a 2-year total of 2 of 27 males (7.4%) being polygynous (Howe 1976, 1978, 1979; Peer and Bollinger 2020). Intraspecific egg dumping is a rare breeding strategy (Bent 1958; Peck and James 1987; Peer and Bollinger 2020). This strategy is unlikely to be successful

because not all eggs would be adequately incubated in extra-large clutches and many young would be lost due to starvation.

The Common Grackle is an omnivore that eats a wide variety of vegetable matter, invertebrates, and vertebrates. It is quite adaptable in its foraging behaviour. It mostly forages on the ground while walking, but also in shrubs and trees. Occasionally, it flies 30 cm up from the ground to capture a flying insect. It uses its bill rather than its feet to uncover food on the ground. The main foraging habitats include woodlot edges, agricultural fields, and urban open spaces and residential areas. Those breeding in marshes mostly forage in adjacent upland habitats, especially woodlots, but capture some dragonflies and damselflies within marshes. In the Boreal Forest Region, it forages mostly in marshes and bogs and this adaptability has allowed it to breed within this area. Its lower density in the boreal forest suggests poorer feeding opportunities than in open arable lands (Bent 1958; Erskine 1971; Howe 1976; Peer and Bollinger 2020; Wiens 1965). In urban areas, it is often a scavenger, picking up crumbs and waste from human foods from the ground, patrolling areas of high human pedestrian concentrations. It also flies into dumpsters to obtain waste food. When bread or crackers are dry and stale, it often soaks them in water to soften them prior to eating them. This appears to be a learned habit, with some birds doing it regularly even if the bread is fresh and others not doing it at all. Dunking by some individuals is common in some areas but does not occur in other areas. Fruits, meat, and insects may be washed by some individuals. On lawns, it often watches robins and steals earthworms that they capture (Bent 1958; Davis 1944; Peer and Bollinger 2020; Pitocchelli 1985; Rand 1967; Wible 1975). There are numerous accounts of the grackle capturing live fish or scavenging dead ones. It uses a variety of fishing techniques. These include flying from a perch near the water and hovering above fish to capture them with the beak, attacking fish from driftwood floating in water, occasionally diving into the water, fishing in deep turbulent water in the manner of gulls and terns, and wading in water and plunging the head under water to obtain fish or crayfish. It appears to prefer live fish to those that are dead. It has captured live golden shiners, common shiners, emerald shiners, threespine sticklebacks, and unidentified minnows. It has eaten dead goldfish, alewives, gizzard shad, and yellow perch (Beeton and Wells 1957; Cahalane 1944; Cottam 1943; Darden 1974; Follett 1957; Iron 1997; Townsend 1919; Zottoli 1976). The Common Grackle often preys upon eggs and nestlings of other birds. It also kills adult birds, often eating only the brain and flesh on the head. This behaviour is most prevalent during winter when food supplies are low, but occurs at all seasons. Its most frequent victim is the House Sparrow, but it has killed American Woodcocks, Barn Swallows, Ruby-crowned Kinglets, American Robins, White-throated Sparrows, and Ovenbirds. It has been observed eating Pine Siskins and American Goldfinches, but it was uncertain whether the grackles killed them (Cummings and Cummings 1989; Davidson 1994; Green 1990; Gross in Bent 1958; Laporte 1974; Middleton 1977c; Taylor 1958). It also attacks, kills, and eats small mammals such as mice and masked and short-tailed shrews. One was observed dive-bombing a bat in mid-air, driving it to the ground, stabbing it with its beak, and flying off with it (Gross in Bent 1958; Mueller 1990; Sparks and Choate 1995). Vogt (1979) observed grackles feeding in association with map turtles in Wisconsin. They removed leeches (the smooth turtle leech) from the leg cavities of turtles while they were basking. The grackle also consumes hatchling turtles in large numbers as they move from their nests to the water. Several other miscellaneous foraging behaviours have been documented. One flock was observed feeding on sphinx moth

caterpillars in a tobacco field. At High Park in Toronto, it captured amphipods in a pond, gathering several together in a pile before eating them. At a small pond, it caught, killed, and devoured small leopard frogs (Gross in Bent 1958). The grackle is highly adapted for opening acorns. It has a specialized keel on its palate that it uses to apply pressure to the acorn, producing an indentation in it. The acorn is rotated and the process repeated until the acorn falls in half. It is capable of opening the acorns of black, Hill's, scarlet, bur, and pin oaks but cannot open the larger acorns of white and red oaks (Schorger 1941). In Niagara Region, it was observed eating chinquapin oak acorns (Sheppard et al. 1936).

In New York, adults often flew 800 m to obtain food for nestlings even though the same food could have been obtained near the nest. Birds at 1 nest flew about 500 m to obtain dead alewives to feed their young even when they were available within a few metres (Hamilton 1951). Females without male assistance are capable of raising a brood of 4 young (Howe 1979; Maxwell and Putnam 1972; Snelling 1968). Young in all nests at a pond in Algonquin Park were fed mostly dragonfly nymphs (Axtell 1955). Young at Michigan nests were fed mostly arthropods, including beetles, odonate nymphs, mayflies, stink bugs, geometer moth caterpillars, crayfish, isopods, spiders, and earthworms; some corn was consumed (Howe 1979). Zottoli (1976) observed adults feeding juveniles pieces of fish. Hamilton (1951) analyzed 130 nestling fecal samples and observed adults feeding their young. Green frog tadpoles were captured in a pond and fed to the nestlings. They were also fed red-backed and dusky salamanders. Parts of a newborn meadow vole and a masked shrew were fed to nestlings. Animal food comprised 89.5% of the volume of nestlings' diet: 48.2% insects, 10.9% earthworms, 8.3% amphibians, 6.6% fish, 5.4% spiders, 0.8% millipedes, 3.4% isopods, 0.3% mammals, and 5.2% snails. Other materials included 3.2% green grass, 1.8% fruit, 1.4% grain, and 4.3% grit. Beetles were the most important insects, appearing in 42.5% of samples. These were predominantly June beetles but ground beetles, click beetle larvae, and small scarab beetles were also consumed. Caterpillars comprised 40.3% of the volume of food and occurred in 52.4% of nestlings that had been fed insects. True bugs, mostly stink bugs, were present in 16.7% of nestlings that had consumed insects. A few ants and a single scorpionfly were consumed. Spiders were frequently fed to smaller nestlings to age 4 days. The grain that was consumed was waste; the fruit was raspberries. Beal (1900) analyzed the diet of 456 nestlings. They had eaten 74.4% animal food and 25.6% vegetation. The animal food consisted of 70% insects and its composition was practically the same as the adult diet. Beetles were fed to older nestlings only, with grubs forming more than 19% of the diet along with 10% ground beetles, 3% weevils, and 5 or 6 other families of beetles totalling less than 1% of the diet. Grasshoppers and crickets were favoured and constituted more than 21% of the diet. Adults selected grasshoppers and other soft-bodied insects for their young and ate beetles and other hard items themselves. Caterpillars comprised 6% of the nestling diet and small amounts of ants, flies, bugs, mayflies, centipedes, and spiders were given to young. Spiders were given to young birds shortly after they hatched. In Wisconsin, Snelling (1968) compared the diets of nestling grackles and Red-winged Blackbirds in a cattail marsh. The nestling period of the 2 species overlapped 23-60% over 6 years with a trend toward decreasing overlap. The grackle was a recent arrival as a breeder in the marsh, so the 2 species may have evolved to minimize the overlap in their nestling periods. Both species were diverse and unspecialized feeders and ate similar-sized prey (mean of 9.79 mm for the grackle and 10.09 mm for the blackbird). There was a 52% overlap in

the diet of the species when they were feeding nestlings. Significant competition for food seemed unlikely. The food for them was abundant and they used somewhat different foraging techniques. Earthworms and scarab beetles were important foods for the grackle but were not eaten by Red-winged Blackbirds. The most important foods for grackle nestlings by volume were 9.13% earthworms, 5.26% skimmers (dragonflies), 27.19% scarab beetles, 13.78% owlet moths, 3.57% geometer moths, 3.55% fulgorid planthoppers, 7.01% fish, and 12.82% bread. Other food items included nematodes, snails, harvestmen and spiders, isopods, crayfish, other beetles (rove, click, darkling, and June beetles and weevils), book lice, other lepidopterans (gossamer-winged butterflies and snout, twirler, and ermine moths), flies (midges and crane, soldier, bristle, and big-headed flies), hymenopterans (ants and sawflies), leafhoppers, true bugs, seeds, and human foods (corn chips, noodles, popped corn, and peanut fragments).

Potvin et al. (1976) summarized the diet of adult Common Grackles in Quebec. During 10-19 May, the diet by volume consisted of 72.5% vegetation, 19.0% animal material, and 8.5% unidentified items. The vegetable matter consisted of 53.0% corn, 12.7% barley, 6.6% smartweed, and 0.2% cherries. The animal food consisted of 15.6% beetles (4.1% ground beetles, 3.3% click beetles, 0.8% rove beetles, 2.5% weevils, 2.5% bark beetles, 1.6% scarab beetles and blister beetles), 2.6% millipedes, and 0.8% isopods. The diet 14-29 July consisted of 43.8% vegetation, 42.8% animal matter, and 8.3% unidentified items. The vegetable matter consisted of 3.5% corn, 27.1% barley, 2.5% oats, 8.3% alfalfa, 1.3% red clover, 0.7% cherries, and 0.5% white sweet clover. The animal food consisted of 2.0% short-horned grasshoppers, 4.0% flies (2.0% parasite flies, 2.0% house flies), 2.0% snout moths, 30.0% beetles (4.0% ground beetles, 4.0% click beetles, 4.0% rove beetles, 8.0% weevils, 8.0% scarab beetles, and 2.0% bess beetles), 3.9% millipedes, 3.8% spiders, and 2.0% earthworms. The diet from 12 August to 16 September consisted of 86.6% vegetation, 9.7% animal matter, and 3.7% unidentified items. The vegetable matter consisted of 79.0% corn, 3.8% barley, 1.7% oats, and 2.1% white sweet clover. The animal food consisted of 1.4% ants, 0.7% snout moths, 0.7% stink bugs, 5.5% beetles (0.7% ground beetles, 1.3% rove beetles, 0.7% scarab beetles, and sap beetles), 0.7% millipedes, and 0.7% spiders. Beal (1897a) analyzed the contents of 2,258 stomachs that were probably included in the 2,346 that Beal (1900) analyzed; 1,890 were adults and the remainder were nestling stomachs. Only 1.6% contained traces of bird eggs and 1 stomach contained the bones of a young bird. Many eggshells were from domestic fowl and were probably obtained from compost piles. Early in spring, it obtains corn from corn cribs and follows plows for insects and grubs. It eats cherries and other fruits as they ripen and corn in the milk stage. In late autumn and winter, it feeds mostly on seeds and grains, becomes more insectivorous in spring, takes small fruits in summer, and attacks ripening corn in September. In all seasons, it probably selects the food items that are most abundant and easily obtained. It eats large quantities of cutworms, June beetles, grasshoppers, crickets, locusts, and pupae and adults of 17-year cicadas and cabbage white butterflies. In late autumn and winter, it eats mast of beech and oaks. There is 1 observation of it killing, skinning, and eating a lizard. The annual diet consisted of 30.3% animal matter and 69.7% vegetable matter. The animal food included insects, spiders, millipedes, crayfish, earthworms, isopods, horsehair worms, snails, fish, treefrogs, newts, lizards, snakes, birds′ eggs, and mice. Insects comprised 27% of the annual diet with a minimum of 3% in February and a maximum of 62.5% in May. Scarab beetles were the most important insects in the diet, including June and rose chafer beetles eaten both as grubs

and adults, with many stomachs crammed full of grubs. Dung beetles and rainbow scarab beetles were common in the diet. It ate weevils every month and they contributed a maximum of 5% of the volume of the diet in June. It ate ground beetles in every month and appeared to prefer them, with a minimum of 7% of the diet in January and 13% in June. Grasshoppers, locusts, and crickets were next in importance in animal foods, particularly grasshoppers which were eaten every month except January with a maximum of 23.4% in August. Caterpillars constituted 2.3% of the annual diet with a maximum of 8% in May. Hymenopterans were represented in the diet mainly by ants. Flies were entirely absent in the samples but have been reported in the diet in other studies. Spiders reached a maximum of 7% in the diet in May. Crayfish were commonly eaten but represented a small proportion of the overall diet. It ate both terrestrial and aquatic snails and a few small clams. The vegetation eaten was very variable and diverse indicating that the grackle is highly opportunistic. Grain consumed included corn, oats, wheat, rye, and buckwheat. Corn was the favourite grain, representing a maximum of 82% of the February diet (all waste grain), 53.2% in September, and 51.5% in October which was crop grain. The fruit consumed included blackberries and raspberries, strawberries, cultivated cherries, mulberries, currants, grapes, apples, blueberries, cranberries, huckleberries, chokeberries, juneberries, and hackberries. Blackberries and raspberries were the favourites and the dominant fruits consumed from May through September, but mostly in July and August. It consumed seeds or nuts of poison ivy, smooth sumac, bayberry, hophornbeam, chestnut, beech, and oaks. Seeds consumed included those of ragweeds, barnyard grass, gromwell, smartweeds, pokeweed, and sheep sorrel. Miscellaneous foods included small bulbs or tubers, galls containing larvae, plant stems, grass and leaves, black locust thorns, and pieces of rotten wood. The overall average diet consisted of 5.6% ground beetles, 4.9% scarab beetles, 2.0% weevils, 1.0% other beetles, 2.3% caterpillars, 7.3% grasshoppers, 2.3% other insects, 1.5% spiders and millipedes, 3.1% crustaceans and molluscs, 0.3% vertebrates, 37.2% corn, 2.9% oats, 4.8% wheat, 1.6% other grain, 2.9% domestic fruit, 2.1% wild fruit, 4.2% weed seeds, and 14.0% mast and miscellaneous. In Algonquin Park, the grackle fed on spruce budworms during an outbreak (Tozer 2012).

Although the ranges and habitats of the 2 species overlap broadly, the Common Grackle is a rare host of the Brown-headed Cowbird. There appear to be a number of reasons for this. The grackle nests earlier than the cowbird. In Illinois, 88.5% of grackle nests were in the incubation stage or later when the first cowbird egg was laid, thereby greatly reducing the potential for parasitism. The grackle is unusual in that it may either accept or reject cowbird eggs, with most species being either acceptors or rejecters. In Illinois, 12.1% of eggs were rejected and 13.4% of Iowa cowbird eggs were rejected. Most eggs are rejected by ejection and the remainder are pierced. Occasional egg rejection is another reason why the grackle is not selected as a host more frequently. Grackles respond aggressively toward cowbirds which may further decrease the incidence of parasitism. Grackle hatchlings weigh more than twice as much as cowbird nestlings, putting the cowbird nestling at a significant disadvantage. Cowbirds are capable of fledging from a grackle nest only when the clutch size has been reduced to allow effective incubation, the cowbird hatches at least 2 days earlier than the grackles, and the cowbird hatchling weighs at least 3 grams. Parasitism has negligible effects on the grackle with the presence of a cowbird nestling having no effect on the grackle nestlings. The only potential negative effect is the removal of grackle eggs by cowbirds (Peer and Bollinger 1997, 2020; Peer and Rothstein 2010; Peer et al. 2010; Rothstein 1975). Peer et al. (2001) reported that there

were only 30 known cases of parasitism, but more may have been documented since. These included 4 of 2,245 nests (0.2%) that were parasitized in Ontario (Peck and James 1998b). Other reported parasitism rates are 0% in Wisconsin (Petersen and Young 1950), 0 of 401 nests in Illinois (Peer and Bollinger 1997), 6 of 727 nests (0.82%) in North Dakota, 3 of 119 nests (3.4%) in Manitoba, 0 of 371 nests in Louisiana (Peer et al. 2001), and 0 of 1,795 nests (Friedmann et al. 1977). Notable are the 3 of 8 nests (37.5%) parasitized in the Saskatoon area (Leighton et al. 2002).

Forest clearing to create agricultural and developed land greatly increased the amount of habitat for the Common Grackle. Its habitat may now be declining or becoming degraded. More intensive farming with subsequent loss of hedgerows reduces nest-site availability. In Nova Scotia, densities were lower in more intensively farmed areas (Erskine 1971) but densities remain high in the extreme southwest of Ontario where agriculture is dominated by large fields of row crops (Zimmerling in Cadman et al. 2007). Modern subdivisions provide little habitat for the grackle because of the high density of houses, small lots, and limited ornamental plantings. Natural succession is occurring in the southern portion of the Canadian Shield, with marginal farmland evolving into forest, thereby reducing the amount of suitable habitat.

In New York, Keller et al. (2003) studied the effects of forest clear-cutting on the grackle. They included it in the sparrow-dominated guild of ground-feeding birds. This guild declined significantly as leaf area increased and the shrub-opening edges it preferred disappeared. This guild represented 37% of the total avian population in 2-year-old clear-cuts and only 9% 6 years after cutting. The grackle was documented in low densities only in clear-cuts 3-5 years old. In southern Ontario, the grackle was equally abundant in uncut forests, those that were selectively thinned, and those where heavy diameter-limit cuts were made (Holmes et al. 2007).

Weather may result in the failure of many nests. Young are often killed in early nests by subfreezing temperatures, and high winds may blow nests out of trees. In the Prairie Pothole Region of Canada, abundance of the grackle was positively correlated with temperature in the previous spring (Forcey et al. 2007; Howe 1976; Maxwell and Putnam 1972; Peer and Bollinger 2020; Petersen and Young 1950).

Human disturbance and predation may result in extensive nest losses and colony desertion. Low reproductive success occurred in a Wisconsin marsh due to researchers. Raccoons followed human trails and depredated nests, food sampling retarded chick growth, adults removed some nestlings with food collars, and many nests were deserted (Snelling 1968). In Ohio, nests disturbed early in the cycle by researchers were abandoned, and nests were deserted when vegetation near the nest was trimmed to afford a better view. No nests were abandoned after the eggs hatched (Maxwell and Putnam 1972). In Illinois, entire colonies were deserted after depredation (Peer and Bollinger 2020). At a Michigan colony, 90% of nests were depredated by domestic cats (Howe 1976). Many grackle nests are closely associated with human dwellings and farm buildings, so cats may be significant predators in much of its range.

Hanowski et al. (1997a) treated Minnesota wetlands with Bti and methoprene to control mosquitoes. This management had no apparent effects on the grackle.

Status

The Common Grackle is much more common now than it was prior to European settlement. There is more habitat available for it now than there ever was in Ontario (McCracken 2003b; Peer and Bollinger 2020). In the Kingston area, it was an abundant summer resident in 1859, 1909, 1965, 1973, and 2008 (Weir 2008). In Elgin County, it was a common breeder in 1891 and 1954 and abundant in 2000 (Lancaster et al. 2004). Baillie and Harrington (1937) considered the grackle one of the most common and widely distributed breeding birds in the province. At that time, it bred from the southern boundaries of the province north at least to Cochrane District and west to Lake of the Woods, and probably considerably further north. The first atlas demonstrated that the breeding range of the grackle encompassed the entire Boreal Forest Region south to the shores of Lake Erie and Lake Ontario. There were also records in the eastern portion of the Hudson Bay Lowland in the Moosonee area north to Attawapiskat. It was an abundant breeder, but became progressively less common northward (Weatherhead in Cadman et al. 1987). James (1991) considered it an abundant summer resident in the south, locally common in the north to Big Trout Lake and Albany, and a vagrant north to Winisk.

The second atlas demonstrated that there had been no significant change in the breeding distribution of the grackle since the first atlas. Its probability of observation decreased province-wide and in all regions except the Hudson Bay Lowland where it experienced a nonsignificant increase. The only significant decline was in the Shield portion of the Great Lakes-St. Lawrence Forest Region. The decline was attributed to natural succession and blackbird control programs in the southern United States. It was most abundant south and east of the Canadian Shield. Its density in this area was surpassed only by densities of the European Starling and Red-winged Blackbird. All these species do well in landscapes dominated by agriculture and urban areas. Density of the grackle decreased in the Shield and northward, probably due to less availability of agricultural lands, settlements, and productive wetlands (Zimmerling in Cadman et al. 2007).

The population of the Common Grackle appears to be declining in the east. Western populations continue to increase and its range is also expanding in the west, due in part to planting of shelterbelts (Campbell et al. 2001; Homan et al. 1996; Peer and Bollinger 2020). There was a considerable increase in its population between the mid-19th and early 20th centuries, probably due to continuing deforestation and planting of grain crops. Population declines may have started early in the 20th century. Extensive planting of corn beginning in the late 20th century increased food supplies and may have levelled off the rate of decline. The grackle has declined at the steepest rate of any blackbird species except the Rusty Blackbird since the Breeding Bird Survey (BBS) was initiated in 1966. By 2003, the population had decreased by 38%, with the decline more severe in the United States at 40%. The decline in the east is attributed to blackbird control programs implemented in the southern United States in autumn and winter. Severe weather in the wintering range may also be a factor (McCracken 2003b; Peer and Bollinger 2020). BBS results indicate that the grackle decreased at annual rates of 0.489% in Canada and 1.17% in Ontario 1970-2021. The trends 2011-21 were annual increases of 2.88% in Canada and 1.03% in Ontario. All results were highly reliable (A.C. Smith et al. 2023). In Great Lakes coastal wetlands, it increased at an annual rate of 8.4% 2011-21 (Tozer et al. 2024).

POSTFLEDGING PERIOD

Young are poor fliers when they leave the nest but quickly become proficient. They usually leave the area of the nest within 1-2 days and disperse as far as 0.5 km to areas of dense vegetation. The duration of parental care is uncertain, but may be several weeks. Young have been observed being fed in early July long after nesting is usually complete. Once the young are independent, family groups coalesce to form flocks. Postbreeding flocks have been observed in Muskoka District as early as 18 June. In late summer and early autumn, grackles join large flocks of other postbreeding species, particularly Red-winged Blackbirds, cowbirds, and starlings (Howe 1976; Mills 1981; Peer and Bollinger 2020; Petersen and Young 1950; Wiens 1965).

During the postbreeding season, the grackle occurs mostly in anthropogenic habitats in the southern portion of the province. These include agricultural fields and farm buildings, rural residential areas, and urban areas. In Algonquin Park, flocks forage on the forest floor, at wetland edges, along shorelines, and in open areas (Sheppard et al. 1936; Tozer 2012). In British Columbia, it prefers human-made clearings in otherwise treed habitats, wetlands, backyards with feeders, homesteads, farm ponds, airstrips, and campgrounds. It also visits farmyards, sewage lagoons, livestock corrals, orchards, harvested cornfields, and riparian woods (Campbell et al. 2001). Agricultural fields close to hardwood forests in bottomland areas appear to be especially attractive (Peer and Bollinger 2020). In Michigan, small numbers occurred both in mature upland and riparian trembling aspen forests (Akresh et al. 2009). Breeding areas may be abandoned by flocks by August in some habitats and areas (Beal 1900).

Communal roosts are an important component of grackle habitat during the postfledging period. Grackles continue to use roosts during autumn migration, winter, and in spring until courtship begins. Numbers of birds at roosts may start to swell 1 or 2 days after the young fledge, beginning as early as mid-June to early July. It roosts with Red-winged Blackbirds, Brown-headed Cowbirds, and European Starlings, with lesser numbers of American Robins, Rusty Blackbirds, and Brewer's Blackbirds. In Niagara Region, roosting occurs regularly in a common reed marsh. In Algonquin Park, grackles roosted in grey alder thickets. Other reported roosting habitats include hardwood woodlots, near food sources such as agricultural fields and orchards, trees along city streets, conifer groves, and cattail and common reed marshes. In Illinois, a family of Barred Owls roosted in a 9-year-old white pine plantation along with 2,500 grackles. An analysis of the owl pellets revealed that they had been eating grackles (Applegate 1975; Black and Roy 2010; Gross in Bent 1958; Lyon and Caccamise 1981; Peer and Bollinger 2020; Stewart 1975b; Tozer 2012).

In North Carolina, roosts were always in or adjacent to urban areas, with few roosting in rural areas. In larger mixed roosts, grackles were the dominant species with most roosts becoming larger and more central after young fledged. By early August, all grackles gathered into a single roost, often returning repeatedly to the same site in successive nights, but also frequently switching roost sites. By early spring, it roosted in scattered sites even when roosting in the same tract of woodland. Some areas were used continually for long periods but specific sites were often different in successive years (Stewart 1975b). Within a 1,000-km^2 area in New Jersey, 22 roosts were located, including 20 in hardwood stands and 2 in common reed. Roosts consisted of 60% starlings, 33% grackles, and lesser numbers of Red-winged Blackbirds, cowbirds, and robins. Hardwood roost sites were 0.13-

10.4 ha, with larger sites supporting more birds. When initially occupied, only a small proportion of the site was used. As the assemblage grew, the roost usually expanded until the entire area was occupied. Important tree species in roosts included maples, gum, oaks, pines, red cedar, and birches. Plantations were used in some sites adjacent to residential areas. Red maple, black gum, and pin oak were the most frequently used hardwoods and red cedar was used in old fields. Tree density in roosts was high (average of 1,741 trees per ha). No sites with a tree density of less than 720 trees per ha were used. Roosts were usually in even-aged stands, and the mean age of roost stands was 18-34 years, with 68% of sites 21-26 years old. There was a significant difference in the average age of roost stands (25 years) and non-roost stands (41 years). The most consistent characteristics of roost sites in addition to stand age were a closed canopy, compact vertical arrangement of twigs, and uniformity of mean twig heights (Lyon and Caccamise 1981). Roosts first became active in early June and the number of active roosts increased through mid-August then declined until the end of the local roosting season in early November. Individual roosts were active 3-20 weeks. The same sites were used each year and their heaviest use occurred over a similar period. Following the population peak in mid-August, the size of individual roosts began to decline, resulting in abandonment of some. Few new roosts were established after mid-August but those that were eventually supported large autumn flights. By early October, few roosts were active; 1-3 became large premigratory roosts while others dwindled until they were abandoned. Before the peak in population, individuals usually remained in a single roosting flock. Later, they switched sites more often as the number of active sites declined, abandoning declining roosts and moving either to developing major roosts or remaining in minor roosts with fewer than 2,000 birds. Roosting sites were not limited because not all were used all the time and some suitable areas were never used (Caccamise et al. 1983). Caccamise and Fischl (1985) identified secondary species that occurred in these roosts in addition to starlings and grackles. They included the Green Heron, Mourning Dove, Common Nighthawk, Chimney Swift, Blue Jay, Purple Martin, Tree Swallow, American Robin, Northern Mockingbird, House Sparrow, Red-winged Blackbird, and Brown-headed Cowbird. The robin was the most abundant secondary species and occurred in every roost except early in the season. Red-winged Blackbirds and Mourning Doves were present for most of the season, but in much lower numbers than robins and not in every roost. The remaining secondary species were less widely distributed and remained for short periods. Morrison and Caccamise (1990) determined that the grackle exhibited fidelity to diurnal activity centres. The mean distance of diurnal grackle sightings was 0.88 km from the centre of the diurnal activity centre and the mean distance moved between sightings was 0.55 km. Four grackles used the same activity centre June to November. One female used 3 activity centres in succession separated by distances of 6.5 and 5.5 km. Although all birds were captured in the same foraging areas, they joined communal roosts at 15 sites. Grackles joined roosts containing both starlings and robins more than 97% of the time. Mean distance between grackle roosts and activity centres was 3.6 km with 2 major roosts more than 4 km away. Grackles switched roosts 15.1% of the time and mostly (39 of 41 cases, 95.1%) switched to roosts within 2 km of the previous night's roost. They switched roosts much more frequently than they switched activity centres. One case of switching activity centres was accompanied by a major shift in the roost.

In the postbreeding period, and also autumn migration and winter, the Common Grackle usually forages in flocks with other blackbirds and starlings. The grackle is one of the most significant

agricultural pest species in North America. It and the Red-winged Blackbird are responsible for most damage to ripening corn and the grackle is the most important species in damaging sprouting corn. It also damages rice crops, other small grains, sunflowers, peanuts, blueberries, and sweet cherries (Peer and Bollinger 2020). Bernhardt et al. (1987) studied how the grackle feeds on ripening corn and found that it had the highest feeding efficiency of the species tested, inflicting the most damage per unit time. It pecked through the husk with the bill closed. Once access to the kernels was obtained, it fed by direct pecking, shearing entire kernels off the cob. Once the husk was open, it would do extensive damage, making 5-10-cm vertical slits in the husk. In field situations, it is more likely to attack ears already damaged by other species. Cummings et al. (1989) summarized damage to sunflower crops by grackles, Red-winged Blackbirds, and Yellow-headed Blackbirds in North Dakota, South Dakota, and Minnesota. Grackles represented 11% of the birds in flocks. Seventy-four percent of damage occurred 3-18 days after antithesis, 70% occurred on sunflower heads with green and green-yellow bowls, and 68% occurred when the heads were half inverted. Soft seeds received 76% of the damage and bird numbers peaked when fields reached the soft-seed stage. Brugger (1988) studied damage to sprouting rice crops in Louisiana by blackbirds. Grackles represented less than 1-8% of the total birds in flocks and did minimal damage compared with female Red-winged Blackbirds. Foraging on rice crops occurred in the winter. Flocks flew as far as 60 km from the roost to forage. Tobin et al. (1982) studied bird damage to apples in New York. Damage to individual crops was less than 1%. The mean percentage of trees receiving at least some damage was 57% and the mean percentage of apples pecked by birds was 5.9%. Most damage was done by the American Crow. The grackle caused minimal damage.

During the postfledging period and autumn migration, acorns are a prominent food (Bent 1958). The grackle also eats wild fruits at this time. In an Illinois woodlot, it gulped fruits whole while foraging in the subcanopy. It foraged an equal amount of time in treefall gaps and forest interior. In 1 year, 100% of the fruit eaten was Virginia creeper. The following year, it ate only fox grapes. It was not observed eating the fruits of red elderberry, pokeweed, poison ivy, greenbrier, or moonseed (Malmborg and Willson 1988). Dennis (1949) reported a flock of 800-900 grackles completely stripping off the fruits of a large stand of flowering dogwood within half an hour in Virginia. They were not well adapted to foraging on dogwood berries. They could easily pull off the fruit but could swallow only a small portion of it, dropping the rest to the ground. Many then fed on the ground, eating both the seed and the fleshy part of the fruit.

MIGRATION

Most Common Grackle populations are migratory except for those breeding in the Gulf Coast states, which are resident birds. Migration occurs diurnally, usually in mixed-species flocks that include Red-winged Blackbirds, starlings, and cowbirds, and less frequently Rusty Blackbirds, Brewer's Blackbirds, and robins. Females tend to migrate about 100 km further south than adult males and juveniles travel 100-300 km further than adult males. Those breeding at latitude 44-45°N migrate about 1,000 km. Those breeding at latitude 34-35°N travel approximately 200 km. The mean distance travelled from the Great Lakes area was 870 km. Severe winter weather may drive birds further south than usual (Dolbeer 1982; Peer and Bollinger 2020). The winter range of Ontario birds covers a broad area from southern Ontario and the Great Lakes states south to the Gulf Coast states, although encounters are rare in Texas and Florida, and along the Atlantic Coast from New Jersey to Georgia

(Brewer et al. 2018). Birds are at the maximum distance from their breeding area in January or February. The mean distance between banding and recovery in a subsequent breeding season for hatch-year birds was 35 km. Mean dispersal distances between years for adults was 26 km for males, 14 km for females, and a mean of 24 km for the sexes. Hatch-year birds dispersed significantly further than adults and 12% moved further than 50 km. Mean distance between successive winters was 357 km for males, 263 km for females, and 282 km overall. Grackles were more faithful to breeding than wintering locations (Dolbeer 1982). Stewart (1975b) analyzed banding recoveries to determine where birds banded in winter in South Carolina were recovered in a subsequent breeding season. A total of 79.4% of birds remained south of Maryland after wintering in South Carolina. Of birds going further north, 6.6% went to Ontario, 5.7% to Pennsylvania, and 4.7% to New York. Birds from New England, more northern states, Ontario, and Quebec wintered in North Carolina rather than moving further south into South Carolina. Eighty-one percent of these birds were from Ontario and 2.0% were from Quebec (Peer and Bollinger 2020).

Males typically arrive 5-10 days before females, but in Hamilton, females did not arrive until a few weeks after the males. Spring flocks are usually comprised of either males or females (Curry 2006; Gross in Bent 1958; Petersen and Young 1950; Wiens 1965). It is possible that males are arriving much earlier now than they did historically and that the gap between the arrival of the sexes has increased. In Hamilton, McIlwraith (1894) reported that males arrived just a few days before females, usually in mid-April. The gap between arrival of the sexes there is now a few weeks and males arrive in late March (Curry 2006). In Manitoba, Murphy-Klassen et al. (2005) analyzed 63 years of migration data and determined that the grackle arrived significantly earlier in the 2000s than in the 1940s. It exhibited the strongest trend toward earlier spring arrival with warmer spring temperatures than any other passerine species. It arrived 2.1 days earlier for every 1°C increase in temperature. In southern Ontario, small numbers arrive in mid- to late February; the peak of migration occurs through March and April. Smaller flocks continue to migrate into mid-May after local breeders are incubating (Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). In the southern Shield, birds arrive in late March or early April; some arrive in early March (Mills 1981; Tozer 2012).

Wilson and McRae (1993) reported 1 grackle at Longridge on 5 September and another at Moosonee on 2 September. They terminated their fieldwork shortly afterwards, so these records may not represent the latest migrants. In Algonquin Park, most leave during October but a few linger into November, mostly at feeders (Tozer 2012). In Muskoka and Parry Sound districts, peak flocks occur in September and October (Mills 1981). In the Kingston area, autumn migration is obvious during October (Weir 2008). In Elgin County, large flocks have moved on by late November (Lancaster et al. 2004).

Habitat used during spring migration is similar to that used during the breeding season. Migration habitat is closely tied to areas with high abundance of food, with both early spring and late autumn migrants visiting feeders when other food sources are less plentiful. Even after arriving at the breeding grounds, grackles may travel as far as 2.4 km from the nesting area to forage. Autumn migration habitat is similar to that used during the postfledging period, with flocks concentrating in agricultural and urban areas. The major postfledging roosts continue to be used during autumn migration, with numbers swelling in September and October. Communal roosting also occurs

during spring migration, but in smaller numbers (Gross in Bent 1958; Mills 1981; Petersen and Young 1950; Tozer 2012).

In the St. Lawrence lowlands of Quebec and Ontario in early autumn, most birds appeared to be from the local breeding population, with two thirds of the breeding population remaining until late autumn from 1 October to mid-November. Blackbird control methods, if implemented in April and early autumn, would affect local breeding populations and reduce late autumn numbers (Weatherhead et al. 1980).

James (1991) considered the Common Grackle an abundant migrant in Ontario. In Niagara Region, an estimated 90,000 were observed in mid-October mixed with other species (Black and Roy 2010). During spring in Hamilton, 5,000 roosted in the Dundas Marsh and 50,000 were seen on a reverse migration in mid-March. In autumn, it flies along the Lake Ontario shoreline with peak numbers of 5,000-7,400 (Curry 2006). At Presqu'ile, 6,000 roosted in the marsh in late August with other blackbird species (LaForest 1993). In Kingston in autumn, flocks of 3,000 grackles are typical mixed among other blackbird species; 12,000 were seen in mid-October (Weir 2008).

WINTER

In winter, the Common Grackle inhabits mostly agricultural and urban habitats. Those in more northerly locations where snow cover may be deep and prolonged tend to remain around feeders. Nocturnal roosts are important in winter, with it roosting mostly with the Red-winged Blackbird, starling, and cowbird; lesser numbers of several other species may be present. Large winter roosts are concentrated mostly in the lower Mississippi Valley, but also in the Atlantic Coastal Plain from Chesapeake Bay southward and in the southern portion of the Piedmont. There are at least 125 major roosts in the southern United States that each support 1,000,000 or more blackbirds and starlings. Peak winter numbers at a Louisiana roost reached 25,000,000 birds. There is considerable intermingling of birds from different breeding populations within and among species in roosts. Birds wintering in a given area come from a broad area of the breeding range (Brugger 1988; Dolbeer 1982; Peer and Bollinger 2020).

In winter, the grackle subsists mostly on waste grain and other anthropogenic food, but also eats some tree seeds (Peer and Bollinger 2020). In the north, it may use feeders all winter. In the normal wintering range, few visit feeders until February when spring migration may be underway. It is less likely to visit rural than urban feeders, probably because natural food is more abundant there. Its favourite feeder foods are mixed seeds, sunflowers, cracked corn, water, and pet food. It infrequently consumes millet, canary seed, safflower, whole corn, milo, wheat, peanuts, suet, peanut butter mixes, bird puddings, fresh or dry bread, baked goods, sugar water, oats, meat scraps, and popped corn (Dunn and Tessaglia-Hymes 1999). Based on 30,311 feeding observations, it preferred cracked corn and 0.5-mm sunflower chips. It preferred platform feeders over tubes and hopper feeders. The mean number of grackles feeding on different seed types per 5-minute observation period were: 5% black oil sunflowers, 7% cracked corn, 5% 0.3-mm sunflower chips, 5% 0.5-mm sunflower chips, 1% niger seed, 3% red milo, 2% safflower, 5% striped sunflowers, 3% white proso millet, and 4% whole peanuts (Horn et al. 2014; Johansen et al. 2014).

Control of blackbirds at winter roosts appears to be the most significant limiting factor for the Common Grackle. There is pressure to control blackbird numbers because of the damage they do

to crops and roosts may harbour the fungus histoplasmosis, a human respiratory disease that can be fatal. From 1974 to 1992, a detergent that eliminates the waterproofing ability of feathers was sprayed on roosts followed by spraying of cold water. This resulted in birds dying of exposure. Hundreds of millions of birds were killed in this manner. In Kentucky and Tennessee, an estimated 28,000,000 were killed 1974-82. This method of control was banned in 1992. Subsequently, DRC-1339 was applied as bait on the ground or spread on rice grains. This chemical kills birds by shutting down liver and kidney functions. Millions of birds were killed by this organochlorine pesticide. The actual number of grackles that have been and continue to be killed in winter is unknown, but it is undoubtedly several millions (Dolbeer 1982; Gross in Bent 1958; McCracken 2003b; Peer and Bollinger 2020). The impacts of blackbird control at winter roosts have been downplayed, using the rationale that birds disperse from roosts to over much of the breeding range, thereby likely having limited effect on local breeding populations (Dolbeer 1982). It seems more likely that the control program has depressed the entire eastern breeding population (Peer and Bollinger 2020). In Illinois, the grackle is declining at an annual rate of more than 7%. Horsley and Ward (2021) demonstrated that nest and postfledging survival rates were high and attributed the decline to winter control programs and possibly exposure to neonicotinoides on agricultural land during spring migration and the breeding season.

Severe winter weather may result in mortality of the Common Grackle. After a storm in Illinois, 8.7% of grackles within a colony died (Odum and Pitelka 1939). Also in Illinois, Graber and Graber (1979) reported a grackle population decline of 18.9% in bottomland forests and 66.7% in urban residential areas after a severe winter storm. They also found a number of grackle carcasses. Stewart (1978) reported less extensive mortality of the grackle at a Kentucky roost following severe winter weather. Ninety-eight percent of the birds in the roost were grackles, but they represented only 9.4% of the dead birds. About 14,500 birds, 32.2% of the total roost, left the evening prior to the mortality suggesting that many responded to the environmental stress by moving further south.

James (1991) considered the Common Grackle a rare to locally common winter resident in the south and occasional and rare to uncommon in the north to Thunder Bay and Moosonee.

The Common Grackle appears to have increased as a wintering species and extended its winter range northward. Freedman and Riley (1980) examined Ontario Christmas Bird Count (CBC) data for 1929-77. It exhibited a trend toward higher abundance and frequency of occurrence, but total numbers remained low. McIlwraith (1894) stated that there were no winter records for the province. Curry (2006) reported that 1 or 2 are present in the Hamilton area every winter, with a maximum of 12. It is uncommon in winter in Niagara Region, Presqu'ile, and the Kingston area; rare in Elgin County and Muskoka and Parry Sound districts; and very rare in Algonquin Park. These are all areas where wintering birds were historically absent. CBC results indicate that it decreased in Ontario at annual rates of 3.67% 1970-2021 and 1.78% 2009-21 (National Audubon Society 2022).

Ovenbird

Seiurus aurocapilla

BREEDING SEASON

Habitat Requirements

All Ontario Ovenbird nests were in forests. Mixed (45% of nests) and deciduous (41.9%) forests were preferred to coniferous forests (12.6%). Open forests with little understorey were preferred to those with a dense understorey. Wet and dry habitats were used without any evidence of preference. Many nests were at woodland edges or near clearings, or beside paths and logging roads (Peck and James 1987). Tree height does not appear to be important, but it requires a closed canopy. It was much more common in mature forests with dry to mesic conditions where there was limited shrub growth (James 1984b).

In the Hudson Bay Lowland near Moosonee, the Ovenbird was common in all deciduous and mixed forest cover (Wilson and McRae 1993).

In the Ontario Boreal Forest Region, the Ovenbird was in a guild by itself, associated with older, tall, closed-canopy deciduous stands with little interspersion of young and old forests. It preferred

areas of lower disturbance and less age-class interspersion of forest stands. Areas that were predicted to have high occupancy in the Nipigon Forest would have 5.9% more canopy closure, 0.6 m taller canopy, less young habitat, more hardwoods, less edge, and less intact forest than current conditions. The most important variable was the amount of deciduous forest cover (Rempel 2007; Rempel et al. 2007). In boreal mixed-wood and coniferous forests near Hearst, it was absent in all lowland stands and clear-cut upland stands 3-5 and 24 years old. In upland habitats, it occurred in clear-cuts 6-19 years old and in uncut stands (Welsh and Fillman 1980). On the northeast shore of Lake Superior, it preferred drier woods where poplar and birch were the dominant species (Baillie and Hope 1943). In the Clay Belt, it was most abundant in trembling aspen, spruce-aspen, jack pine, and jack pine–black spruce stands. It occurred mostly in dry and mesic stands that were moderate to rich in nutrients (Welsh and Lougheed 1996).

In jack pine stands near Gogama in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, James and Peck (1995a) considered the Ovenbird characteristic of pine stands once trees reached a height of 10 m and of mixed jack pine–deciduous stands once trees became 12 m tall. The main habitat requirements were dense canopy cover; a sparse tall shrub layer, although density occasionally reached 50% coverage; dense coverage by low shrubs and herbaceous species in pine stands; and herbaceous growth in leaf litter in deciduous woods, with these areas growing up with bracken fern later in summer. Jack pine forests mixed with trembling aspen, white birch, white pine, sugar maple, and hemlock near Parry Sound supported low to moderate Ovenbird densities. These stands had low canopy closure of 25-50% or less with numerous openings due to rocks, wetlands, or logging (James 1979a). In Muskoka District and Haliburton County, areas around singing posts and nests had high canopy coverage and low ground and shrub coverage. It was associated with very high canopy volume mixed-wood forests with intermediate tree density, typical of mature undisturbed forest (Clark et al. 1983). In Peterborough County, it consistently chose territories in mature forests with tree heights of 16-22 m, with 60-90% canopy closure. Relative to random sites, it selected nest sites with lower ground cover, larger trees, and flatter areas, where the leaf litter was thick, and at distances of more than 20 m from forest edge (Burke and Nol 1998). In Algonquin Park, it was abundant and well distributed throughout every forest type except wet spruce swamps (MacLulich 1938). It was absent in bogs and in black spruce, balsam fir–black spruce, and black spruce–white cedar stands in Algonquin Park. It was the most abundant species in trembling aspen–white birch stands and was also dominant in aspen-birch–balsam fir stands, but occurred at lower densities. It was the dominant species in immature white pine and balsam fir–

black spruce–hardwoods stands and second in abundance in northern hardwoods stands. It also occurred in stands dominated by hemlock. It was characteristic of deciduous stands where it was consistently one of the most abundant species (Martin 1960). In Algonquin Park, it was least common in stands cut 10-18 years previously and more common in both recently cut stands and those where no logging had taken place. It was one of the most abundant species in white pine stands (Kingsley and Nol 1999). Also in Algonquin Park, it avoided large open areas of bracken fern and grasses in aspen forests but used similar areas in conifer-birch stands. It avoided wet areas in sugar maple stands (Stenger and Falls 1959).

Near Ottawa in the off-Shield portion of the Great Lakes–St. Lawrence Forest Region, high importance habitat features for the Ovenbird were the percent coverage of living ground cover, leaf litter depth, shrub height, canopy cover, and percentage of deciduous trees. Moderately important features were the diameter at breast height (DBH) of trees, tree density, and tree species richness. Tree height was of low importance (Lee et al. 2002). In the Kingston area, McLeish and Robertson (1997) concluded that upland white cedar stands could provide quality breeding habitat. In southeastern Ontario, leaf litter was positively correlated with its density, pairing success, and productivity. Pairing success was correlated with sapling density and canopy cover. Nest success was correlated with percent cover by forbs (Richmond et al. 2012). In Durham Region, it was present in all forest types surveyed, including those with open canopies and a black spruce bog with a red maple–poplar swamp on 1 side. It was a late successional species associated with deciduous tree species (Speirs and Orenstein 1975).

In the Carolinian Forest Region in the South Walsingham Forest in Norfolk County, abundance of the Ovenbird was significantly correlated with the shrub layers 0-0.3 m and 0.3-1.0 m from the ground, and shrub stem density. It was one of the least discriminating species, occurring in all types of forested habitat. It was the second-most abundant species (McCracken et al. 1998).

Throughout its range, the Ovenbird is an obligate forest species, although it occasionally nests in early successional areas created by clear-cutting. In New York, it became a dominant species 24-25 years after clear-cutting in deciduous forest. Mixed and deciduous woods are preferred over coniferous stands, but it may be common in certain types of coniferous woods, particularly those dominated by white pine and balsam fir. It avoids pine-spruce stands, but nests where spruce is mixed with deciduous species or balsam fir. It may be common in coniferous plantations, especially those dominated by white pine. Densities are higher in plantations that have been thinned and have some deciduous undergrowth. In plantations, it may be second in abundance. It is the dominant species in many stand types, or second in abundance. It is particularly abundant in stands dominated by aspen and/or white birch, mixed upland spruce–balsam fir, oak and oak-pine, pines, and sugar maple. In New Jersey pine and oak barrens, it was one of the most abundant species in oak stands, second in abundance in oak-pine stands, and third in abundance in pine-oak. In Wisconsin, it was rare in pine and oak barrens, but common in barrens that were nearly forest (Back 1979; Bielefeldt and Rosenfield 1994; Brooks 1940; Brush 1987; Campbell et al. 2001; Capen 1979; Crawford and Titterington 1979; Drapeau and Darveau in Gauthier and Aubry 1996; Erskine 1977; Falardeau et al. 1999; Hanski et al. 1996; Holmes and Sturges 1975; Keller et al. 2003; Kirk et al. 1996;

Lambert and Hannon 2000; Lent and Capen 1995; McLaren and McLaren 1981; Mossman et al. 1991; Schieck et al. 1995; Sinclair et al. 2003; Sweeney and Dijack 1985; Thompson and Capen 1988).

The Ovenbird is mostly associated with upland mesic stands that are rich in nutrients, but exceptions occur. It tends to prefer woodlands with moderate slopes. In Illinois, floodplain forests usually lack Ovenbirds, but some lowland forests support notable populations on second-level ridges above the floodplain. In Michigan, small populations occurred in forested swamp nearest a river, it avoided the next 2 bands of forested wetland, and significantly higher densities occurred in the outer band of upland forest. It was considered an upland species. In balsam fir–white cedar stands in eastern Quebec, it occurred both in riparian and nonriparian stands, but was significantly more abundant in nonriparian stands. It was also more frequent in nonriparian than riparian stands of balsam fir in Newfoundland. In Missouri, it was absent in mature riparian forest. In Wisconsin upland forests, it was associated with mesic stands and was the most abundant species. It was most abundant in stands of the more mesic half of the moisture gradient and very conspicuously increased in importance and density with increasing mesic conditions (Bond 1957; Campbell et al. 2001; Faanes and Andrew 1983; Flack 1976; Graber et al. 1983; Inman et al. 2002; Kirk et al. 1996; LaRue et al. 1995; Mossman and Hoffman 1989; Pagen et al. 2000; Robbins et al. 1989; Wenny et al. 1993; Whitaker and Montevecchi 1997). The Ovenbird occasionally occurs in treed swamps. In New Jersey, there was no significant difference in its abundance in upland oak-pine forests and hardwood swamps, and it was the most abundant species in both habitats. In other areas, it is equally abundant in upland xeric oak-hickory forests, mesic stands, and lowland deciduous forests (Chapman 1907; Morse 1989; Rich et al. 1994). In Newfoundland balsam fir stands, it was significantly more abundant in rich than poor stands. Observations were equally split between poor and rich sites in 40- and 80-year forests, but significantly more birds were seen in rich sites in 60-year-old stands (Thompson et al. 1999).

The Ovenbird may occur in almost all ages of forest, except for very young stands. It reaches its highest abundance in intermediate to mature stands and is least abundant in very early seral stages and old-growth forests. In Ontario white pine forests in the Canadian Shield in the Great Lakes–St. Lawrence Forest Region, it was more abundant in old-growth than mature stands, but not significantly. In mixed jack pine stands near White River, it was significantly more abundant in 40-100-year-old stands with a large component of jack pine than in stands 3-25 years old. It was 1 of 6 species that were indicators of mature forest. In the Boreal Forest Region of Ontario, it was rare in stands 12 years old and younger and common in stands 18-220 years old. In clear-cuts, it is significantly more abundant in stands 9-10 years old than those 4-5 years old, and abundance increases with increasing stand age until stands are at least intermediate aged. In aspen-birch stands, it is absent in the seedling-sapling stage, first appearing in the sapling-pole stage and increasing through to mature stands. It was absent in stands younger than 15 years. Similar relationships have been documented in pine and mixed stands. In Alberta aspen stands, its relative abundance in different age classes was 2.13 in young stands, 2.78 in mature stands, and 1.71 in old-growth stands. In Wisconsin, it was more than twice as common in climax stands as in pioneer stands. In Newfoundland balsam fir stands, it preferred stands 40 years old to those 60 or 80 years old, but possibly because there was a higher percentage of deciduous growth in the younger forests. In regenerating fields surrounded by forest in New Jersey, the Ovenbird was absent in fields

that had been regenerating for 10 and 20 years, but present in a 40-year-old field. In Quetico Park, its average importance values were 8 in early-successional stands (1-23 years), 28 in intermediate stands (67-73 years), 18 in mature stands (112 years), and 0 in old-growth stands. In Pennsylvania, it occurred in 36.4% of old-growth forests, 74.6% of forests state-wide and 82.7% of forests on the Appalachian Plateau. It had a negative old-growth affinity, probably because of its preference for heavy ground cover which was virtually absent in old-growth forest. It increased over a 30-year period in a New Hampshire forest. During this time, the forest changed from having a dense canopy and low shrub layer to having a more patchy canopy, a denser subcanopy, and a more sparse low shrub layer, which improved habitat (Apfelbaum and Haney 1985; Back 1979; Bond 1957; Capen 1979; Haney 1999; Hoffman 1989a; Holmes and Sherry 2001; Kirk et al. 1996, 2012; Lent and Capen 1995; Pagen et al. 2000; Schieck et al. 1995; Suthers 1988; Temple et al. 1979; Venier and Pearce 2005; Welsh 1993).

In North Dakota, the Ovenbird occurred in areas with 50-75% forest cover (75% was the maximum extent of forest cover) and in areas with 91-100% forest cover in New York. It showed a strong response to increasing forest cover and was the only species that had a sharper positive response in landscapes with more than 30% forest cover. It was absent where there was less than 20% tree cover within 100 m (Cunningham and Johnson 2016, 2019).

Numerous studies identified vegetation parameters correlated with Ovenbird abundance. The most consistently reported habitat parameters are canopy height of 16-22 m, 60-90% canopy closure, deep deciduous leaf litter, and sparse to moderate coverage by short shrubs. Less important vegetation parameters include total basal area (BA) particularly by larger trees, tree density, moss cover, downed woody material, density of snags larger than 20 cm DBH, increasing deciduous cover and decreasing coniferous cover, moderate slopes, herbaceous coverage and species diversity, shrub species diversity, and abundance of invertebrates in the leaf litter (Anderson and Shugart 1974; Askins et al. 1987; Beals 1960; Bushman and Therres 1988; Campbell et al. 2001; Collins et al. 1982; Falardeau et al. 1999; Gross in Bent 1953; Grundel and Pavlovic 2007a; Lynch 1987; Mossman and Hoffman 1989; Niemi and Pfannmuller 1988; Parker et al. 1999; Pérot and Villard 2009; Robbins et al. 1989; Schieck et al. 1995; Stauffer and Best 1980; Sweeney and Dijack 1985; Temple et al. 1979; Thompson and Capen 1979; Thompson et al. 1999; Van Horn and Donovan 1994; Wenny et al. 1993). In New Hampshire and Maine, it was positively correlated with the number of deciduous trees larger than 10 cm DBH, the total foliage density of coniferous trees larger than 10 cm DBH, and the total foliage volume of deciduous trees smaller than 2 cm DBH. It was negatively correlated with the number of coniferous trees larger than 10 cm DBH, the number of woody stems per ha, and the total foliage volume of both deciduous and coniferous trees 2-10 cm DBH (DeGraaf et al. 1998).

Some exceptions to these vegetation preferences have been documented. In Tennessee, the Ovenbird was found in forest stands with open canopy and subcanopy layers and a dense understorey. In Indiana, it was positively associated with tree density, but occurred in open stands with as few as 200 trees per ha. Some authors stated that the Ovenbird occurred in areas of dense shrub growth. It usually avoids areas of very high shrub density and may nest in areas that are devoid of woody vegetation in the understorey. In some cases, it was associated with increasing coniferous coverage rather than deciduous coverage. In Minnesota, it occurred where there was more than

50% coniferous tree coverage. Its association with coniferous coverage might be secondary because it consistently occurred in areas of mixed deciduous-coniferous cover. In Maryland, it was more abundant where coniferous ground cover and hemlock, deciduous, and short shrub coverage were high. In Iowa, its abundance was negatively correlated with herbaceous cover and abundance of snags (Anderson and Shugart 1974; Collins et al. 1982; Gates and Giffen 1991; Grundel and Pavlovic 2007a; Stauffer and Best 1980).

Habitats used by the Ovenbird in Maine and Minnesota were quite dissimilar. In Minnesota, it occupied areas with tall canopies, moderate coniferous cover, few small trees, and more large trees. In Maine, it was associated with high percent canopy cover, variable coniferous cover, and many trees in the smaller age classes (Collins 1983a).

In a Connecticut woodlot over a 59-year period, there was a progressive shift to larger trees, a sparser shrub layer, and a less diverse tree canopy dominated more by oaks and maples as a result of a decline in hemlock. The Ovenbird declined within the woodlot but remained stable throughout the state. Buchanan et al. (2016) considered it a hemlock associate and its decline may have been related to the decline of this tree. In Pennsylvania and New Jersey over a 15-year period, hemlock declined from 56% of the total basal area to 46% due to the hemlock woolly adelgid. The decline in hemlock resulted in an increase in deciduous understorey. The Ovenbird population increased in response to the loss of hemlock (Toenies et al. 2019).

In Missouri, the Ovenbird avoided streams and in New Brunswick its abundance was significantly lower near streams. Density increased with distance from edge and it demonstrated an avoidance reaction to streams (Parker et al. 1999; Wenny et al. 1993). In Maryland, Gates and Giffen (1991) found no evidence of stream avoidance by the Ovenbird. Avoidance of streams in some areas could potentially be related to vegetation characteristics, such as shrub density rather than actual stream avoidance.

The Ovenbird is an area-sensitive species, requiring forests much larger than its territory size. In contiguous forests near Quebec City, Ovenbird territories were aggregated, possibly in response to the clustered distribution of suitable ground cover (Bourque and Desrochers 2006). Similar findings were reported in Missouri, with territories clumped together and areas of apparently suitable habitat remaining unoccupied. The placement of clumped territories may vary annually, and may be a result of social interaction rather than habitat structure. The sociability of the species requires that forests be large enough to accommodate more than 1 pair, although single pairs occur within some woodlots (Van Horn and Donovan 1994). The size of forest required varies regionally, even within the province. Also, a distinction must be made between forests that merely contain Ovenbirds and those that support viable populations. Those residing in small forest fragments may be unpaired or have minimal reproductive success due to predation, parasitism, and low density of prey items. In the Ottawa area, Villard et al. (1993) studied the Ovenbird in woodlots 4.5-25.9 ha and found that pairing success was lower in fragments than in contiguous forest, but not significantly. It may inhabit small patches in this region. It is restricted to forests larger than 100 ha in Elgin County, but is one of the most common species where it is present. It is not found some years even at Springwater Forest, one of the largest and most mature forests in Elgin County (Lancaster et al. 2004). James (1984b) concluded that it required 70 ha or more of contiguous forest in Ontario. In the Region of Waterloo,

it was rare in woodlots 3-4 ha in area. It was more frequent in larger woodlands, but only 50-67% of forests 20-50 ha were occupied (Friesen et al. 1999a). In southern Ontario, its abundance was positively associated with woodlot size, amount of forest cover 100 m or further from edge, and amount of forest cover within 2 km. It was negatively correlated with the amount of regional forest cover. These relationships were not significant (Austen et al. 2001). Burke and Nol (1998, 2000) characterized the amount of forest required in Peterborough County and central Ontario to support a source population. High-quality habitat was not attained until fragments contained a minimum of 20 ha of core habitat (100 m from edge), or at least 80 ha in total. They concluded that it required forests larger than 500 ha to maintain populations. Smith et al. (2011) analyzed point count data for southern Ontario from the second atlas. The amount of forest in the surrounding landscape had an important and consistently positive effect and this was the most important variable for the Ovenbird at all scales examined. In the Ottawa area, its abundance was best predicted by the amount of surrounding forest cover and woodlot size. The amount of surrounding forest cover was a more important variable than patch size, although this was also important (Lee et al. 2002). These studies suggest that the Ovenbird will inhabit smaller woodlands when there is a greater percentage of forest cover. Elgin County has approximately 15.2% forest cover compared with 29.4% for Ottawa (Riley and Mohr 1994).

Forest size requirements for the Ovenbird have been reported from other areas. In South Carolina, its probability of detection was 7% in 0.5-ha and 1.0-ha deciduous forests, 8% in 2.5-ha forests, 9% in 5.0-ha forests and 12% in 10.0-ha forests. The deciduous stands were all surrounded by pine forest. The probability of detection was 0% in all similarly sized forests surrounded by fields and shrubs (Kilgo et al. 1997). In aspen woodlands surrounded by grassland in North Dakota, its probability of occurrence was 45% in 1-ha woodlots, 60% in 5-ha woodlots, 65% in 10-ha woodlots, 80% in 100-ha woodlots, and 90% in 1,000-ha woodlots. It was predicted to reach 50% probability of occurrence in aspen groves 8-20 ha and should almost always be found in larger stands (Grant and Berkey 1999). In the mid-Atlantic states, the maximum probability of detection was reached at 450 ha, the probability was reduced to 50% at 6.0 ha, and the 3 smallest woodlots in which it was detected at least twice were 2.5, 1.2, and 0.8 ha. It was estimated that 2,650 ha were required to maintain a viable population, the highest for all species studied (Robbins 1979; Robbins et al. 1989). Hayden et al. (1985) considered the 2,650 ha to be an overestimate and concluded that 341 ha was the minimum area requirement for it in Maryland. Estimates reported from other areas were 4.0 ha in New Jersey and 24 ha in Illinois (Bushman and Therres 1988). In Maryland, Lynch (1987) reported its probability of occurrence at 10% in 1-ha woodlots, 25% in 3.2 ha, 41% in 10 ha, 60% in 32 ha, 65% in 100 ha, 69% in 320 ha, and 63% at 3,300 ha. In Wisconsin, its frequency of occurrence in differently sized woods was 4.0% in 6.1-14 ha, 20.0% in 16.2-32.4 ha, and 29.5% in woodlands larger than 32.4 ha. The Ovenbird was 45% more common in larger forests. In pioneer stands, it was more abundant in larger patches, but this effect was less pronounced in more climax stands (Bond 1957). In South Dakota, it was absent in small tableland woodlots 0.7-3.5 ha but was present in large riparian forests (Gentry et al. 2006). In Rhode Island red maple stands surrounded by upland forests, it occurred in low density within the swamp and there was no relationship between patch size and abundance. This may have been because the landscape was 60% forest and area sensitivity had broken down (Golet et al. 2001). In Iowa, the minimum width of wooded riparian strip that supported it was 175

m (Stauffer and Best 1980). In Alberta, it inhabited riparian buffer strips 100 and 200 m wide, but not those 20, 40, or 80 m wide (Lambert and Hannon 2000). In Missouri, it occurred in wide (400-530 m) riparian strips, but not in narrow (55-95 m) strips (Porneluzi et al. 2020). In Pennsylvania, Porneluzi et al. (2020) suggested that 1,000 ha may be needed in areas of lower density and that the presence of a forest larger than 5,000 ha was necessary to ensure viable populations in nearby woods. The amount of regional forest was considered important to Ovenbird abundance in Connecticut, Maryland, and the mid-Atlantic states (Askins et al. 1987; Lynch 1987; Robbins et al. 1989), but not in Michigan (Crozier and Niemi 2003). Robinson (1992) found the Ovenbird in woodlots as small as 14 ha in southern Illinois. Woodlots this small in Missouri, central Illinois, and the eastern United States generally lack Ovenbirds. He suggested that the Illinois woodlots might be attractive because there are no large (500 ha) upland forests within a 200-km radius. McShea and Rappole (1997) determined that song rates were higher in larger forests and where the Ovenbird was more abundant. Survey results might underestimate the abundance of the Ovenbird in smaller forest fragments.

Many authors consider the Ovenbird a forest-interior species that avoids forest edge. Freemark and Collins (1992) assumed that it was a forest-interior species because it was area sensitive but Villard (1998) pointed out that there was no information to establish a linkage between area sensitivity and edge avoidance. Mazerolle and Hobson (2003) cautioned that early morning surveys may falsely indicate that Ovenbirds are avoiding edge. During early morning, males spend most of their time defending their territories, with foraging activities occurring later in the day. Males with territories along edges spend the early morning defending the interior portion of their territory because there are no neighbours on the edge side. Edge use varied with the time of day, with the mean time of observation in edge habitat occurring at 1139 hours compared with 0936 hours in the interior. Studies conducted in early morning only are likely to underestimate usage of forest edge habitat. A few studies determined that the density of nesting Ovenbirds is greater in forest interior than edge and concluded that this is due to edge avoidance (Kroodsma 1984; Wenny et al. 1993). In Vermont, densities of Ovenbirds were 40% lower at edges than in forest interior. The proportion of area defended as territories did not differ between edge (39.6%) and interior (36.7%). Ortega and Capen (1999) concluded that lower density near edges was related to variation in territory size and that it did not actively avoid forest edges. In New Hampshire, it was equally abundant at edges of clear-cuts and distant from edge (King et al. 1997).

The Ovenbird is not an obligate forest-interior species. There are occasions when it exhibits an aversion to edge, when it appears indifferent to edges, and when it actively selects edge and avoids forest interior. In Michigan, Hann (1937) did not find any nests closer than 20 m from forest edge. In Peterborough County, the mean distance of nests from forest edge was 125.5 m in forest fragments compared with 81.9 m for random sites. In larger forests, nests averaged 250.8 m from edge compared with 192.1 m for random sites. Burke and Nol (1998) concluded that random sites within small tracts contained little core area and had few sites available for nesting at distances of 190 m from edge. Smith et al. (2011) found that increasing amounts of core area had a stronger positive effect when the amount of forest was low. It is likely that Ovenbirds nesting in small patches or in areas with limited forest cover show a greater tendency to avoid edge. Edges may contain higher densities of predators and cowbirds and lower densities of invertebrate prey. Edge avoidance is more likely in forests within agricultural and urban landscapes than where forests are fragmented

by forestry and natural features such as wetlands, water bodies, and burns. In Saskatchewan, Mazerolle and Hobson (2003) studied Ovenbirds in relation to forest edge in an agricultural landscape. Their results were the opposite of those of Burke and Nol (1998, 2000). More than 20% of Ovenbird observations were less than 25 m from edge and activity centres were closer to edge than randomly derived activity centres. Forty-seven percent of sightings were less than 50 m from edge, and this habitat was only 33.3% of home ranges. Similar results were obtained when edge was defined as 25 m. Nests tended to be closer to edge (44 m) than the mean distance of random points (58 m). In this study area, forest edges had the greatest biomass of insect larvae and arthropod abundance was not correlated with leaf litter or soil moisture, which increased with distance from edge. Burke and Nol (2000) found that invertebrate abundance was low in the edges of the forests that they studied. Differences in the abundance of food relative to edge might partially explain the apparent preference of edge by Ovenbirds in Saskatchewan and edge avoidance in Ontario. In Saskatchewan, there was no evidence that edge habitats were lower in quality than forest interior, but edge habitat was inferior in Ontario. In Alberta, it tended to avoid edges created by clear-cuts but the response was not significant (Villard et al. 2007). In Wisconsin, it tended to nest in higher density near forest clear-cut edges (Flaspohler et al. 2001). The highest nesting density reported for the Ovenbird in southern Illinois was at the edge of a pine plantation (Graber et al. 1983). In a 33-year Pennsylvania study, all territories were on edge and Ovenbirds could not be enticed into forest interior using broadcasts of their calls. There were 14 territories each year, almost always at the same location. The mean litter depth in territories was only 1.64 cm, less than found on any territories in Ontario. It appeared to be avoiding the eastern chipmunk, a known nest predator. Chipmunks were found in 97% of off-territory surveys and it took an average of 2.1 minutes to detect one. On territories, chipmunks were found on only 14% of surveys and it took an average of 7.2 minutes to detect one. One territory was occupied for 2 years and abandoned the third. No chipmunks were detected on it the first 2 years, but chipmunks were present the third year (Morton 2005). In a 15-year study in New York, nests were in locations with significantly lower chipmunk populations (Emmering et al. 2018). It appears as though the Ovenbird does not respond to edge per se, but instead selects areas with a greater abundance of food and low densities of predators and possibly brood parasites. In individual woodlands, it may be more common in the interior or at edges, or be uniformly distributed. Edge avoidance is most likely to occur in agricultural landscapes and in small forest patches due to lower food abundance and higher densities of predators and parasites in edge.

All Ontario nests were on the ground, mostly in areas with deep dead-leaf ground cover. Most nests (50.0%) were among ferns, grasses, and herbaceous plants; 39.1% were at bases of trees, saplings, shrubs, and stumps, often concealed by overhead branches; 7.3% were under fallen branches; 2.7% were in moss hummocks; and 0.9% were under arched tree roots. Most nests were hidden in the surrounding vegetation, but 3 were exposed. Nests were both in depressions in the ground and on level ground (Peck and James 1987). In Peterborough County, nest sites were on mid- to upper slopes and were characterized by a low percentage of bare ground (less than 7%), moderate herbaceous and sapling cover, low seedling and shrub coverage, high canopy cover, deep leaf litter, moderate slopes, and distances of approximately 3 m from the nearest tree (Burke and Nol 1998).

Although nests are rarely closer than 20 m to a forest edge, most are in or near openings in forests. In Michigan, most were less than 10 m from an internal roadway, creek bed, lane, or open spaces within the woods. The average distance of nests from open spaces was 4.4 m. The 7 furthest were 12-20 m away from an edge or opening. If these 7 were omitted from the calculation, the average distance from an opening was 2.8 m. All nests got a little sunshine each day, albeit a very small amount. Nests have been reported in and near openings in Ontario, Quebec, British Columbia, New Jersey, and throughout much of its range. The Ovenbird avoids areas of dense shrubbery for nesting, but nests may be at the base of herbaceous vegetation, saplings, or trees. They may also be hidden under clubmosses, ferns, and low-hanging branches. A high proportion is built in open areas among leaves. All reported nests except one were on the ground; the exception was in the hollow of a large pine log (Beals 1960; Campbell et al. 2001; Chapman 1907; Gross in Bent 1953; Hann 1937; Maciula 1960; Mousley 1916a, 1926; Porneluzi et al. 2020).

Males begin defending a territory as soon as they arrive in spring. When the nest site is selected, territory boundaries undergo some changes, shifting the centre of interest from the male's favourite singing perch to the nest, and there may be an initial shift when females arrive. There is little change in the territory thereafter unless later nests are built. In some areas, there is a buffer between territories and foraging may occur in these undefended areas. In other populations, territories are contiguous and foraging occurs within the territory. Territorial boundaries are usually respected, but territories may overlap in some cases. In Saskatchewan, territories overlapped by 20% in contiguous forest and 34% in forest fragments. During the premating, mating, incubation, and nestling periods, the area used by the male in a day was almost as large as the entire territory. During the nest-building and egg-laying periods, the male uses approximately half the territory on a daily basis. Territory size is influenced by the type of forest community, density of birds, whether the male is paired, whether the territory is on forest edge or in forest interior, whether the territory is in contiguous or fragmented forest, and food availability. Older and larger males have larger territories than those that are younger or smaller. The higher the habitat quality and the more abundant the food resources, the smaller territories were. Habitat quality is also linked to food availability, so food abundance may be the most important criterion in defining territory size. Where birds can forage off the territory, the linkage between food availability and territory size is weak (Drapeau and Darveau in Gauthier and Aubry 1996; Hann 1937; Mazerolle and Hobson 2004; Ortega and Capen 1999; Smith and Shugart 1987; Stenger 1958; Stenger and Falls 1959; Van Horn and Donovan 1994; Zack and Falls 1979). In Vermont, ground cover was significantly less in territories (4.3%) than in unoccupied areas (4.8%). Territory size decreased with decreasing ground cover. Proximity to a road was more important in defining territory size than habitat, suggesting an effect on habitat quality that was independent of vegetation structure. Edge territories were significantly larger (0.53 ha) than those in forest interior (0.39 ha). Overall territory size ranged from 0.20 to 0.69 ha (Ortega and Capen 1999). In Tennessee, occupied territories had a higher percentage of canopy closure, the largest tree classes, and a lower percentage of ground cover, shrub cover, and conifer BA than unoccupied areas (Smith and Shugart 1987). In Quebec, territory boundaries were most often associated with fern cover, vegetation-covered rocks, and shrub diversity, suggesting that these served as landmarks rather than resources (Porneluzi et al. 2020). Territories may contain habitats that are not used. A Pennsylvania site had several areas dominated by large boulders which likely reduced the area of

the forest floor that was suitable for foraging. The average territory size was 1.0 ha in rocky areas compared with 0.5 ha in other areas (Bernard et al. 2001). In Algonquin Park, several territories had open, unforested areas within them that were not used (Stenger 1958).

Five studies examined territories of Ovenbirds in Algonquin Park (Martin 1960; Stenger 1958; Stenger and Falls 1959; Zack and Falls 1975, 1979). In 1 study, most territories were separated by about 18 m and 30 m in sugar maple stands where territories were larger. Some territories were contiguous or overlapped. Territory depth extended from the ground to 8-12 m above ground, which corresponded to the height of the lowest branches in the canopy. These were often used as singing perches. In 1 area, singing perches were scattered throughout the territory with no particular concentrations, and no song posts were used repeatedly. In another area, song perches were patchily distributed within the territory and often occurred in clusters. The density of song perches decreased toward the periphery of the territory. Nests are within the territory, but may be at its edge. In 1 study, territories were 0.02-1.6 ha (average 0.23 ha). Another study found that territory size ranged from 0.3 to 1.7 ha. Territory sizes differed by forest type and averaged 0.7 ha in aspen, 0.9 ha in conifers-birch, 1.0 ha in mixed woods, and 1.3 in sugar maple, suggesting that aspen stands are superior habitat. The territory sizes of 2 males were smaller when they were unmated than when they became mated. The territory location did not change when birds renested. When renesting, 2 males increased the size of their territory and one decreased it: 1.1 to 1.5 ha, 0.6 to 1.4 ha, and 0.6 to 0.4 ha. Territory sizes of first and second nesting attempts for individual males in different habitats were 0.61 and 0.45 ha in aspen, 0.61 and 1.38 ha in mixed forest, and 1.09 and 1.46 ha in mixed woods. Mean territory sizes in nonbudworm years were 0.83 ha (range 0.5-1.1 ha) compared with 0.48 ha in budworm years (range 0.4-0.6 ha) for first nests, and 1.4-1.5 ha in nonbudworm years compared with 0.3-0.5 ha in budworm years for second nests. In nonbudworm years, third nests were not attempted; territory sizes were 0.5-0.6 ha in budworm years for third nests. During budworm years, there was no significant difference in territory size between first and replacement nests, but territory sizes increased significantly for replacement nests in nonbudworm years. During budworm years, territories were more densely packed in addition to being smaller. The average distance between territory centres was 92.3 m in budworm years and 108.6 m in nonbudworm years. At 1 site, the mean area used for foraging was 6,346 m^2 (range 4,600-8,450 m^2), the mean territory size was 5,146 m^2 (range 2,454-8,154 m^2), and the 95% territory size was 3,649 m^2 (range 1,611-5,592 m^2). The mean percent of the foraging search path that was outside the territory was 31.43% (range 14.64-61.66%) and 39.23% (range 18.15-67.90%) was outside the 95% core territory area. Near Lake Nipigon, 9 territories averaged 0.77 ha (range 0.44-1.21 ha; Kendeigh 1947).

In Saskatchewan, the territory size was 1.41 ha in forest fragments and 1.28 ha in contiguous forests. The mean home range size of individuals with territories abutting an edge was 1.95 ha (Mazerolle and Hobson 2003, 2004). In Michigan, territory size was 0.2-1.8 ha, average territory size was 0.26 ha in Wisconsin, average territory size was 0.65 ha in New York (range 0.10-1.21 ha), 13 Illinois territories were 0.5-2.2 ha (averages 1.0 and 1.7 ha over 2 years), 23 Tennessee territories averaged 0.27 ha (range 0.13-0.38 ha), Missouri territories were 0.88-1.40 ha, and Quebec territories averaged 0.27 ha with a range of 0.2-1.8 ha (Drapeau and Darveau in Gauthier and Aubry 1996; Graber et al. 1983; Hann 1937; Kendeigh 1945; Loss and Blair 2011; Smith and Shugart 1987; Van Horn and Donovan 1994). In Quebec sugar maple stands, territories were larger (0.60 ha) in forests

that had declined than in healthy stands (0.34 ha; DesGranges et al. 1987). In response to timber harvesting in Alberta, territory sizes decreased in residual adjacent habitat. In 100-m wide residual strips, territory size decreased from 1.76 to 1.45 ha after harvest. Territories decreased from 1.60 to 1.36 ha in 200-m wide strips (Lambert and Hannon 2000).

Natal philopatry rates appear to be low. In Michigan, 1 of 68 young (1.5%) returned to nest in its natal area. It established a territory 300 m from its natal nest and mated with the female that had been there the year before (Hann 1937).

Adult site fidelity is fairly high. Schlossberg (2009) calculated site fidelity at 32% from a sample of 908 birds from 8 studies. The rate of adult return varies depending upon age of the bird, mating success, and habitat quality. In New Brunswick over a 9-year period, 322 of 525 males (61.3%) returned in at least one of the following breeding seasons (Haché et al. 2016). In Michigan, 24 of 46 adults (54.5%) returned, including 52.4% of females and 56.5% of males. Both sexes returned to their previous territory, if possible. Old males have a good chance of obtaining their former territories either by arriving early or driving away other males. Over several years of study, only 1 male moved its territory. It occupied an adjacent territory that perhaps overlapped the old one. Females go first to their old territory. If the male there already has a mate, she moves to an adjacent territory. Eight females returning to their original territory had nests 2.6-48 m (average 19.2 m) from their previous nest site (Hann 1937). In a 21-year study in Pennsylvania, no Ovenbirds moved between 2 study sites that were 1.5 km apart. Bernard et al. (2011) concluded that long-term dispersal by older birds was rare and that failure to return was probably a result of death. Return rates at the 2 sites were 72.9% and 57.4%. There was no significant difference in return rates for birds that had nested successfully or unsuccessfully the previous year. Despite high rates of territory fidelity, territories tended to drift apart. The distance from the first territory increased each year that a bird returned but the direction of the shift was not constant. Shift distances were different among age classes, with first-year shifts greater than subsequent years. The mean shift distance from centre to centre of territories was 41.6 and 76.5 m for the 2 sites. Nearly all shifts between years were less than a territory width. Birds moved a mean distance of 65.5 m from their first-year territory. Thirty-seven lifetime shifts were beyond 100 m with the furthest 302.8 m. The high site fidelity at these Pennsylvania study areas may have been because Ovenbirds were in high quality, homogenous habitat. Another Pennsylvania study determined that annual return rates for males over a 2-year period were 67% and 62%, with 85% being after-second-year birds (Morton 2009). In Missouri, males that were paired but failed to raise young rarely returned (9.1%), but the return rates of unpaired males (41%) and paired males that were successful (54%) did not differ from each other. Return rates were similar in both fragmented and unfragmented landscapes. Of 47 returning males, 30 (64%) had territories with more than 50% overlap with the previous year's territory, and 12 (26%) were adjacent to or overlapped with less than 50% of the previous territory. The remaining 5 (10%) were not adjacent, but were separated by less than 200 m. Unpaired males returned to essentially the same location the next year. Upon returning, previously unpaired males achieved a rate of pairing success (73%) that did not differ from previously successful males (80%). Territories that were successful were more likely to support successful pairs the subsequent year and unsuccessful territories were more likely to be unoccupied or be settled by an unpaired male the following year (Porneluzi 2003; Porneluzi and Faaborg 1999). In Saskatchewan, 41.0% of 398 males returned to the same site at least once. Return rates were 44.4%

in contiguous forest, 43.1% in forest fragments within a largely forested landscape, and 35.1% in forest fragments within an agricultural landscape. There was no significant difference in return rates among the 3 types of forests, but Ovenbirds in small fragments in agricultural landscapes had lower return and survival rates. The probability of a male returning was dependent upon its pairing success the previous year. Only 11% of unpaired males returned compared with 41% of paired males, but there was no significant difference in the return rates of males that were successful or unsuccessful the previous year. Significantly more yearling males were recruited into forest fragments in agricultural settings (90%) than in fragments in forested landscapes (73%) and contiguous forests (70%). Eighty-eight percent of returning males relocated less than 100 m from their previous territory. There were no significant differences in distances moved by returning males in different landscapes or by successful or unsuccessful birds. Increased immigration into small agricultural woodlots seemed to compensate for the low return rate to these fragments. The larger proportion of older birds in contiguous forest could be due to floaters obtaining territories as they get older rather than from failed breeders dispersing from small agricultural woodlots to larger forests (Bayne and Hobson 2002a). Villard et al. (1992, 1995) studied numerous woodlots near Ottawa and found that this region constituted a metapopulation for the Ovenbird. Local extinctions and recolonizations occurred within individual woodlots but the total number of occupied woodlots remained fairly constant. Patches that experienced population turnovers were smaller than those where it was continuously present, but were not significantly larger than patches where Ovenbirds were never recorded. In New Brunswick where single-tree selection removed 30-40% of the BA of trees, the return rate of males was 69.1%. Return rates were similar in treatment and control plots during the first year after treatment, but were 15.8% and 12.7% lower on treatment plots 2 and 3 years postharvest, respectively. A lower proportion of after-second-year birds returned to treatment than control plots suggesting that the cut plots were of inferior quality. Dispersal movements were short with only 2 males moving more than 100 m from their previous territory. The proportion of first-year birds breeding in control and treatment plots was similar suggesting that they were not forced to breed in suboptimal habitat (Haché and Villard 2010). In New Hampshire, 46% of adults fitted with geolocators returned, similar to the return rate of 53% of adults without geolocators (Hallsworth et al. 2013). In New Jersey, only 3 of 172 adults (1.7%) returned. This was marginal habitat that consisted of a 40-year-old field that had regenerated with second growth (Suthers 1988). In Illinois, only 16.7% of adults returned, indicating a high rate of turnover. These were isolated fragments distant from potential source woodlands where there was a high predation rate. This area was poor habitat (Robinson 1992).

Limiting Factors

Eggs have been found in Ontario nests from the last week of May until the end of July, with most present in the first 3 weeks of June (Peck and James 1987). In Algonquin Park, most eggs hatched between 26 and 28 June and the maximum biomass of invertebrates occurred during the first half of July during the nestling period (Stenger 1958). Nests there are under construction from mid-May until early July, eggs are present from late May to late July but chiefly in June, nestlings are present from early June to early August, and dependent fledglings occur from late June to mid-August. July and August nests are probably replacement nests (Tozer 2012).

The female begins building the nest 1-6 days after she arrives on the territory. The time required to build first nests is 5 days. Successive nests may be completed in 4 days or less. The first egg is laid 1-3 days after the nest is complete. Eggs are laid at the rate of 1 a day. Incubation may begin in the afternoon or evening before the last egg is laid or as late as the day after the last egg is laid. The incubation period at 5 Ontario nests was 11-12 days. In Michigan, the incubation period ranged from 11 days 12 hours to 14 days (average 12 days 5.6 hours). All eggs of a clutch have approximately the same incubation period and there is no difference in the incubation period in cool or warm weather or in parasitized or unparasitized nests. Young may leave the nest in an emergency when they are 6 days old, but typically remain in the nest longer. In Michigan, the average nestling period was 7 days 22.5 hours (range 6 days 13 hours to 8 days 12 hours). In North Carolina, the average nestling period was 7.6 days and was 8.0, 7.8, and 7.0 days over 3 years. Larger broods fledged sooner than smaller broods, with averages of 8 days for 2-nestling broods, 8.1 days for 3 nestlings, 7.7 days for 4 nestlings, and 7.25 days for 5 nestlings. In Minnesota, most young fledged when they were 8 days old, but some fledged on day 7. Abundant food resulted in a shorter nestling period. Increased temperatures in May and June corresponded to a decrease in the nestling period, although this relationship was weak. The nestling period is as long as 10 days in some areas. The short nestling period may be an adaptation to reduce predation risk. Predation rates during the nestling period are double those during incubation. In North Carolina and Tennessee, the average length of the nesting cycle was 31.4 days for first broods and 30.1 days for renesting and second broods. Averages were 7.1 days for nest building (5.8 days for later nests), 2.5 days for egg laying, 13.2 days for incubation, and 8.7 days for the nestling period (Chapman 1907; Gross in Bent 1953; Hann 1937; Harrison 1984; Mousley 1926; Nice 1931; Peck and James 1987; Stodola et al. 2010a; Van Horn and Donovan 1994).

The Ovenbird typically raises a single brood, but there are rare records of second broods, including one from Algonquin Park during a spruce budworm outbreak. Two second broods were reported in Michigan and 3 were documented in Tennessee. A New York population appeared to raise 2 broods. Renesting occurs regularly if a nest is disarranged or lost. The probability of renesting in Tennessee and North Carolina was 75% at the nest construction stage, 67% at the egg stage, and 70% at the nestling stage. The distance of 15 replacement nests from the first nest averaged 42 m in Michigan (range 18-66 m). In Ontario, clutches of 2-6 eggs have been reported, with 4 and 5 eggs most frequent (mean 4.3 eggs). In Algonquin Park, both first and replacement clutches averaged significantly larger in budworm than in nonbudworm years. During budworm years, first clutches averaged 5.0 eggs compared with 4.2 eggs in nonbudworm years; replacement clutches averaged 4.5 and 3.7 eggs, respectively. In budworm years, no clutches contained fewer than 4 eggs and 1 female laid 5 eggs in her third nesting attempt. In nonbudworm years, replacement clutches all contained 3 or 4 eggs. Throughout its range, the Ovenbird lays 3-6 eggs, but mostly 4 or 5. First nests typically have 5 eggs; later nests have 3-5 eggs. In Michigan, all 3-egg clutches and all but a single 4-egg clutch were laid by females that had previously laid a clutch. The maximum number of eggs laid by an individual bird in a season was 10 eggs (Chapman 1907; Gross in Bent 1953; Hann 1937; Kendeigh 1945; Peck and James 1998a; Podolsky et al. 2007; Zach and Falls 1975, 1976a).

The age of first breeding is 1 year. Birds nest every year thereafter if they can find a mate. The sex ratio is male biased so there are unpaired males in all populations, even within contiguous forest. One unpaired Illinois male defended 2 territories 200 m apart. The mating system is typically

monogamous, but rare cases of bigamy and polyandry have been reported. If an adult receives no fledglings to care for or loses them, it may remate if it is not too late in the season. Pairs usually do not remate in subsequent years, but this happens occasionally. Remating occurs only if both birds return to the same territory and another female has not mated with the male by the time the original female arrives (Hann 1937, 1940; King et al. 2000; Robinson 1992; Van Horn and Donovan 1994; Villard et al. 1993).

The Ovenbird forages by walking on the ground, picking food from the substrate, and hunting among dead leaves. Most food is obtained in the leaf litter on the forest floor. It does not scratch with its feet, but occasionally turns over a leaf with its bill. It gleans some insects from low ground vegetation or from sides of decaying logs. In Vermont, 90% of prey attacks were by gleaning and 10% were aerial. Foraging substrates were 77.5% ground, 2.5% foliage, 2.5% air, 2.5% tree trunk, and 1.0% branch. Over 2 years in Algonquin Park, only once was one observed attempting to feed in a tree, and it was extremely awkward at this. During a spruce budworm outbreak in the same area, it frequently fed in infested white spruce and balsam fir, taking larvae, pupae, and adults. More than 100 observations of arboreal feeding were made. It searched in small conifers that could be reached from the ground and also along the main branches of larger trees. Spruce budworm moths that it flushed were often pursued and captured aerially. In Algonquin Park, the distribution of prey was patchy and foraging sites contained significantly more food than areas that were not searched. The Ovenbird is responsive to the distribution of its food supply and concentrates searches in areas of high food abundance. It systematically forages along pathways, avoiding areas that have already been searched. Areas of high prey density are remembered, and initial foraging bouts on subsequent days focus on sites that previously supported abundant prey. In Tennessee, prey abundance was correlated with percent canopy cover and density of trees 15.3 cm DBH and larger, and negatively correlated with the density of shrubs, density of trees 2.5-7.5 cm DBH, and the BA of conifers. Stands dominated by larger trees with a closed canopy and few shrubs in the understorey supported the greatest abundance of prey. The Ovenbird usually takes larger prey in preference to smaller prey, but size selection is less important with familiar prey. The close relationship between prey density and territory size in some populations suggests that food supply limits the size of the breeding population in some areas (Lent and Capen 1995; Morse 1989; Stenger 1958; Smith and Shugart 1987; Zach and Falls 1975, 1976b, 1976c, 1979). Burke and Nol (2000) concluded that food availability was probably a limiting factor in small woodlands in central Ontario.

Stomachs of 5 nestlings in Algonquin Park contained 35.4% caterpillars, 17.3% unidentified larvae, 15.4% weevils, 12.3% snails, 9.2% lepidopteran adults, 10.8% unidentified beetles, 6.1% fly larvae, 1.5% flies, and 1.5% bugs. In Michigan, the food brought to young nestlings consisted of green and brown geometer moth larvae and small earthworms. As the young grew, adult insects were added to their diet, including crane flies, moths, ants, and beetles. Nestlings have eaten spruce budworm larvae, click beetles, and fireflies. In Ohio, there was little evidence that fledglings adopted a frugivorous diet and they appeared to eat a variety of arthropods. In Algonquin Park, the Ovenbird exhibited a low preference for eating ants. Several young collected a few days after they left the nest had a diet similar to that of the adults (Hann 1937; Mousley 1926; Stenger 1958; Zach and Falls 1975, 1979).

A sample of 98 adult stomachs collected over an 11-year period in Algonquin Park consisted, by weight, of 24.0% unidentified larvae, 20.7% ground beetles, 10.7% unidentified beetles, 19.9% weevils, 12.3% ants, 6.1% spiders, and 4.4% miscellaneous beetles. Other items that constituted less than 5% of the diet included rove beetles, beetle larvae, fly larvae, snails, millipedes, hymenopterans other than ants, flies, bugs, and lepidopteran and fly pupae. The major invertebrate groups in the diet occurred in similar proportions as the litter samples from the forest floor. Some soil invertebrates were eaten less than their abundance, but these were subsurface species that were not generally available to Ovenbirds. There was no selectivity for food items from the forest floor. The diet varied annually, providing further evidence for lack of selectivity. Caterpillars occurred in the diet in greater proportion than they occurred in leaf litter indicating that some were gleaned from trees, that there is selectivity for caterpillars, or that an increased number occur on the ground during the shortest period of greatest abundance. Near Lake Nipigon, the diet of 8 adults included 39.0% beetles (8.5% ground beetles, 8.2% click beetles, 4.8% scarab beetles, 0.4% weevils, and 17.2% unidentified). Hymenopterans were second in abundance at 19.4%, including 9.4% ants, 5.0% sawflies, 1.1% ichneumonid wasps, a parasitic wasp, and unidentified species. Spiders were third in abundance (11.4%), followed by flies (fungus gnats and marsh flies) at 5.1%, 1.9% harvestmen, 0.1% lacewings, and 5.4% unidentified invertebrates. In Quebec sugar maple forests, 93% of food items were beetles and a high proportion of these were brown leaf weevils. Other items included slugs, centipedes, earthworms, aphids, crickets, mosquitoes, and black flies. The Ovenbird does not exhibit a strong vagrancy response to outbreaks of the spruce budworm. When an outbreak occurred in Algonquin Park, food supply remained high after 15 July, territories were smaller and more densely packed, and there was a greater tendency to replace lost nests. A laboratory study demonstrated that it fed both on early and late-instar gypsy moth larvae and that it was more likely to feed on larger larvae. Four birds collected in Maine during a spruce budworm outbreak had eaten 14% budworm larvae and pupae by volume (DesGranges et al. 1987; Gross in Bent 1953; Hann 1937; Kendeigh 1947; Mitchell 1952; Mousley 1926; Patten and Burger 1998; Stenger 1958; Vitz and Rodewald 2012; Whelan et al. 1989; Zach and Falls 1975, 1979). The Ovenbird responds positively to spruce budworm outbreaks and may increase its population slightly (Morris et al. 1958; Venier et al. 2009).

The Ovenbird is a common host of the Brown-headed Cowbird. It typically accepts cowbird eggs, but occasionally abandons the nest and builds a replacement nest. As many as 7 or 8 cowbird eggs have been found in a single Ovenbird nest, but usually only 1 or 2 cowbird eggs are laid in a nest. Early nests are parasitized more frequently than later nests due to the cowbird's early laying period and the presence of more potential hosts later on. The female cowbird often removes an Ovenbird egg after laying her own egg. Parasitized nests contain fewer Ovenbird eggs than unparasitized nests: 2.7 compared with 4.1 eggs in Massachusetts, and 3.0 compared with 4.8 eggs in Minnesota. In Michigan, 18% of Ovenbird eggs were lost due to removal by cowbirds. Some nests were deserted and replaced resulting in a net loss of 13.5% of eggs. The incubation periods of the cowbird and Ovenbird are similar. The cowbird does not have a significant advantage by hatching earlier but a single cowbird nestling consumes as much food as 2 Ovenbird nestlings. There is no evidence to suggest that Ovenbird nestlings starve, and a high proportion of nests fledge both Ovenbirds and cowbirds. One Michigan nest fledged 2 cowbirds and 4 Ovenbirds, and nests with 2 cowbirds fared as well as those with only one. Due to egg removal and loss of some young from

competition with cowbirds, parasitized nests fledge fewer Ovenbirds than unparasitized nests: 1.7 compared with 4.1 fledglings in central Ontario, 2.4 compared with 3.8 fledglings in Massachusetts, and 2.5 compared with 4.4 fledglings in Minnesota. In central Ontario, 67% of parasitized nests produced at least 1 Ovenbird fledgling. The cowbird has a longer nestling period than the Ovenbird, remaining in the nest an additional 1-2 days. The host parents continue to feed the cowbird nestling until it leaves the nest. Of 40 cowbird eggs laid in Ovenbird nests in Michigan, 22 hatched, 10 fledged, and only 5 left the woods. Cowbird survival from egg laying to independence was 12.5% compared with 24.2% for the Ovenbird. In Minnesota, 1 fledgling from a parasitized nest and fledglings from unparasitized nests were radiotracked. The fledgling from the parasitized nest died 26 days after fledging and showed no signs of predation but its stomach was empty. All fledglings recovered from nonparasitized nests had signs of predation and their stomachs contained food. An adult was observed accompanying the fledgling from the parasitized nest on 33.3% of observations compared with 68% of observations for fledglings from nonparasitized nests. It was suggested that parasitism could affect survival of fledglings because of parents spending additional time feeding cowbird fledglings (Burke and Nol 2000; Hann 1937, 1947; Harrison 1984; Hersek et al. 2002; Lowther 1985, 1997; Peterson et al. 2012; Robinson 1992).

Cowbird parasitism rates on the Ovenbird range from 0% to 100%. The rate of parasitism depends upon local abundance of the cowbird and landscape and forest-size characteristics. Parasitism rates are higher in agricultural than forested landscapes and in smaller than larger woodlands. Parasitism rates frequently approach 0 in contiguous forest. In Ontario, 34 of 298 nests (11.4%) were parasitized, comparable to the 10% rate reported in Quebec. In Manitoba, Saskatchewan, Alberta, and the Northwest Territories combined, 36.8% of nests were parasitized. Parasitism rates in fragmented landscapes include 72% in Missouri, 40% in Illinois, 19% in Wisconsin and Minnesota, 29% in Massachusetts, 17% in Saskatchewan, 80% in Wisconsin, 52% in Michigan, 0% in Georgia and South Carolina where no ground-nesting species were parasitized, 33% in Connecticut, 36% in Ohio, and 100% in Iowa. In Missouri, 32 of 65 nests (49.2%) were parasitized in 890-ha and 1,146-ha forests, but the dominant cover in the larger landscape was not described. In 3 Missouri woodlots 575-1,146 ha, 50 of 94 nests (53.2%) were parasitized. Parasitism rates reported in forested landscapes include 6.1% in Minnesota, 4% in Wisconsin and Minnesota, 1.6% and 5.0% in Minnesota, 4% in Missouri, and 0% in Ontario, New Brunswick, North Carolina, Minnesota, Tennessee, New Hampshire, and Saskatchewan (Brittingham and Temple 1996; Burke and Nol 2000; Drapeau and Darveau in Gauthier and Aubry 1996; Gross in Bent 1953; Hann 1937; Hanski et al. 1996; Harrison 1984; Hersek et al. 2002; Jenkins and Faaborg 2016; Jenkins et al. 2016; Kilgo and Mossman 2003; Manolis et al. 2002; Peck and James 1998a; Pérot and Villard 2009; Peterson et al. 2012; Podolsky et al. 2007; Porneluzi and Faaborg 1999; Porneluzi et al. 2020; Robinson 1992; Sodhi 1995; Van Horn and Donovan 1994).

South of the Canadian Shield, habitat loss and fragmentation are the greatest limiting factors for the Ovenbird, and this is true through most of its range. Effects of fragmentation are significantly greater in landscapes dominated by agricultural or urban land uses than in forested landscapes. The Ovenbird has been described as one of the most sensitive species to alteration of its habitat. Fragmentation has effects at different scales: at the landscape scale, at the local scale where

reduction in forest size can have impacts, and as a result of fragmentation of individual woodlots by roads, utility corridors, and other disturbances.

At the landscape scale, fragmentation reduces the amount of forest cover in a given region and increases distances among wooded areas. Smith et al. (2011) concluded that the overall negative effects of fragmentation were more important where the amount of habitat was low in southern Ontario. This has a direct effect on area sensitivity, with Ovenbirds requiring larger forests in landscapes with less forest cover. In southern Ontario, there was about a 12% reduction in its probability of occurrence in woodlands with every 1 km increase in distance from a large forest. Colonization of sinks is predominantly through natal dispersal. Occupied forest fragments were mostly less than 14 km from large forests and much less than this on average (Nol et al. 2005). Bélisle et al. (2000, 2007) translocated territorial males in Quebec and Alberta and measured the time it took them to return in different areas. The amount of forest cover was the only factor that affected return rates and timing. The probability of a male returning to its territory increased by 1.06% for each 1.0% increase in forest cover. A bird translocated in a landscape with 80% forest cover would be 99% more likely to return than one in an area of 20% forest cover. Reduction of the percent coverage of forest may disrupt habitat selection processes, reduce colonization of isolated forest patches, and ultimately alter population structure and dynamics. In the eastern United States, only about 17% of detections of the Ovenbird on Breeding Bird Survey (BBS) routes were in fragmented landscapes (Donovan and Flather 2002). In Peterborough County, densities of singing males were 25 times higher in the largest than the smallest woodlots, and density increased significantly with increasing core area (forest habitat 100 m or more from edge; Burke and Nol 1998). In the Hull-Ottawa area, densities in contiguous forest were approximately twice those in fragments (Villard et al. 1993). Density of the Ovenbird was lower in large than small patches near Ottawa, however (Lee et al. 2002). Higher territorial density in larger forest fragments and contiguous forests than in small woodland fragments has been reported from Saskatchewan, Missouri, New Jersey, and Pennsylvania (Gibbs and Faaborg 1990; Hobson and Bayne 2000; Keller and Yahner 2007; Mazerolle and Hobson 2002; Porneluzi and Faaborg 1999; Porneluzi et al. 1993; Van Horn and Donovan 1994; Villard et al. 1993). In Pennsylvania, parameters that were most important in defining density were the percentage of forest within 2 km, forest size, core area, and distance to a large forest. Densities were higher in Saskatchewan where there was a higher percentage of forest cover within 5 km (Hobson and Bayne 2000; Porneluzi et al. 1993). Forest fragments either have larger proportions of their area that are unsuitable habitat or they are less saturated with males (Mazerolle and Hobson 2004). In Missouri and the Midwest, the proportion of edge habitat occupied by males is less than in forest interior, and this relationship has also been observed in Ontario (Burke and Nol 1998; Porneluzi and Faaborg 1999). If some birds avoid edge or have to have larger territories to obtain sufficient food, then smaller woodlots would have lower densities of males. This is because a higher proportion of the habitat of small woodlots is near edge. In contrast, Flaspohler et al. (2001) found no differences in density between forest edge and interior in Wisconsin, but there was a tendency for greater density at edge. In this area, the potential ecological trap of high nest density and low nest success in edge was partially offset by larger clutch sizes in edge.

Even in contiguous forests, there may be unpaired males but the percentage of unpaired males increases as forest size decreases. In eastern Ontario, less than 25% of males were paired in small

woodlots; most pairs were paired in large woodlots (Brenner and Nol 1996). In the Hull-Ottawa area, pairing success over 2 years was 82.4% and 76.5% in contiguous forests and 58.6% and 58.3% in forest fragments. Pairing success was greater in denser populations but the relationship between pairing success and density levelled off and became weak once densities exceeded 4 males per 10 ha (Villard et al. 1993). Also in the Ottawa area, mean pairing success was significantly higher in 3 extensive forests than in 22 forest patches. Pairing success was unrelated to landscape forest cover (Lee et al. 2002). In Peterborough County, pairing success increased most significantly with increases in woodlot core area and ranged from 0% in the smallest woodlots to 100% in the largest. Pairing success was correlated with the density of territorial males. Lower male pairing success in smaller woodlots has also been documented in Saskatchewan, Pennsylvania, Missouri, New Jersey and Illinois (Bayne and Hobson 2001b; Gibbs and Faaborg 1990; Mazerolle and Hobson 2002; Robinson 1992; Van Horn and Donovan 1994; Van Horn et al. 1995). In Saskatchewan, the proportion of paired males was positively correlated with density in woodlots in agricultural landscapes, negatively correlated with density in forest fragments within forested landscapes, and uninfluenced by density in contiguous forests. The effects of fragmentation in agricultural settings on pairing success are most severe where the density of males is lower (Bayne and Hobson 2001b). Most studies that demonstrated an increase in pairing success with increasing forest size were undertaken in agricultural landscapes. This relationship does not appear to occur in woodlots in landscapes dominated by forest. In Missouri, New Brunswick, and Pennsylvania, there were no significant differences in pairing success in forest fragments and contiguous forests in forested landscapes. Fragmentation effects on Ovenbird pairing success appears to be largely restricted to agricultural and urban landscapes (Porneluzi and Faaborg 1999; Porneluzi et al. 1993; Rodewald and Yahner 2000; Sabine 1996; Sabine et al. 1996). In Saskatchewan, males further from edge had a greater probability of attracting a mate. In Vermont, pairing success was lower within 150 m of roads than in forest interior. In Missouri, there were more paired males with territories further than 300 m from edge, but this was not always a significant relationship (Bayne and Hobson 2001b; Ortega and Capen 1999; Van Horn et al. 1995). In another Saskatchewan study and at a Pennsylvania site, pairing success of males was as high on edges as in forest interior (Mazerolle and Hobson 2003; Morton 2005).

Habitat quality and food abundance are often lower in smaller than larger woodlands and in territories of unpaired than paired males. In many areas, the food supply is limited such that habitat quality and food abundance are synonymous. In Peterborough County, the biomass of leaf-litter invertebrates was significantly higher within territories than in random areas and significantly higher in large than small woodlots. Woodlands with more than 20 ha of core area had 10-36 times more invertebrate biomass than woodlots with less than 20 ha of core area. The average invertebrate biomass was higher at random sites in large woodlands than at nest sites in small woodlots. Smaller forests contained significantly lower percentages of leaf litter, more bare ground, and significantly reduced seedling and shrub layers than larger forests. Small tracts lacked deep litter which is important in nest-site selection and abundance of invertebrates. Small woodlots appeared to have poor habitat in terms of food supply. Even in large woodlands, Ovenbirds preferentially selected areas with high food abundance. Desiccation of leaf litter is most pronounced near forest edge. This leads to a decline in food availability which may result in lower density of birds and reduced pairing

success near edge (Burke and Nol 1998). Also in Ontario, small woodlots contained less food in the litter, a possible cause of low pairing rates. It appeared to choose nest sites in smaller fragments that had a sparser shrub layer and denser canopy layer than random sites, and larger fragments may have contained more of these suitable nest sites (Brenner and Nol 1996). Similar results were documented in Missouri, Vermont, and Pennsylvania, with habitat quality and food abundance probably being the most important factors in defining pairing success and distribution of the Ovenbird in small and large fragments and in relation to edge (Ortega and Capen 1999; Rodewald and Yahner 2000; Van Horn et al. 1995; Wenny et al. 1993). In a forested landscape in New Brunswick, there were no significant differences in invertebrate biomass in contiguous forests and forest fragments or in territories of paired and unpaired males. Leaf-litter invertebrate biomass was correlated only with canopy cover (Sabine et al. 1996). In Saskatchewan, there was no difference in the invertebrate biomass in territories in forest fragments and contiguous forests, although the composition of the invertebrates varied. Vegetation structure varied significantly between fragments and contiguous forests and this was the most important factor in determining pairing success and possibly predation rates. Contiguous forests had more hardwood stems, taller trees, larger diameter trees, and more shrubs taller than 2 m, and fewer shrubs shorter than 2 m and less coarse woody debris than forest fragments. Females prefer mature forests with large hardwood trees, so the vegetation differences could affect pairing success. The vegetation parameters that were correlated with invertebrate biomass were leaf-litter depth, increasing shrub density, and decreasing coarse woody debris (Mazerolle and Hobson 2002).

Nest predation rates are typically higher in small than large forest fragments, but this is not always the case. In central Ontario, Burke and Nol (2000) reported predation rates of 55.4% in small woodlots, 41.0% in large woodlots, and 20.0% in contiguous woodlands. Predation rates declined significantly with an increase in the amount of woodland core area. Brenner and Nol (1998) found no relationship between forest size and predation rates in southern Ontario. In Saskatchewan, artificial nests were depredated at higher levels in forest fragments than in extensive woodlands (Mazerolle and Hobson 2002). In Pennsylvania, nest survival rates were lower in agricultural than forested landscapes due to differential effects of predation. Squirrels were significantly more abundant in agricultural landscapes 1 year, but not the other. There were no significant differences in population densities of chipmunks and Blue Jays between landscape types, but there were significantly more American Crows in agricultural than forested landscapes. Lower survival in agricultural landscapes was best explained by the greater abundance of some avian and mammalian predators (Rodewald and Yahner 2001). In central Ontario, Burke and Nol (2000) found no difference in nest predation rates in relation to distance from forest edge. Predation rates were 29% 0-50 m from edge, 56% 50-100 m from edge, 16% 101-200 m from edge, and 32% more than 200 m from edge. Predation rates were unaffected by edge due to the lack of avian predators near edge and the presence of small predatory mammals throughout forest fragments. In Pennsylvania, there was no difference in survival rates in relation to edge (Rodewald and Yahner 2001). In Saskatchewan, artificial ground nests at edges of woodlots in agricultural settings were 25% more likely to be destroyed than those at the edges of woodland fragments in forested landscapes or of contiguous forests (Bayne and Hobson 2001b). In Illinois, artificial Ovenbird nests 20 m from edge had significantly higher egg predation rates than those 200 and 400 m from edge (Linder and

Bollinger 1995). Predation rates are higher in small than large woodlots and in agricultural than forested landscapes. There may or may not be higher predation rates closer to forest edge depending upon the predators that are present. Porneluzi et al. (2020) concluded that predation across 17 states increased with the amount of fragmentation within a 10-km radius.

Parasitism rates of the Ovenbird by the Brown-headed Cowbird are higher in small than large woodlots. In central Ontario, 29.3% of nests were parasitized in small woodlots, 16.4% in large woodlots, and 0% in contiguous forests. In 6.76% of nests in small fragments only cowbird young were produced compared with 1.56% in large fragments (Burke and Nol 2000). Also in Ontario, parasitism was greatest in small- and intermediate-sized woodlots and rare in large woodlands (Brenner and Nol 1996). In Missouri, 6% of Ovenbird pairs raised cowbird young in forest fragments, significantly more than the 1% in contiguous forests (Porneluzi and Faaborg 1999). In Saskatchewan, no nest parasitism occurred in contiguous forests or in forest fragments within forested landscapes. In forest fragments in agricultural landscapes, 17% of nests were parasitized, with all but 1 nest parasitized 1 year (Bayne and Hobson 2002a). In suburban woodlots ranging from 10 to 132 ha in Massachusetts, a higher percentage of nests was parasitized in small (37.5%) than large (34.7%) woodlots, but not significantly (Hersek et al. 2002). In Missouri, Wisconsin, and Minnesota, nest failure due to parasitism was only a factor in forest fragments where 16.7% and 5.27% of the daily mortality rate was attributed to parasitism. In contiguous forests, 2.5% and 4.0% of nests were parasitized compared with 80% and 58% in forest fragments (Donovan et al. 1995). In Ontario, the parasitism rate was significantly higher within 100 m of edge than more distant from edge (Burke and Nol 2000) and this relationship has been observed in other locations (Ford et al. 2001; Ortega and Capen 1999). Porneluzi et al. (2020) concluded that brood parasitism across 17 states increased with the amount of fragmentation within a 20-km radius.

Reproductive success is lower in smaller than larger forests, and smaller populations are frequently sinks with adults failing to produce enough young to replace themselves. In central Ontario, woodlot size was the most important factor affecting reproductive success. Significantly more young were fledged per nest in contiguous forests than in either small or large forest fragments. Ovenbirds in contiguous forests produced almost 2 times as many young as those in large fragments and almost 7 times as many as those in small fragments. The number of nesting attempts required to maintain populations were 4.1 in small fragments, 1.3 in large fragments, and 0.8 in contiguous forests. Populations were sinks in small forests, close to maintenance levels in large fragments, and sources in contiguous forests. Populations remained constant over the study, suggesting a source-sink population. Most fragments with nesting Ovenbirds produced at least 1 fledgling over the course of the study and some fragments occasionally functioned as sources. Sink populations can have a positive influence on metapopulation size and longevity provided that source populations remain. Only 1% of forest fragments in central Ontario are sources (woodlands larger than 200 ha), and 82% have no core area and are sinks (Burke and Nol 2000). In Ontario, 6 nesting attempts were required to produce a single young in small woodlots compared with 1 in a contiguous forest. Woodlots with less than 50 ha of core area resulted in no Ovenbirds being produced despite the high density of singing males (Benner and Nol 1996). Similar results have been reported from other areas, but the size of forest that is required to be a source varies. In Missouri, the average clutch size and proportion of pairs raising young in contiguous forests were significantly

higher than in forest fragments. Some of these effects in forest fragments may have been mitigated by renesting. Populations in contiguous forests were self-sustaining, but those in forest fragments as large as 2,000 ha were not (Porneluzi and Faaborg 1999). In Massachusetts, woodlands as small as 120-132 ha acted as sources. These woodlands were surrounded by a forested suburban landscape so that edge effects were not as extreme as for isolated woodlots in agricultural landscapes (Hersek et al. 2002). Podolsky et al. (2007) cautioned that not accounting for renesting and double brooding in models can greatly underestimate annual productivity and that these activities may account for 40% or more of annual fecundity. In Pennsylvania, the proportion of successful males was significantly higher in contiguous forests (59%) than forest fragments (5.9%). Only 1 male in forest fragments was successful in raising young and he was in the largest (126.5 ha) fragment. It was concluded that forests as large as 183 ha did not support sustainable Ovenbird populations (Porneluzi et al. 1993). In Saskatchewan, nest survival rates were lower in small woodlots in agricultural settings, intermediate in woodlots in forested landscapes and highest in contiguous forests (Bayne and Hobson 2001b, 2002a; Hobson and Bayne 2000).

Fragmentation may affect survivorship of males. In Saskatchewan, the apparent survivorship of males was significantly higher in woodlots larger than 20 ha (58%) than in those smaller than 15 ha (34%). Although the probability of recapture rate was higher in forest fragments in agricultural landscapes, male survival rates were significantly lower in these forests than in forest fragments in forested landscapes and contiguous forests (Bayne and Hobson 2002a).

Linear corridors through forests are the final type of fragmentation effects. In Vermont, Ortega and Capen (1999) studied the effects of narrow (7-10-m wide) dirt and gravel roads through forests on the Ovenbird. They concluded that habitat quality for it may be lower within 150 m of unpaved roads in extensively forested landscapes, affecting territory density and possibly reproductive success. In New Jersey, Rich et al. (1994) examined the distribution of the Ovenbird in relation to 8-m wide corridors for unpaved roads, 16 m for paved roads, and 23 m for hydro corridors. Its abundance was significantly reduced on edge transects of corridors 16-23-m wide, but not along those 8-m wide. Corridors 16-23-m wide created an edge effect. Edges also attracted avian predators and parasites. In the Northwest Territories, Machtans (2006) examined the response of Ovenbirds to seismic lines, which were 6-m wide clear-cuts. It was the most sensitive species to this type of disturbance, declining in abundance and shifting territories away from seismic lines. It was not observed crossing these lines. Bayne et al. (2005a, 2005b) examined the effects of seismic lines 6-10 m wide in Alberta. All but 1 Ovenbird was observed on both sides of a line, but birds spent significantly more time than expected on 1 side of the line. The average percentage of the territory on the predominantly used side of the line was 78%. There was no change in abundance or density of the Ovenbird as a result of the lines, but they tended to act as territory boundaries. There was little evidence that it declined in response to seismic lines but there is potential for population-level effects as the density of lines increases. Lankau et al. (2013) continued this research and concluded that Ovenbirds excluded seismic lines from their territories due to a lack of protective cover (lower tree and shrub coverage) and because of reduced food resources due to large areas of bare ground. These effects appeared to be mitigated only once the depth and extent of leaf litter was restored and the amount of woody vegetation returned to forest-interior conditions. Bayne et al. (2016) compared its abundance near energy sector disturbances and in adjacent forest interior in the

western boreal forest. It was 2-19% less abundant along seismic lines, 2-24% less abundant along pipelines, and 11-69% less abundant at well pads than in adjacent forest interior. In Michigan, Valentine et al. (2019) used artificial Ovenbird nests to determine if forest fragmentation due to well pads had an effect on predation. Predation rates on nests 5, 20, and 35 m from edge were similar to those at nests in forest interior and in control woodlots. In West Virginia, it avoided well pads, access roads, and pipelines and was significantly less abundant close to them. Over time, it shifted its distribution within the forest to avoid the area most heavily affected by well pad development and, to a lesser extent, away from linear infrastructure. It declined by 35% in response to these features (Farwell et al. 2019).

Forest management may have detrimental effects on the Ovenbird. It is considered by most authors to be one of the most adversely affected species when forestry practices are implemented. Other studies found few effects. In the Boreal Forest Region of Ontario, Rempel et al. (2007) modelled the effects of forest management on the Ovenbird. Even when all guides for habitat maintenance were adhered to, a decline was predicted because of a decline in hardwoods. A decline was also predicted due to natural disturbances, but this decline was markedly less than declines due to forestry. Vanderwel et al. (2009) summarized the effects of partial harvesting of late-successional forests in the Boreal Forest Region of Ontario. A decrease in population was observed when 50-70% of the forest cover was retained. When only 30% of the forest cover was retained, it became locally extirpated. It declined by 25% when 15% of the forest cover was removed, by 50% when 30% of the forest cover was removed, and by 75% when 45% of the forest cover was removed. Partial harvesting negatively affects habitat by removing canopy trees, reducing litter depth, and promoting growth of understorey shrubs (Vanderwel et al. 2007). Near Sault Ste. Marie, Holmes and Pitt (2006) examined the effects of single and group selective harvesting on the Ovenbird. It declined significantly in 2 of 3 cut-blocks, but showed signs of recovery 3-6 years later. Its abundance was positively associated with canopy cover, BA (especially of trees larger than 50 cm DBH), and leaf litter, and negatively associated with grass and sedge cover, low shrub cover, downed woody cover, and density of tall shrubs. Reduced canopy cover due to thinning could result in a drier leaf-litter layer and lower prey densities. Densities declined after harvesting and the productivity of the remaining individuals was also reduced. In Algonquin Park, it was 50% less abundant in recently logged stands and stands logged 15-20 years previously. The reduced canopy cover and increased shrub growth as a result of thinning was detrimental. Higher air and soil temperatures and lower soil moisture result in reduced beetle populations that serve as prey for the Ovenbird (Tozer 2012). In Algonquin Park, Kingsley and Nol (1999) concluded that the Ovenbird was not adversely affected by uniform shelterwood logging in white pine stands. Also in Algonquin Park, Tozer et al. (2010) examined the effects of group-selection logging. In typical group-selection, 5% of the stand area was removed; intensive group-selection removed 20% of the stand area. The Ovenbird decreased slightly in the second year due to typical group-selection and showed no response to intensive group-selection. The decrease was likely due to a reduction in leaf litter and an increase in ground cover. Numbers did not change with intensive group-selection because birds crowded into the residual forest where the canopy was left intact. In Algonquin Park, its abundance was 50% lower in areas harvested by single-tree selection and in stands logged 15-20 years previously than in uncut stands. It was positively associated with deciduous canopy cover and density of trees 10-20 cm DBH (Jobes et al. 2004). Leblanc (2010)

studied responses of the Ovenbird to single-tree-selection in Algonquin Park hardwood forests. No differences were detected in daily nesting success, pairing success of males, or in nesting behaviour among treatments. In recently (1-15 years) harvested stands, it was selective for nest sites with deep leaf litter and BA associated with larger trees because these microhabitats were limited. After 20-25 years, nest site and total BA were the only microhabitat parameters that remained below preharvest levels. In the Carolinian Forest Region, selective harvesting and diameter limits cuts had no effects on the Ovenbird (Holmes et al. 2004). In the Canadian Shield in Ontario, it was equally abundant in early successional clear-cuts and burns but significantly less abundant in mid-successional clear-cuts than mid-successional burns. It was significantly less abundant in early successional than mature stands but significantly more abundant in mid-successional than mature stands (Zimmerling et al. 2017).

Effects of forest management on the Ovenbird have been reported from other areas. In Quebec, strip-cutting had a detrimental effect; it took 12-15 years for its abundance to reach the levels of neighbouring uncut areas (Drapeau and Darveau in Gauthier and Aubry 1996; Falardeau et al. 1999). In New Brunswick, lower breeding density and reproductive success occurred as a result of single-tree selection and in selection cuts that removed 30% of tree cover every 20 years. The return rate of males was negatively affected by single-tree selection. The Ovenbird was the species most affected by forestry (Bourque and Villard 2000; Haché and Villard 2010; Pérot and Villard 2009). In Nova Scotia, it was one of the most abundant species in unharvested forests, was absent in recent clear-cuts and on thinned plots, and occurred in much lower densities in strip-cut plots than in uncut forests (Freedman et al. 1981). In Saskatchewan, it was significantly more abundant in sites that were at or below rotation age, so forests were not harvested before they provided optimum habitat (Cumming and Diamond 2002). In Alberta, Lambert and Hannon (2000) examined the effects of harvesting trembling aspen stands, leaving riparian buffer strips of 100 or 200 m where trees averaged 60-70 years old. The harvest did not affect numbers within 100-m strips, although territories shifted toward the lake. The 200-m wide buffers retained the Ovenbird at preharvest levels. There was no change in pairing success in either width of buffer, and the authors concluded that the effects of forest fragmentation may be considerably less in areas of extensive forest. In Alberta, it declined in cut-blocks but numbers recovered by the third year after harvest. It increased with increasing BA after cutting and with increasing retention of trees in cut-blocks. There was evidence for an effect of harvesting on the Ovenbird, but it was short lived (Tittler et al. 2001). Another Alberta study determined that it decreased when 25% of trees were removed in deciduous forests and became extirpated when 50% or more of trees were removed. In deciduous forests with a shrubby understorey, it declined when 25-50% of trees were removed and became extirpated when 80-100% of trees were removed (Harrison et al. 2005). In New York, it showed a decline in population with increased intensity of logging. Habitat became less and less suitable as the intensity of logging increased. The population recovered substantially over 6-7 years, but only to half the level of unharvested forest (Webb et al. 1977). Declines in numbers of Ovenbirds as a result of selective logging have been documented in Missouri, Arkansas, Illinois, Wyoming, Minnesota, and Pennsylvania (Hanowski et al. 2002, 2005; Niemi and Hanowski 1984a; Porneluzi et al. 2020; Robinson and Robinson 1999; Yahner 2003). In Pennsylvania, areas where snags were retained in improvement cuts supported lower densities of Ovenbirds than where snags were removed. There was

significantly greater coverage by shrubs in stands where snags were retained and this may have created less favourable breeding habitat (Stribling et al. 1990).

Three studies were conducted on the effects of clear-cutting in forested landscapes. In New Hampshire, clear-cuts were 12 ha or less and cowbirds were absent. There was no evidence of edge avoidance or lower pairing success on edges. Although nest survival was lower on edge, the proportion of pairs fledging young and the condition of fledglings did not differ between edge and interior nests. King et al. (1996) concluded that the effect of small-scale clear-cutting on the Ovenbird was slight in this extensively forested area. Edge effects could be further minimized by making clear-cuts as close to circular as possible and by creating fewer but larger clear-cuts to minimize edge creation. In Minnesota, there was strong evidence for an edge effect on Ovenbirds nesting near regenerating clear-cuts in a forested landscape. Nesting success increased with distance from the nearest clear-cut edge. Differences in nest success rates were due to increased predation rates near edge (Manolis et al. 2002). In Minnesota, territory density in patches that were recently thinned or near clear-cuts was 1-3% greater than in uncut and interior patches. Territory density increased by 19% as upland openings increased from 1% to 22%. Pairing success decreased from 92% to 88% as territory density increased from 0.7 to 2.5 males per ha. Territory settlement patterns were inconsistent with an ideal distribution where densities are highest in the least fragmented landscapes which should contain high quality patches. The reason for this is that the costs of dispersing from a low-quality patch may exceed the costs of remaining (Mattsson and Niemi 2008).

Loss and Blair (2011) studied the effects of invasion of woodlands by common earthworms on the Ovenbird in Wisconsin. Earthworms consume leaf litter and organic layers below the litter, mix soil horizons, reduce the abundance of mycorrhizal fungi and arthropods, and alter nutrient dynamics. Presence of earthworms was not directly associated with Ovenbird daily survival rate, but earthworms affected vegetation. There was a significant positive correlation between presence of earthworms and sedge cover and a significant negative relationship with average litter depth. At 0% sedge coverage, nest success rate of the Ovenbird was 74% compared with 37% for 100% sedge coverage. Nest concealment decreased with increasing sedge coverage, mostly by Pennsylvania sedge. This sedge thrives in response to earthworms because it has a competitive advantage in the absence of other plants, tolerates disturbed soils, and does not depend on mycorrhizal fungi. Ovenbird success rates were 84% with 9.7 cm litter depth compared with 45% at 0 cm. Decreased litter depth can result in decreased arthropod abundance, reduced food availability, and more exposed nests. Earthworms significantly affected the productivity of Ovenbirds. In Ontario, it is likely that a high proportion of woodlands south of the Shield are infested with earthworms and there are local earthworm infestations further north.

Near Peterborough, 14 of 27 of Ovenbird nests (51.9%) failed due to predation. Nests in sites with more cover were more likely to fledge young. Abundance of raccoons and squirrels was positively correlated with housing density. Eastern chipmunks were negatively correlated with housing density. The effects of housing extended only 100 m for chipmunks and squirrels, but 2 km for raccoons. Squirrels were positively associated with the percentage of understorey vegetation. Forest fragments surrounded by greater amounts of less intensive agriculture (hay, pasture, old field) within 2 km tended to have greater invertebrate biomass. Nests are more likely to survive if more

seedlings and forbs are present regardless of the type and relative abundance of mammalian predators, and more invertebrates are likely to be present under these conditions (Richmond et al. 2011).

Acid precipitation and other air pollutants that affect tree health or soil acidity may have adverse effects on the Ovenbird. In Quebec, many sugar maple forests are declining, which results in a loss of crown foliage. Density of Ovenbirds was 42% lower in stands affected by dieback than in healthy stands. Insect abundance appeared to be lower in dieback forests (DesGranges et al. 1987). In Maine, there was no difference in territory size in acidified and control watersheds. Territory size decreased as calcium concentrations in potential prey (adult beetles) increased. Calcium limitation can be a determinant of territory size (Pintar and Olsen 2021). In Pennsylvania, Pabian and Brittingham (2011) added lime to forest plots to increase soil calcium concentrations. Where calcium was added, territory density was 1.8 times higher and clutch size was 1.1 times larger than in control sites. Two times as many young were produced from limed than control plots. At high calcium concentration areas, nests were initiated earlier and as many as 3 replacement clutches were laid. Ovenbirds in low calcium areas rarely laid replacement clutches. Snail abundance was positively correlated with calcium concentrations. Snails may be important in the diet to aid in eggshell formation. Soil acidification due to acid precipitation has the potential to decrease its productivity, especially in the Canadian Shield in Ontario.

Natural disturbances that affect canopy closure may affect the Ovenbird. A decline occurred in Vermont due to changes in habitat structure from an extensive ice storm. In Minnesota, a dramatic decline in density occurred following loss of elms to the Dutch elm disease. This resulted in an increase in density of ground vegetation and light levels that made habitat less suitable (Porneluzi et al. 2020). It is possible that loss of ash trees due to the emerald ash borer will further degrade Ovenbird habitat.

In central Ontario, Clark et al. (1983) concluded that the Ovenbird could be expected to occur near cottage lots in mature woods provided that the forest was not disturbed. Cottages lots where only a few trees were removed and the ground and shrub layers were left intact would probably deter Ovenbirds from nesting. Stauffer and Best (1980) considered the Ovenbird intolerant of any habitat alterations. They predicted that it would be reduced in numbers if the canopy was partially removed or if the woody understorey was thinned.

Woodlots were formerly frequently grazed by livestock. This was highly detrimental to Ovenbirds because it removed both herbaceous and woody cover in the understorey and inhibited tree regeneration (Graber et al. 1983; Hann 1937). These practices have largely been abandoned in Ontario, but grazing by the white-tailed deer creates a similar problem (Vitz and Rodewald 2011). In Delaware, Tymkiw et al. (2013) found no significant differences in the abundance of the Ovenbirds in areas of low, moderate, and high deer density.

Prescribed burns and other fires in forests are highly detrimental to the Ovenbird. In Georgia, it was the species most negatively affected by fire and this was also true in pine-oak forests in North Carolina. Burns opened up the canopy and reduced shrub coverage. Habitat may be degraded for many years following a high-intensity fire. Six years after a fire in Georgia, densities were only about half those before fire, or even much lower in some areas. In addition to reducing shrub density, leaf-

litter depth is greatly reduced by fire, thereby reducing food availability and nest cover. In Indiana, maximum abundance of the Ovenbird occurred when the frequency of fires within a 15-year period was 0. Abundance dropped to 0 when fire frequency reached 4 in 15 years (Grundel and Pavlovic 2007a; Klaus et al. 2010; Porneluzi et al. 2020; Rose and Simons 2016).

In Waterloo Region, woodlands adjacent to houses supported fewer forest-dwelling bird species than those without houses nearby. This relationship was not particularly strong for the Ovenbird (Friesen et al. 2005). In North Carolina, its abundance declined significantly with increases in housing density (Lumpkin and Pearson 2013).

In Alberta, the Ovenbird's song frequency overlapped that of noise from compressor stations, potentially causing masking of songs. Significantly more males were paired at control sites (92%) than at compressors (77%). Densities of males were greater at controls than at compressors. The noise may have interfered with intersexual communication. Noise level may be 1 factor that females use in mate selection (Habib et al. 2007). In Alberta, Bayne et al. (2008) found no significant difference in its abundance at quiet well pads and noisy compressor stations.

Streby et al. (2009) determined that blow flies appeared to have no effects on nestlings, but the survival rate and minimum first-detection distance from the nest were significantly lower for fledglings from infested nests. Of 9 infested fledglings, 8 died within 3 days of leaving the nest. Seven exhibited no signs of predation and the eighth was apparently depredated by a small mammal. Seventy-four percent of non-infested fledglings survived the same period. Infected broods were more active with nearly constant scratching and twitching, and this may have attracted predators. Non-infested broods remained chiefly motionless. The adverse effects of blow fly infestations are not manifested until the fledgling stage.

In Minnesota, young forced to fledge early by researchers experienced a significantly higher survival rate than those that fledged at a typical fledging age. Premature fledging did not adversely affect survival rates and the ability to fledge early may be a predictor of higher probability of fledgling survival (Streby et al. 2013).

Blake et al. (1992) examined the effects of drought on the Ovenbird in Wisconsin and Michigan. It declined over a 5-year period and its abundance varied significantly among years in both states. Abundance was influenced by drought or drought-related factors with declines in drought years. Drought effects were less severe early in the year when temperatures were mild and moisture from winter snowfall was still present.

Price (2004) concluded that the Ovenbird's range could contract in southern Ontario if the average summer temperature increased by 2°C. In North Carolina, Lumpkin and Pearson (2013) determined that its abundance increased with increasing temperatures.

Status

The Ovenbird has always been common to abundant in Ontario. Highest densities occur in mature deciduous forests in Ontario, New Brunswick, Maine, Wisconsin, and Minnesota (Mattsson and Niemi 2008; Van Horn and Donovan 1994). McIlwraith (1894) considered it present in suitable habitat throughout the province. In eastern Ontario, it was very common in deciduous forests in the 19th and 20th centuries, and it is still an abundant breeder in the Kingston area (Weir 2008). Baillie and

Harrington (1937) described it as a common summer resident throughout most of Ontario north to southern Kenora District and James Bay and concluded that it likely bred throughout this range. It had also been documented during the breeding season at Lake of the Woods and at latitude 52°N along the Manitoba-Ontario border. Fleming (1907) considered it a rare breeder in the Toronto area; it is likely that this area had been largely deforested by that time. In the Dorset area in the 1960s, it was the second most abundant species (Mills 1981). During the first atlas, it was common and widespread throughout Ontario, except in the northern portion of the Hudson Bay Lowland, where it was scarce or absent. It was most abundant in the Great Lakes–St. Lawrence Forest Region, particularly in the southern Canadian Shield (Armstrong in Cadman et al. 1987). James (1991) considered it an abundant summer resident across the province, becoming rare through the Boreal Forest Region north to Big Trout Lake and Fort Albany, and occasional somewhat further north. In heavily forested areas in south and central Ontario, the Ovenbird is very abundant and is usually outnumbered only by the Red-eyed Vireo. In Peterborough County and white pine stands in Algonquin Park, it was the most ubiquitous species (Burke and Nol 1998; Kingsley and Nol 1999). In the Shield portion of the Great Lakes–St. Lawrence Forest Region, the Ovenbird was the most abundant species in white pine stands and constituted 11.9% of all birds (Kirk et al. 2012). In the South Walsingham Forest in Norfolk County, it was second in abundance to the Red-eyed Vireo, and represented 12.56% of all bird records (McCracken et al. 1998). It is much less common in southwestern Ontario where there is less forest cover. In Elgin County, it was common to very common until 1954 but an uncommon breeder by 2000 and apparently absent some years (Lancaster et al. 2004). Black and Roy (2010) considered it an uncommon breeder in Niagara Region.

The second atlas demonstrated that there had been no change in the breeding distribution of the Ovenbird since the first atlas. In the Hudson Bay Lowland, it was restricted to river corridors where there were suitable stands of mature balsam poplar and trembling aspen. Habitat distant from rivers is unsuitable. Province-wide, there was no significant change in its probability of observation. A significant decline occurred in the Carolinian Forest Region, possibly due to continuing forest fragmentation. It is absent in many areas of the extreme southwest because the existing woodlots are very small and the percentage of regional forest cover is very low. Heavy logging has likely contributed to its decline in portions of Huron, Lambton, and Middlesex counties. Significant increases were documented in the Boreal Forest Region and the Great Lakes–St. Lawrence Forest Region in the Shield. It was predicted that continued declines or losses would occur in many areas due to forest disturbance and fragmentation. Highest densities occurred in the Great Lakes–St. Lawrence Forest Region in the Shield, and high densities also occurred on Manitoulin Island and the Bruce Peninsula. Areas of moderate density south of the Shield included the Oak Ridges Moraine, Norfolk Sand Plain, Niagara Escarpment, and eastern Ontario north of the St. Lawrence River (Burke in Cadman et al. 2007).

Based the BBS, the Ovenbird experienced an initial increase followed by a decline. Overall, it increased 1965-79, but declined 1978-87. BBS data for 1980-89 indicated significant population declines at the periphery of its breeding range, but significant increases in the core of its range (Porneluzi et al. 2020; Van Horn and Donovan 1994). BBS data indicate that it decreased at annual rates of 0.188% in Canada and 0.461% in Ontario 1970-2021. Trends 2011-21 were annual decreases of 0.335% in Canada and 1.42% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings go through 4 phases: the hopping stage at 8-11 days of age, the early flying stage at 11-20 days, the semi-dependent phase at 20-30 days, and the independent phase at 30-40 days. During the hopping stage, young can travel on the ground about as fast as a person can walk. During this phase, fledglings may remain in practically the same place for several days. During the early flying stage, young can fly 5-30 m, but go in a circle if flushed and return to the same area. During the semi-independent stage, young walk with their parents, picking up food as they go, but continue to be fed by the adults. During the independent phase, the adults leave the young and usually leave the woods that were used for nesting. At this time, the young wander solely or occur in small groups of 2-3, occasionally in the company of an adult. Young birds associated together at this time are not necessarily from the same brood. When the first chick leaves the nest, either the male or female leads it away and the other mate is left responsible for the remainder of the brood. Young are initially led 15-25 m from the nest and are subsequently taken further. Fledglings under the care of an individual adult are kept separate from each other. The male and his young tend to remain in the nesting territory until the young are independent, but the female and her young may move considerable distances (Hann 1937; Streby et al. 2011a, 2013b; Van Horn and Donovan 1994; Vitz and Rodewald 2010).

Shortly after the young leave the nest, adults and fledglings move to areas with denser vegetative cover. In Ohio, postfledging habitat was significantly different from nesting habitat and had 1.8 times as many woody stems, 14% less canopy cover, and 11% fewer small trees. There were no differences in the number of medium- or large-sized trees at postfledging and nesting sites. There were significant differences in postfledging habitat and random sites, with 40% more woody stems and 8% more canopy cover at postfledging sites compared with random areas. Surviving fledglings used habitats with 15% more woody stems than those that perished, mostly due to predation. Some fledglings used regenerating clear-cuts, but these were not preferred. More frequently used habitat was dense understorey in mature forest, including riparian thickets, forest edges, tree-fall gaps, and dense foliage of recently fallen trees (Vitz and Rodewald 2011). In Missouri, habitat used by fledglings differed significantly from habitat at nest sites. Juveniles occurred in areas with denser foliage 0-2 m from the ground (72.0% compared with 58.9%), less litter depth (2.0 cm compared with 2.6 cm), higher shrub density (2,363 compared with 1,677 per ha), higher ground cover, and more live tree stems (1,263 compared with 959 per ha) than nest sites. Juveniles occurred closer to edge (mean 132 m compared with 168 m) than nests (Jenkins et al. 2016). Stoleson (2013) captured 38 adults and 20 fledglings in clear-cuts compared with 19 adults and 16 fledglings in adjacent mature forest. The capture rate of Ovenbirds was significantly higher in forest. The Ovenbird preferred mature forests to clear-cuts during the postfledging season. In many areas, postfledging Ovenbirds make heavy use of regenerating clear-cuts and it is frequently the most abundant forest-breeding bird found in this habitat. Fledglings rarely use clear-cuts until they are independent of their parents, usually around age 24 days. Simultaneous capture of adults and young is not a reliable indicator of family groups because the young move to shrubby habitat after they are independent. In Ohio clear-cuts, capture rates were 2 times higher in areas with a canopy taller than 4.5 m than those with a canopy shorter than 2.5 m. In Minnesota clear-cuts, the strongest predictors of adult abundance were density of shrub- and ground-level invertebrates with canopy

height and woody debris being less important parameters. The strongest predictor for fledgling abundance was availability of shrub-level invertebrates, which was twice as important as the next strongest predictor of leaf-litter depth. In Ohio, there was no significant difference in capture rates in small (4-9 ha) and large (13-18 ha) clear-cuts, although clear-cut edges may be avoided to reduce predation risk (Marshall et al. 2003; Streby et al. 2011a, 2011b; Vitz and Rodewald 2006, 2007). In New Hampshire, areas occupied by fledglings had fewer large trees and more understorey structure than nest sites and random points. Fledglings selected habitat with a dense understorey of shrubs and saplings. These were mostly dense areas of regeneration of canopy species such as beech and hemlock, but also included patches of hobblebush, raspberries, and blowdown. There was no association between fledgling presence and litter depth. Mature hardwoods and mixed woods were most preferred; coniferous forests and regenerating forests were much less preferred. Pole-sapling stands and non-forested habitat were not used (King et al. 2006). In Michigan, Akresh et al. (2009) studied the abundance of adults and fledglings in upland and riparian forests. The upland habitat was an even-aged aspen stand. The riparian forest had an aspen overstorey and a shrubby understorey of alder and honeysuckles. Adults did not nest in the riparian forest, but after the young fledged, adults were captured less in upland forest and more in riparian forest. Seventy-three percent of juveniles were captured in riparian forest indicating that both young and adults quickly dispersed to the area with denser shrub coverage.

Porneluzi et al. (2014) netted in Missouri during the postfledging period 2-15 years after an oak-pine-hickory forest was clear-cut. Ovenbird capture rates showed a significant curvilinear trend that increased gradually to a peak 7-10 years after harvest followed by a decline. In Missouri, Burke et al. (2017) radiotracked juvenile Ovenbirds that were captured in deciduous clear-cuts 3-6 years old. The mean distance between moves was 133.5 m. Seventy-five percent of birds remained in the clear-cut where they were captured. The probability of use was much greater for stands in the small-tree class than in pole or sawtimber classes. The probability of use was much greater for clear-cuts than for partial cuts or unharvested stands. One bird travelled 1.14 km to another study area and returned the same day where it remained for another 10 days. It used early successional habitat for all its stops.

Streby and Andersen (2012, 2013a) radiotracked fledglings from nests in mature deciduous and mixed forests in Minnesota. Every fledgling made 1-day movements ranging from 300 m to 3 km 5 days or less after becoming independent. Within 24 hours of fledging, fledglings were 3-108 m (average 36 m) from their nests. Fifty-eight to 74% of fledglings were outside their natal territory within 24 hours. Within 5 and 10 days of fledging, 98% and 100% of fledglings were outside their natal territory, respectively. Stands occupied after these movements differed from habitat in the natal areas. Of birds from the deciduous stand, which had a sparse shrub layer, 50% moved to sapling-dominated clear-cuts, 40% moved to forested wetlands, and 10% moved to mature deciduous forests. Of birds leaving the mature mixed woods, 10% moved to sapling-dominated clear-cuts, 30% to forested wetlands, and 60% to mature mixed woods. Birds spent 1-10 days (mean 5 days) in these stands before making a second 1-day long-distance movement of 300 m to 6.1 km. Birds made a third long-distance movement after another 1-10 days (mean 4 days). Only 10% of birds tracked for 5 or more days did not make use of sapling-dominated clear-cuts or forested wetlands. Birds from the deciduous site selected among cover types. Usage of sapling-dominated

clear-cuts was more than twice as much, forested wetlands 6 times as much, and mature forest less than half as much as expected based on availability. Birds from the mixed forest also selected, using mature forest, sapling-dominated clear-cuts, and forested wetlands more than shrub-dominated clear-cuts. There was a disproportionately low use of shrub-dominated clear-cuts. All fledglings used areas with dense woody undergrowth. Regenerating clear-cuts can be important habitat for fledglings, but not until saplings become established.

Areas of dense shrub or sapling coverage are very important to Ovenbirds during the postfledging period. Areas that are potentially suitable nesting habitat may not be occupied if birds do not have access to dense woody cover once the young leave the nest. These dense areas are probably most important in providing protection from predators, but they may also be rich in invertebrates and fruit (King et al. 2006; Streby et al. 2011a; Vitz and Rodewald 2010, 2012).

In Ohio, Vitz and Rodewald (2013) captured young Ovenbirds in regenerating hardwood clear-cuts. Fledglings were released in the clear-cut where they were captured, in a different clear-cut, or in mature forest. Birds that survived the 52-day monitoring period inhabited areas containing 1.5 times the number of woody stems as those that did not survive. Birds released in clear-cuts had the highest survival rates, but not significantly greater than in mature forest. Juveniles used areas with 1.4 times the number of woody stems than occurred in random areas. Birds were most often found in mature forest (80% of observations), followed by regenerating clear-cuts (11%), and mid-successional stands (9%). Of mature-forest locations, 16% were in riparian thickets and 6% in treefall gaps. Birds released into mature forest were later found in this habitat 91% of the time, but also in mid-successional forests (6%) and clear-cuts (3%). For fledglings released into clear-cuts, 76% of subsequent locations were in mature forest, 14% in clear-cuts, and 10% in mid-successional stands. Survival of young Ovenbirds was not determined by access to large patches of early successional habitat. They used a variety of habitats that provided dense understorey vegetation, including within mature forests, and did not appear to be especially attracted to regenerating clear-cuts.

In Saskatchewan forests, male Ovenbirds did not avoid forest–clear-cut edges during the postfledging period and were more abundant at forest edges. The percentage of positions within 50 m of edge (75%) was greater than expected if males randomly used areas within the forest (58%). The proportion of observations within 25 m of edge was also greater than expected (46% compared with 30%). Males without young had a higher percentage of observations within 50 m of edge (80%) than those with young (65%) but there was no difference in the percentage of observations within 25 m of edge. Forest edges may be a barrier to movement, resulting in a concentration around edges (Bayne and Hobson 2001a).

Fledglings may move considerable distances from the nest to postfledging habitat. In Ohio, the mean time of dispersal between these 2 habitats was 29.2 days (range 24-34 days). The centre of the natal home range was separated from the postfledging habitat by an average of 1.3 km (maximum 3.7 km). There was no evidence that presence of dense vegetation near the nest reduced the distance travelled (Vitz and Rodewald 2010). The range of distance moved by independent fledglings in Ohio was 0.07-18.2 km. Birds gradually moved greater distances over the first 4 weeks after capturing them in clear-cuts. Birds released in mature forests moved the furthest (mean 975 m). Those released in different clear-cuts moved a mean of 855 m compared with 468 m for those

released in the same clear-cut. No birds attempted to return to the original capture location (Vitz and Rodewald 2013).

In Missouri, there was no difference in the overall numbers of male and female nestlings or in the survival rates of male and female fledglings. Twenty days after fledging, females moved 350-750 m further than males from the nest. Prior to this, male and female movements were similar. Some females moved as far as 1 km from their nest. The maximum distance travelled by male fledglings was 250 m (Jenkins et al. 2017).

In Minnesota, Streby and Andersen (2013b) determined survival rates of Ovenbird fledglings 1-8 and 9-16 days after leaving the nest and correlated the results with habitat. During the first 8 days after fledging, young that crossed a logging road at least once during this period were twice as likely to be depredated as those that did not cross a road. Next in importance in defining survival was the habitat adjacent to the mature forest where they fledged. Survival was lower for fledglings adjacent to young regenerating clear-cuts and higher for those near older regenerating clear-cuts and forested wetlands. Road crossing had the greatest impact on survival 9-16 days after fledging. Young that crossed logging roads were 33% less likely to survive than those that did not. Reclamation of abandoned logging roads could have a positive effect on populations of Ovenbirds.

In New Brunswick, Haché et al. (2014) studied survival and movements of postfledging Ovenbirds in plots treated 4 and 5 years earlier by selection harvesting and in control plots. Shrub density was higher in treated plots than in controls. Of 55 fledglings, 45.5% were still alive on day 14; 60% of mortality occurred 2-10 days after fledging. Some fledglings moved as far as 355 m during the first 2 weeks, but most remained near their nest. Mean distances between the nest and location on day 14 were 138.5 m in treated plots and 212.2 m in controls. Only 3 fledglings moved from control plots. They moved into plantations or coniferous riparian areas with open ground cover. Postfledging movement rate was not influenced by habitat variables, predator abundance, or body condition. Variations in eastern chipmunk and red squirrel abundance were key factors influencing fledgling survival, and they were responsible for 80% of predation events.

In Saskatchewan, Bayne and Hobson (2001a) examined whether forest fragmentation affected dispersal of adult males during the postfledging period. Males without young were more likely (83%) to cross gaps in the fragmented landscape than those with young (14%). Four birds without young permanently left the woodlot where they were first encountered and moved to 2 or more fragments 1.05-5.63 km away. The widths of gaps crossed by them was 100-300 m. Six males left their original woodlot, crossing at least 50 m of adjacent cropland to another woodlot, and returned the following day. Only 1 was seen attending young. In contiguous forest, there was no difference in the frequency in which males with young (33%) and those without young (30%) crossed gaps less than 25 m wide. Males with young in contiguous forest frequently crossed small gaps but those with young in forest fragments rarely left. Forest fragmentation did not affect dispersal of adults without young and did not constrain movement patterns of successful breeders. Although the Ovenbird is capable of crossing gaps, it may preferentially move through forested areas when dispersing from the breeding territory. The fact that successful breeders usually did not disperse from small forest fragments suggests that these woodlots must have habitat that is suitable both for breeding and postfledging to accommodate nesting Ovenbirds.

Not all fledglings maintained a stable home range in New Hampshire (King et al. 2006). In Ohio, the mean home range of fledglings while they were still in the natal area was 5.0 ha. This far exceeded the size of breeding territories. The use of large areas after fledging may contribute to patterns of area sensitivity, at least in fragments smaller than the natal home range. Once a patch exceeds this size, these effects are likely to be reduced because family groups may have overlapping home ranges (Vitz and Rodewald 2010). In Saskatchewan, there was no difference in home range sizes of males during the postfledging period among woodlots in forested and agricultural landscapes. Males without young had significantly larger home ranges (7.2 ha) than those with young (2.2 ha). Most males remained within a few 100 m of their capture location regardless of landscape type. Males with young remained in a 2-3 ha area around the capture site, suggesting they remained near their territory. Home ranges during the breeding season in forest fragments (1.8 ha) and contiguous forests (1.6 ha) were similar to those of males with young during the postfledging period (Bayne and Hobson 2001a).

Jenkins and Faaborg (2016) studied the effects of cowbird fledglings on Ovenbird fledglings in Missouri. There was no significant difference in mortality rates of Ovenbirds from parasitized and unparasitized nests. Ovenbirds from unparasitized nests moved further from the nest (150 m) than broods with a cowbird fledgling (60 m). The negative effects of cowbird parasitism did not extend into the postfledging period.

MIGRATION

The Ovenbird appears to be a nocturnal migrant. During spring, males migrate before females. In Michigan, male arrival was spread out over a few days and they arrived 9-14 days before the first female. The average time between arrival of all males and females was 7 days; females arrived simultaneously. The age classes may migrate separately in spring and autumn. Some studies indicate differential timing and others do not. The length of stopover during migration is significantly briefer in spring than autumn. During spring in Louisiana, the average length of stopover was 1.68 days (maximum 3 days). Lean birds stayed longer than fat birds. In Maine, the minimum length of stopover was 2.4 days in spring and 5.1 days in autumn. During autumn migration in New York, Ovenbirds stayed 1-14 days. The fat content of birds remaining only 1 day was at least 11% of the total body mass but all with fat content of less than 6 percent remained at least 4 days. One bird stored sufficient fat to continue migration after 8 days, yet remained an additional 6 days. The wind was from the north on the night it departed, but was from the south previously. This bird possibly waited 6 days for favourable flying conditions (Brewer et al. 2018; Hann 1937; Moore and Kerlinger 1987; Morris et al. 1994; Seewagen and Guglielmo 2010; Van Horn and Donovan 1994).

The Ovenbird mostly arrives in Ontario at the beginning of May and migration is over by the end of May; it may arrive as early as mid-April. Peak migration occurs during the second and third weeks of May (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). During 1975-2000, the midpoint of Ovenbird migration at Long Point was 15 May and there was no difference in timing of spring migration in relation to climate change when either the date of first arrival or the quartile method was used (Mills 2005a).

Determination of the timing of autumn migration is confounded by the fact that birds move to shrubby, atypical breeding habitat once the young have fledged. It is difficult to distinguish between birds that are occupying postbreeding habitat from those that are migrating. Records of autumn migrants in July and early August probably represent birds in postfledging habitat. In the southern Shield, migrants are on the move from late August to mid-September, with some remaining until early October (Mills 1981; Tozer 2012). In southern Ontario, the peak of migration occurs in the first 2 weeks of September. Birds may arrive in late August and most have left by late September or early October, with stragglers remaining until mid-December (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). Throughout its range, the Ovenbird begins autumn migration in early to mid-August and the northern breeding grounds are vacated by the end of September (Gross in Bent 1953).

Several studies examined habitat preferences of the Ovenbird during migration. In Pennsylvania, it was detected more frequently in less fragmented landscapes and was more likely to occur in larger than smaller woodlots. It was found in smaller habitat patches during migration than during the breeding season (Keller and Yahner 2007). In oak savannahs and woodlands in Indiana, abundance of spring migrating Ovenbirds was positively associated with tree density. Relative abundance was 0.5 at 400 trees per ha and reached almost 1.0 at 600 trees per ha (Grundel and Pavlovic 2007a). In British Columbia, migrants may inhabit floodplains, fields, trembling aspen sapling forests, brushy thickets, areas of thick undergrowth, and occasionally suburban areas and city parks (Campbell et al. 2001). In Saskatoon, it occurs primarily in wooded areas such as riverbank parks, but may venture out of shrubbery and walk across lawns (Leighton et al. 2002). In Illinois, spring migrant populations were highest in bottomland forests in the southern portions of the state and in upland forests centrally. In autumn, highest densities were in bottomland forests in the south but it was equally common in bottomland and upland forests centrally. It used all types of woody habitats that were surveyed during autumn (Graber et al. 1983). During spring migration in Wisconsin and Minnesota, it was significantly more abundant in upland than riparian forests (Kirsch et al. 2013). During spring migration in Pennsylvania, Smith and Hatch (2008) observed and captured significantly more Ovenbirds in forest than shrub habitat. In Pennsylvania during spring, it was significantly more abundant in mature upland forest than in mature riparian forest. The main differences in the habitats were that the upland forest had 74% canopy closure and 39% shrub coverage compared with 83% canopy closure and 19% shrub coverage in the riparian forest (Rodewald and Matthews 2005). Spring migrants prefer forests to shrublands; forests with dense shrub coverage are preferred to those with sparse coverage. Rodewald and Brittingham (2002) examined the distribution of autumn migrating Ovenbirds in Pennsylvania woodlands. In decreasing order of abundance, it occurred in forest interior followed by suburban forest, forest edge, forest-agricultural edge, pole-stage forest, and shrub-sapling-stage forest. There was no difference in its abundance in these habitats. Rodewald and Brittingham (2004) updated this study. Significantly more Ovenbirds were found during autumn migration in forest interior than in shrub-sapling-stage forest. Numbers within the other habitat types were not significantly different from those occurring in forest interior or shrub-sapling-stage forest.

In North Carolina, Parnell (1969) studied habitat and substrate preferences of the Ovenbird during spring migration. It was absent in wet and dry thickets and occurred in most forest types, but

selected pine-hardwoods, pine, and oak-hickory stands over floodplain and beech forests. Forty-six percent of observations were in a low tree, 22.6% in a shrub, 21.7% on the ground, and 9.7% in the canopy. Birds occurred at heights of 0-7 m (average 1.2 m). In low trees, 0% of observations were at the top of the crown, 13.7% in the inner crown, 32.3% in the lower crown, and 0% on the bole. In shrubs, 3.2% of observations were at the top of the crown, 7.3% were in the inner crown, 0.8% in the lower crown, 7.3% in dense thicket, 4.0% in brush piles, and 0% in grasses. On the ground, 4.0% of observations were in dense thicket, 0.8% in grasses, 0% at the edge of water, and 16.9% in the open. In the canopy, 0% of observations were at the top of the crown, 1.6% in the inner crown, and 8.1% in the lower canopy.

Tozer (2012) reported a case of site fidelity in a grey alder thicket in Algonquin Park. An Ovenbird banded on 30 August 1960 was recaptured in the same location on 27 August 1961, 27 August 1962, and 19 August 1963.

The autumn of 1975 was unusually cold in Ohio. During migration that year, Tramer and Tramer (1977) reported an Ovenbird eating fruit from a yew. Arboreal arthropods and insects were scarce that year, forcing it to eat fruit. During autumn migration in New York, Lebbin et al. (2007) suspected that Ovenbirds were foraging nocturnally at a site illuminated by football-stadium lights.

Massive kills of the Ovenbird frequently occur during migration. These are usually associated with frontal movements, most frequently cold fronts in association with high pressure systems. Under these conditions, it may strike tall structures such as office buildings and television and communication towers. Many are killed by flying into windows of houses. At the Lennox generating station chimneys near Kingston, 1,127 were killed 1972-82. Probably more Ovenbirds have been killed at central Illinois television towers than any other species (Graber et al. 1983; Leighton et al. 2002; Van Horn and Donovan 1994; Weir 2008). Loss et al. (2014) summarized bird-building collision data for the United States. At all building types combined, the Ovenbird was 21.8 times more at risk of collisions than average for bird species. At 1-3 storey residences, it was 112.1 times more vulnerable, 30.4 times more vulnerable at low-rises, and 43.7 times more vulnerable at high-rises. It is one of the species most vulnerable to striking high-rise buildings in Toronto (Colling et al. 2022).

Strode (2003) studied the effects of climate change in Illinois and North Dakota on the timing of spring migration by the Ovenbird. Over 100 years, there was no significant change in temperature in southern Illinois, but over a 40-year period spring advanced an average of 8.6 days in North Dakota. The Ovenbird arrived earlier on its breeding grounds, suggesting that it was responding to climate change.

James (1991) considered the Ovenbird a common to abundant migrant. This is true for most of the province, but it is an uncommon migrant in Niagara Region, Elgin County, and sparsely forested areas in the southwest (Black and Roy 2010; Lancaster et al. 2004).

Hussell et al. (1992) summarized trends in numbers of Ovenbirds banded at the Long Point Bird Observatory 1961-88. It experienced a significant decline of 2.9% per year. Numbers fluctuated considerably with a decrease during the first decade and a weak increase the following decade, followed by a large decline. This pattern was exhibited by several other species and may be influenced by spruce budworm outbreaks.

WINTER

The Ovenbird is rare and irregular during winter in Ontario (James 1991). Most winters, it is likely that there are no Ovenbirds present in the province. It is uncertain if an Ovenbird has ever survived an entire winter in Ontario. One remained in an urban Hamilton garden from 26 November until 12 January. It survived by eating high-fat foods put out for it (Curry 2006). One was at Presqu'ile on 2 January where it sought shelter under large spruce trees. It was last seen 2 days later following a heavy snowstorm (LaForest 1993). One was observed in Toronto on 6 February and was last seen on 7 March. It took shelter under spruce trees and near a washroom that emanated warm air. It was observed feeding on peanut particles at a feeder. Another Ovenbird survived at an Ottawa feeder until 28 February (Bryant 2002).

The Ovenbird normally winters as far north as North Carolina, but there are casual winter occurrences north to the Great Lakes and New England. It usually does not winter where the average January temperature is less than 0°C and is most abundant where this temperature is 10°C or higher. Mulvihill and Leberman (1977) reviewed 80 extralimital winter records: 61% in December, 25% in January, 9% in February, and 9% in March. Multiple records occurred in winters or portions of winters that were unusually mild with little snow cover. Deaths typically coincided with periods that had both cold temperatures and significant snow accumulations.

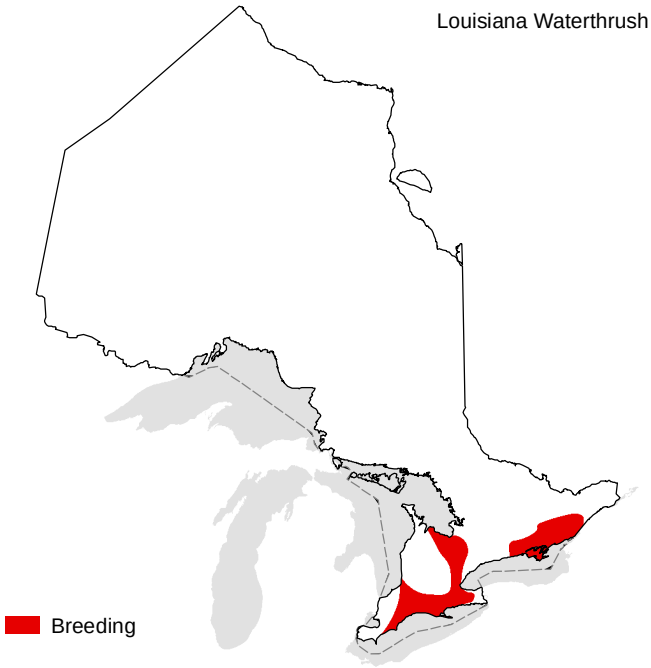
Louisiana Waterthrush

Parkesia motacilla

BREEDING SEASON

Habitat Requirements

Breeding habitat of the Louisiana Waterthrush in Ontario consists of deciduous woodlands that are swampy or contain flowing streams with more or less vertical earthen banks. Two nests were in a mixed forest dominated by hemlock in Elgin County (Peck and James 1987, 1998a). It prefers heavily wooded ravines with running water, particularly in east Elgin where the soils are sandy. One nest was along a small tributary at the bottom of a steep hemlock-dominated ravine (Lancaster et al. 2004). In the Hamilton area, it occurs in rocky ravines containing streams, particularly where there are larger waterfalls along the Niagara Escarpment (Curry 2006; McIlwraith 1894). In southern Ontario, its distribution is dictated by climate, the presence of forested creek and river valleys, and abundance of large swamps that contain ponds and vernal pools. It occurs at elevations lower than 300 m and in regions above the 6°C isotherm for annual temperature. It prefers mature deciduous and mixed forests where there are shaded watercourses with underbrush and old logs lining stream banks. It prefers steep-sided talus slopes facing southward and selects cold, clear streams most frequently for nesting. The forests that are inhabited are often late successional and dominated by



sugar maple and hemlock. Less frequently, it inhabits mature deciduous and mixed swamps with standing pools of open water. Closed forest canopies and presence of water are essential habitat components (Austen et al. 1994; McCracken 1991, 2006). At Chesney Bog, it nested in a mature mixed swamp surrounding a bog. The swamp was dominated by white pine and red maple, with lesser amounts of white cedar and yellow birch. This habitat supported 593 trees per ha that were 7.6 cm or larger in diameter and 87 trees per ha 22.9 cm or larger. The total basal area (BA) was 16.1 m^2 per ha. Canopy closure was 85% and the average canopy height was 16.8 m (range 9.1-27.4 m). There were 17,890 shrub stems per ha with the 5 most frequently occurring species being winterberry holly (29.7% of total shrub stems), white cedar (23.3%), red-osier dogwood (8.0%), black ash (5.5%), and yellow birch (5.4%). Portions of the swamp are quite hummocky and support vernal pools (personal observation). At Former Camp Ipperwash, it nested in mature, mixed mesic forest dominated by sugar maple and hemlock with numerous vernal pools. There was also extensive mature deciduous swamp dominated by pumpkin ash, silver maple, and cottonwood adjacent to and interspersed within the mixed forest (personal observation). It also nested at Vanessa Swamp, a mature deciduous swamp with vernal and semi-permanent pools (personal observation).

Throughout its range, preferred habitat of the Louisiana Waterthrush is along watercourses in mature deciduous and mixed forests. Preferred streams are clear and cold, often with springs, and have a steep gradient. These watercourses have a series of riffles and pools, and waterfalls are often present. Typical stream substrate is cobbles and gravel, with cobblestones optimal because the interstitial spaces provide habitat for aquatic macroinvertebrates and the stones provide foraging perches for this waterthrush. Most selected streams are permanently flowing, but some may be reduced to isolated pools by the time the young fledge. Its presence in Georgia was correlated with the percentage of mayflies, stoneflies, and caddisflies in the benthic macroinvertebrate population and also to the invertebrate Family Biotic Index. Waterthrush presence is used as an indicator of high stream quality in that state. Streams it inhabits are frequently in ravines and may have talus slopes and often undercut banks, exposed tree roots, and logs along the shoreline. Watercourses that it uses are typically small first- to third-order headwater streams, but it occasionally inhabits larger streams and small rivers. In Minnesota, there were several streams populated with this waterthrush, but it avoided areas where the valley became broad and flat with limited forest canopy. Much less frequently, it may nest along slow-flowing streams through swamps, and these watercourses typically have a soft substrate of silt or mud (Bent 1953; Chapman 1907; Coffin and Pfannmuller 1988;

Eaton 1958; Eliason and Fall 1989; Graber et al. 1983; Mattsson and Cooper 2006; Mattsson et al. 2011, 2020; Mossman 1988; Mossman and Hoffman 1989).

Upland forests inhabited by the Louisiana Waterthrush are most often dominated by sugar maple and often have a component of basswood, mountain maple, and conifers, especially hemlock or white pine. The conifers provide essential cover in the spring prior to the leaf-out of deciduous trees. In both upland and swamp forests, it is restricted to mature, late-successional stands. It prefers low to moderate shrub density in the understorey and avoids areas with dense, woody undergrowth (Buffington et al. 1997; Bushman and Therres 1988; Eaton 1958; Eliason and Fall 1989; Noon et al. 1979; Prosser and Brooks 1998).

Prosser and Brooks (1998) prepared a habitat suitability index (HSI) model for the Louisiana Waterthrush in Pennsylvania. It was designed to be used in areas containing first- to third-order streams in the mid-Atlantic states. It preferred high-quality headwater streams with well developed pool and riffle sequences; large blocks of forest-interior habitat where herbaceous cover was sparse and shrub coverage was moderate to sparse; areas of fallen trees with exposed root masses; and riparian banks with abundant crevices. It was absent in highly fragmented landscapes and where sediments from agricultural and urban lands had negatively affected water quality and stream substrates. The HSI model ranked habitats on a scale of 0 (unsuitable) to 1 (optimum). The model for forest canopy closure was: more than 80%, 1.0; 60-80%, 0.7; 40-59%, 0.2; and less than 40%, 0. The model for percent shrub cover was: for 0.1-1.5 m tall shrubs, 75% or more coverage 0.1, 24-74% coverage, 0.3, and 25% or less, 0.5; for shrubs taller than 1.5 m, 75% or more coverage, 0.4; 24-74% coverage, 1.0; and 25% or less, 0.8. The model for percent deciduous forest cover was: 0-29%, 0.5; 30-69%, 1.0; 70-100%, 0.5. The model for percent herbaceous cover less than 20 cm tall was: 75% or more, 0; 24-74%, 0.3; 25% or less, 1.0; for percent herbaceous cover 5-20 cm tall, 75% or more, 0.3; 24-74%, 0.7; 25% or less, 1.0; and for percent herbaceous cover less than 5 cm tall, more than 75%, 0.7; 24-74%, 1.0; 25% or less, 1.0. The model for stream type was: first- or second-order stream with well developed pool and riffle areas, 1.0; first- or second-order streams with steep topography, continuous rapid riffles, a straight channel or run, or flat water, 0.7; third-order stream comprised mostly of riffles and pools, 0.5; and third-order stream that was mostly a run or greater than third-order stream, 0.2. The model for stream substrate was: clear streams with coarse or sandy substrate, 1.0; clear streams with fine substrate, 0.5; turbid streams with coarse or sandy substrate, 0.5; turbid streams with fine substrate, 0. The model for stream bank slope and cover type was: a mix of soil, roots, and rocks forming crevices with an overhanging bank with more than 60° slope, 1.0; the same bank type with 30-60° slope, 1.0; the same bank type with less than 30° slope, 0.7; more than 75% rock banks, 0.1 for all slope categories; and more than 70% herbaceous coverage, 0.1 for all slope categories. The landscape model was: forest with interior habitat larger than 350 ha, 1.0; within 100 m of the edge of a large forest but within the forest, 0.8; shrubland or highly fragmented forest, 0.5; emergent wetland, agricultural field, or open water, 0.2; and urban, 0.

The other habitat type used by the Louisiana Waterthrush consists of mature treed swamps. These may contain either streams or small ponds and vernal pools. The presence of water is essential to this species in both upland forests and swamps. In most regions, swamps are much less preferred than watercourses in upland forests and it tends to be uncommon to rare in swamps. The exception

is in Missouri where it is uniformly distributed in swamps. In swamps in South Carolina, it occurred exclusively in late-successional stands dominated by black gum, red maple, and tulip tree. These stands had an average of 92.5% canopy closure, 18.3 m canopy height, 36.0% green ground cover, 35.8% coverage by water, 139 shrubs per ha, and a BA of 43.7 m^2 per ha. In the mid-Atlantic states, its probability of observation was positively correlated with BA, forest area, moisture gradient, and foliage density between 0.3 and 1.0 m from the ground. It was negatively correlated with the percentage of the canopy that was occupied by conifers (Bent 1953; Buffington et al. 1997; Chapman 1907; Graber et al. 1983; Robbins et al. 1989).

In North Carolina, the Louisiana Waterthrush was not observed in the canopy or in low trees; 62.5% of observations were in shrubs and the remaining 37.5% were on the ground. It was observed at heights of 0 m to more than 15 m, with an average of about 4.5 m for singing males, 0-6.9 m for other activities, and an overall average of 1.2 m from the ground. It was associated with the ground and low tree layer in beech and floodplain forests (Parnell 1969).

In Connecticut, Craig (1985) compared habitat use by the Louisiana and Northern waterthrushes. The 2 species occurred together and their territories overlapped widely with no apparent signs of aggression. In Louisiana Waterthrush territories, the percent coverage by herbaceous species was 6.7% cinnamon fern, 8.7% sensitive fern, 9.2% skunk cabbage with a total of 17.4% forbs, 17.9% ferns, and 19.9% moss. Louisiana Waterthrush territories had significantly more fast-flowing water, were less densely vegetated with trees and shrubs, and had less coverage by conifers, moss, ferns, and alders than those of the Northern Waterthrush. The amount of fast-flowing water may be the most important difference between the habitat of the 2 species, with Louisiana Waterthrush territories containing 23.7% fast-flowing water compared with 3.8% in Northern Waterthrush territories.

The Louisiana Waterthrush appears to be area sensitive throughout its range. In Maryland, the smallest woodland it occurred in was 42.2 ha and it did not reach 100% occurrence until woodlands were larger than 340 ha. In Maryland and the mid-Atlantic states, the critical forest size was estimated at 100 ha. Its probability of detection was 10% at 75 ha, 20% at 1,000 ha, and 25% at 3,200 ha. The forest size where its probability of detection was greatest was larger than 3,000 ha and the probability declined to 50% at 200 ha. The 3 smallest forests where it was detected at least twice were 24.7, 24.7, and 184.1 ha (Bushman and Therres 1988; Hayden et al. 1985; Robbins 1979; Robbins et al. 1989). In Illinois, all forests studied by Robinson (1992) were relatively small (maximum size of 65 ha), yet supported the Louisiana Waterthrush. In riparian forests in Maryland and Delaware, its probability of detection increased significantly with forest width: 9% in 50-m wide forests, 11% in 100-m wide, 15% in 200-m wide, and 65% in 800-m wide forests (Keller et al. 1993).

Some authors (Bushman and Therres 1988; Freemark and Collins 1992; Hayden et al. 1985) considered the Louisiana Waterthrush a forest-interior species. There appear to be no strong data to support this. Nests averaged 58 m from a transmission line corridor in Maryland and Bushman and Therres (1988) considered this evidence of edge avoidance. Given that the average distance from edge was only 58 m, many nests must have been much closer than this to edge. No information was provided on the minimum distance from edge. The forests studied by Robinson

(1992) in Illinois contained abundant edge and there were no woodlots where birds could nest more than 250 m from edge.

The female roosts in the nest at night from the start of incubation until the young are fledged. Males have roosted in hemlock trees and on exposed roots under overhanging creek banks (Eaton 1958; Mattsson et al. 2020).

Ontario nests were in depressions in earthen banks of streams and pools and in natural cavities in stumps surrounded by water. Five nests were 0.2-1.2 m above water (average 0.7 m). Nests in banks were concealed by roots and overhanging vegetation (Peck and James 1987). Another Ontario nest was on a sloping bank of a stream 0.9 m above the creek surface under live and dead fronds of Christmas fern (Peck and James 1998a).

Nests in upland forests are typically imbedded in the bank of a stream, often among tree roots, in cavities in the bank, on bedrock shelves, or under the edge of a ledge. Nests in swamps are usually in roots of upturned trees, often at the edge of a pond or pool of water. In Georgia, 162 nests were oriented in every direction, but many faced southwest and few faced east. In New York, 10 of 13 nests faced south and the others faced east. In Illinois, 5 nests faced south, 5 west, and none east or north. Preferred nest sites are adjacent to streams and are in small hollows or cavities within the root mass of an upturned tree or under a fallen log. Cavities where the nest is protected from above are preferred, but some nests are only partially covered or even completely exposed. Nests in stream-bank cavities were 0.2-7 m above a stream, but most are less than 2 m above water. In swamps, where most nests are in upturned tree roots, the nest may be as high as 1.8 m above ground or water. Nests are not reused, but nest cavities may be. Of 113 nest cavities used the previous year in Georgia, 7 were reused by a different pair and 3 were used by the same male mated to a different female. Four Pennsylvania nest sites were used in multiple years by different birds. One nest cavity was used twice in the same breeding season in 2 years following a flood event in both cases (Bent 1953; Chapman 1907; Eaton 1958; Eliason and Fall 1989; Forbes and O'Regan 1960; Graber et al. 1983; Harrison 1984; Mattsson et al. 2020).

The Louisiana Waterthrush is strongly territorial, mostly before the females arrive and again during incubation. Males sing in tree perches 5-12 m from the ground or on talus slopes, but usually about 9 m from the ground, and rarely on the ground. For birds nesting along a watercourse, only the stream is defended and it is used as a travel corridor within the home range. In Ontario, territories are rarely, if ever, contiguous to one another. The size of territories within swamps in Ontario was 2 ha. In Connecticut swamps, territories averaged 0.67 ha. In upland habitats, territories were linear and followed the watercourse. In New York, territories extended approximately 400 m along a watercourse. Nests tended to be near the centre of territories so that nests were spaced about 400 m apart. Nests were only 200 m apart on 1 stream where a waterfall formed territory boundaries. One male included 2 streams that were close to each other in his territory. In Illinois, stream territories averaged 930 m in length. They averaged 358 m in Connecticut, 520 m in Georgia, and 283 m in northeastern Pennsylvania, with an overall range in territory length of 90-1,200 m. Stream quality affects territory length, with streams that are acidified or degraded due to other pollutants or sediments supporting longer territories and lower densities of waterthrushes. In Pennsylvania, territories averaged 630 m in length on acidified streams compared with 370 m on circumneutral

streams. The average area of stream territories is 2 ha, assuming an average width of 50 m and average length of 400 m. The accuracy of these assumptions is uncertain. Some authors stated that it rarely uses the upland habitat adjacent to streams. In Minnesota, a pair nested along a river that was more than 100 m wide and the male often flew across the river to forage on the opposite shoreline. It was unknown if the far side of the river was an undefended feeding area or part of the territory. It has been estimated that a home range size of about 25 ha is required over the course of the breeding season to successfully raise young (Craig 1984; Eaton 1958; Eliason and Fall 1989; Friis and Brett 2012; Mattsson et al. 2020; McCracken 2006; Mulvihill et al. 2002, 2008).

Natal philopatry rates are low. In Tennessee, 0 of 49 nestlings returned. At the same site, 113 fledglings were banded and 4 (3.5%) returned. Three were banded in July when they may have been dispersing, but the fourth bird probably hatched locally. In Pennsylvania, 1 nestling returned to breed the following year and a male banded as a nestling in New York was collected 2 years later 4 km from its natal site (Goodpasture 1977; Mattsson et al. 2020; Mulvihill et al. 2002). In West Virginia, Frantz et al. (2019) banded 222 nestlings over 6 years. Natal site fidelity was consistently low and ranged from 0% to 5.1% annually, with an overall return rate of 1.7%. Highest return rates occurred in years when adult breeding densities were lowest, suggesting that natal dispersal might be density dependent. When areas are saturated with breeding birds, dispersal by yearlings may enhance individual survival or the prospects of finding unoccupied suitable breeding habitat.

In Tennessee, 20 of 152 adults (13.2%) returned. Some made multiple returns with 1 returning after 8 years, 1 after 5 years, 3 after 4 years, 8 after 3 years, 10 after 2 years, and 17 after 1 year (Goodpasture 1977). Of 201 Pennsylvania territories, 18% of males and 15% of females returned at least once, and 13% of males and 7% of females returned at least twice (Mulvihill et al. 2009). Also in Pennsylvania, females exhibited high territorial fidelity, with as many as 50% reoccupying their previous year's territory (Mulvihill et al. 2002). In Illinois, 2 of 3 adults returned the next year in 1 area and 0 of 4 returned at another site (Mattsson et al. 2020; Robinson 1992). In West Virginia, Frantz et al. (2019) banded 187 adults over a 6-year period. Adult return rates were 63% in the first 2 years but declined to 32% at the end of the study. Habitat quality declined during the study due to disturbances from shale gas extraction.

Limiting Factors

Eggs have been reported in Ontario nests from 1 June to 8 July (Peck and James 1998a). McCracken (1991, 2006) concluded that eggs could be present in Ontario nests from early May until mid-July, including renesting attempts.

Nest-site searching may be delayed 1-2 weeks after pair formation unless this occurs later in the season. The delay appears to be related to food availability. Nest building begins about the same time that spring vegetation begins to leaf out. Most nests are completed in 2-5 days but replacement nests may be built quicker. In some nests, there is a delay of 1-7 days before the first egg is laid. Egg laying begins immediately in other nests. One egg is laid per day. Incubation may begin the day before the last egg is laid. The incubation period is 11-14 days, mostly 12-14 days. All young hatch over a 24-hour period. Young may leave the nest when they are 9-12 days old, but mostly when they are 11 days old. The nest cycle length was 22.9 days in Pennsylvania and 21.7 days in Georgia. In Pennsylvania over several years, the breeding season extended 107 days from the

earliest clutch initiation to the latest observation of provisioning of fledglings. Initiation of egg laying in first clutches ranged over more than 6 weeks. A total of 48-55 days were required from clutch initiation to fledgling independence, approximately half the breeding season (Eaton 1958; Forbes and O'Regan 1960; Harrison 1984; Mattsson et al. 2011, 2020; Mulvihill et al. 2009).

The Louisiana Waterthrush typically raises a single brood in a season (Eaton 1958), but rare cases of double brooding have been reported further south in its range. It is highly unlikely that any second broods are raised in Ontario. In Pennsylvania, 5.6% of pairs that successfully fledged young from their first nest attempted a second brood; 4.8% and 8.4% of birds attempted second broods in 2 Georgia studies. In Pennsylvania, the mean date of first clutch initiation was significantly earlier for birds attempting to raise a second brood (29 April) than for birds raising a single brood (4 June). Only those birds that initiate nesting shortly after arrival have an opportunity to raise a second brood. Of 24 pairs that initiated nesting early, 8 attempted a second brood and 5 were successful. Pairs attempting second broods fledged an average of 7.0 young compared with 2.3 for single-brooded pairs. No individual attempted a second brood in more than 1 year and double brooding did not occur every year. At least 58.9% of females attempting second broods were experienced breeders returning to the same territory. Only 1 yearling female was involved in a second brood and all males attempting a second brood were after-second-year birds. Almost all cases of double brooding occurred along high-quality circumneutral streams, suggesting that food availability may be a factor influencing the incidence of double brooding. Only 1 case of double brooding occurred along a stream that was moderately affected by acidification. Prey levels at the end of fledging of the first brood may be important determinants in defining the incidence of second broods (Eaton 1958; Mattsson and Cooper 2007; Mattsson et al. 2011, 2020; Mulvihill et al. 2009). It commonly renests if the first nest is lost. The replacement clutch may be initiated 1-6 days after the first is lost (Eaton 1958; Mulvihill et al. 2002). In Pennsylvania and Georgia, its probability of renesting was 65.8% and 54.2%, respectively. The higher incidence of renesting further north was because of greater food availability due to the longer daylight hours (Mattsson et al. 2011). In Pennsylvania, 38.2% of pairs that had their first replacement nest fail attempted a third nest (Mulvihill et al. 2020). In Georgia, 36 of 75 first nests (48.0%) that failed were followed by a replacement nest. Third and fourth nesting attempts were uncommon: 3 of 26 pairs (11.5%) attempted third nests and 1 of 1 attempted a fourth nest. Of 10 abandoned nests, replacement clutches were laid in 4 cases and adult mortality was involved in the other 6 cases. Loss of the first nesting attempt was more influential on productivity because replacement nests contributed little to productivity (Mattsson and Cooper 2006). Clutches of 4-5 eggs were reported in Ontario (average 4.5; Peck and James 1998a). Elsewhere, it lays 3-6 eggs with 5 eggs the most frequent clutch size. The size of first clutches was 4.8 in Pennsylvania and 4.7 in Georgia; the size of replacement clutches was 4.3 and 3.8, respectively. In Pennsylvania, clutches of nests along circumneutral streams were significantly larger (4.8 eggs) than those along acidified (4.5 eggs) streams (Bent 1953; Chapman 1907; Eaton 1958; Graber et al. 1983; Mattsson and Cooper 2007; Mattsson et al. 2011; Mulvihill et al. 2008). Presumably streams affected by organic pollution and sediments would also contribute to smaller clutch sizes.

The age at first breeding is 1 year and birds nest every year thereafter provided they can find a mate (Mattsson et al. 2020). The mating system is typically monogamous. Of 283 males (1.4%) were polygynous in Pennsylvania. Polygyny may be promoted by females' high site fidelity. Females may

mate with the territorial male even if he has another mate. The sex ratio may be female biased, contributing to the potential for polygyny. In 1 case, the primary female lost her clutch. The male extended his territory by 250 m, drove off the male that was defending this area, nested with the female of the male that he had ousted, and renested with the primary female. One male nested with another female 1 km away. One male was polygynous in 2 successive years. Nests of secondary females overlapped only with the late stages of fledgling care of the first nest. One female was polyandrous and double brooded, switching mates between broods. In 6 other cases of double brooding, the pair remained united for both broods. Occasionally mates reunite in subsequent years. In Georgia, 9 of 29 matings (31.0%) comprised of individuals present the previous year consisted of birds mated with their previous mate (Mattsson et al. 2020; Mulvihill et al. 2002, 2009).

Early in the season, the Louisiana Waterthrush forages entirely in streams. Later in the season, if streams dry up, it may feed in adjacent upland forests or along lakeshores and exposed riverbeds. Swamp-dwelling birds forage at edges of pools and ponds. The male and female often forage together prior to incubation, but forage alone during the incubation and nestling stages. One adult flies downstream and the other upstream to forage and birds move upstream while feeding. It forages by wading and walking along logs, flat bare rocks, on branches, and at the water's edge. The use of microhabitats for foraging changes as the breeding season progresses. In Illinois, from territory acquisition until the end of laying, 90% of foraging manoeuvres were directed at water; 7% at soil, rocks, or dry leaf litter (ground); 2.5% at foliage; and 0.5% at flying insects. During incubation, 60% of foraging was directed at water, 19% at the ground, 20% at foliage, and less than 1% at flying insects. During the nestling period, 63.5% of foraging was directed at water, 23% at the ground, 11% at foliage, and 2.5% at flying insects. In Connecticut prior to leaf-out, 80% of foraging was directed at water and 20% at the ground, with no foraging observed on foliage or flying insects. After leaf-out, 53.3% of foraging was directed at water, 28.3% at the ground, 14.2% at foliage, and 4.2% at flying insects; these differences were significant. It captures both submerged and floating organisms. It finds prey items by flipping leaves to pick up animals beneath, poking its bill into crannies, picking food items directly out of the water by wading, and jumping from the ground to capture flying insects. It takes prey from water 2 cm or less in depth. When feeding on woody plants, it walks on stout branches and picks prey from foliage and stems. During a stonefly outbreak in New York, it foraged along deciduous and coniferous branches several metres above ground. Foraging techniques include picking prey from rocks, mud, moss, leaf litter, and vegetation; leaf-pulling (pulling dead leaves from water or litter to inspect them for prey); hawking (sallying upward for flying insects); and hovering. In Connecticut, foraging methods changed significantly as the season progressed. Prior to leaf-out, 53.3% of foraging attacks were by picking, 44.0% by pulling, 0% by hawking, and 2.6% by hovering. After leaf-out, 86.6% of foraging attacks were by picking, 5.5% by pulling, 30% by hawking, and 4.9% by hovering (Craig 1984, 1987; Eaton 1958; Eliason and Fall 1989; Mattsson et al. 2020).

Craig (1984) compared the foraging ecology of the Louisiana and Northern waterthrushes. Both species exhibited similar behaviours when foraging, had similar attack rates, and fed on submerged and floating organisms. The 2 species foraged similarly prior to leaf-out but there was a significant divergence in the foraging sites used after leaf-out. The Louisiana Waterthrush foraged mostly on the ground and at aquatic sites. The Northern Waterthrush had a wider range of foraging substrates

including ground, water, and foliage. There was an overlap in use of foraging sites of 98% before leaf-out and 92% after leaf emergence. The foraging methods of the 2 species overlap to a greater degree than for other closely related species.

Small items are initially fed to nestlings, but by the time they are 5 days old, they may be brought prey as large as cicadas. At 1 nest, most food items brought to nestlings were mayfly nymphs or adults. Along an acidified watercourse where mayflies were almost completely absent, young were fed novel prey items such as terrestrial salamanders. In New York, 1 nestling′s stomach contained 85% insect fragments by volume, 5% snails, 5% adult beetles, and 5% grit. Another contained 85% insect fragments, 10% beetle adults, and 5% grit. In Arkansas and Pennsylvania, DNA sequencing was used to determine nestlings′ diet. The researchers hypothesized that the nestling diet would be comprised predominantly of mayfly, stonefly, and caddisfly taxa and that the diet would change over the course of the nesting season in response to changes in the aquatic insect community. Contrary to predictions, lepidopterans occurred in 92% of fecal samples and they were significantly more common in the diet than any other order in Pennsylvania and any other order other than flies in Arkansas. Flies (70% occurrence) and mayflies (61% occurrence) were frequent in the diet. Among the mayfly, stonefly, and caddisfly orders, mayflies were most frequently represented, contributing to 93% of taxonomic units. Stream mayflies, whose nymphs typically occur in rapidly flowing water, occurred in 58% of Arkansas fecal samples and 61% of Pennsylvania samples and were the only family of mayflies found in the diet in Arkansas. Stoneflies and caddisflies were detected in only 9 samples from Pennsylvania, representing 7% and 1% of taxa, respectively. These orders were not detected in samples in Arkansas. The diet included aquatic megalopterans and terrestrial spiders, beetles, true bugs, hymenopterans, orthopterans, and book lice. The frequency of occurrence of flies in the diet did not vary seasonally at either study area. Frequency of occurrence of lepidopterans and mayflies did not vary seasonally in Arkansas but differed significantly from late May to early June in Pennsylvania. The Louisiana Waterthrush is less dependent upon aquatic prey than previously thought, with only mayflies being important in the diet. In these study areas, it did not rely predominantly on pollution-sensitive aquatic species. The usefulness of using the Louisiana Waterthrush as a predictor of high-quality streams, and the contention that water quality impairment is a significant threat to it may be overstated or incorrect (Craig 1984; Eaton 1958; Trevelline et al. 2016).

In New York, fly larvae (midges, soldier flies, and crane flies) and beetles (water-scavenger and click beetles and weevils) were the dominant foods of adults, but the Louisiana Waterthrush highly preferred mayflies and stoneflies. Nymphs of these orders were taken 1-2 days before they emerged and waterthrushes feed heavily on subimagos and adults during emergence. Other prey consisted of caddisflies, bugs, earthworms, millipedes, and alderflies. In Connecticut, 96.0% of prey was aquatic. The diet consisted of 40.7% caddisflies, 20.3% flies, 13.6% mayflies, 13.6% oligochaetes, and 3.4% isopods based on observations of prey captures. Other food items included dragonfly nymphs, predaceous diving beetle larvae, crane fly larvae, snails, mosquito larvae and adults, terrestrial millipedes, and caterpillars. Other items that the Louisiana Waterthrush eats include locusts, ants, scale insects, small fish, cicadas, geometer moths, scorpions, bugs, small frogs, and larval salamanders. Compared with prey availability, it strongly preferred fly larvae, especially midges, and strongly avoided isopods. It selected prey more than 13-19 mm in length, took prey longer than 19

mm in proportion to its availability, and underutilized prey 7 mm or shorter and 7-13 mm in length. It ate prey as large as 30 mm (Bent 1953; Craig 1984, 1987; Eaton 1958; Harrison 1984; Mattsson and Cooper 2006; Mattsson et al. 2020; Mulvihill et al. 2009).

Craig (1984, 1987) compared the diet of the Louisiana and Northern waterthrushes. The Louisiana Waterthrush ate significantly more caddisfly larvae and fewer flies (mostly midges) than the Northern Waterthrush. The most significant difference between the diet of the 2 species was the size of prey consumed. The Northern Waterthrush showed no size preferences; the Louisiana Waterthrush preferred prey 13-19 mm in length. Caddisflies comprised 52% of prey larger than 13 mm in Louisiana Waterthrush territories compared with 31% in Northern Waterthrush territories. The biomass of aquatic insects larger than 13 mm was 15% higher in Louisiana Waterthrush territories than in Northern Waterthrush territories. The 2 species were not ecologically separated by interspecific territoriality, divergence in foraging sites, or divergence in foraging methods. They appeared to select territories with different sizes of aquatic invertebrates. Fast-flowing water supports a higher density of larger invertebrates which may explain the Louisiana Waterthrush's preference for fast-flowing streams.

The Louisiana Waterthrush is a common host of the Brown-headed Cowbird. Cowbirds remove a waterthrush egg prior to laying one of their own. Young waterthrushes are occasionally jostled out of the nest by cowbird nestlings and 1 young cowbird killed 3-4 young waterthrushes just before they fledged. The cowbird occasionally lays before the Louisiana Waterthrush does, and these eggs are sometimes buried in the nest. Most cowbird eggs are laid during the waterthrush's laying period and these eggs are either accepted or punctured and ejected. The Louisiana Waterthrush frequently fledges both species. Parasitized nests may produce 50% fewer waterthrush fledglings than unparasitized nests due to egg loss and lower success rates. Nests with greater exposure from above and those with a larger gap between the top of the nest and the cavity roof are more likely to be parasitized. Nests nearer forest edge were more likely to be parasitized in southern Illinois. In Ontario, 2 of 11 nests (18.2%) were parasitized. Two of 9 (22.2%) and 9 of 16 (56.3%) were parasitized in 2 New York studies. In Illinois, 81% of nests were parasitized in 1 study, but only 33% were parasitized at a site 35 km away. In Pennsylvania, 7% of 74 nests were parasitized in the northeast, 0% of 31 centrally, and 3% of 117 in the southwest. In Georgia, 0 of 173 nests were parasitized (Bent 1953; Eaton 1958; Hahn and Hatfield 1995; Mattson and Cooper 2007; Mattsson et al. 2020; Peck and James 1998a).

Habitat loss does not currently seem to be a major limiting factor for the Louisiana Waterthrush in southern Ontario, although habitat degradation is taking place in some areas. It is likely that considerable habitat was lost historically due to forest clearing. This, in turn, may have dried up some streams that potentially provided habitat in the past. Due to past land management practices, there are few swamp forests remaining in southern Ontario large enough to support the Louisiana Waterthrush. The remaining swamps are under pressure from agricultural drainage and drainage may dry up vernal pools and ponds that are essential within its territory (Austen et al. 1994; McCracken 1991, 2006).

Habitat degradation is the most significant limiting factor for the Louisiana Waterthrush. Degradation may result from opening up the forest canopy, air and water pollution, and changes in stream hydrology.

Friis and Brett (2012) and McCracken (1991) stated that forest thinning was a medium threat because this opens up the canopy, increases water temperature and sedimentation, results in erosion, and decreases the diversity and biomass of aquatic invertebrates. It is possible that this threat is overstated. To have any appreciable effect on water temperature, considerable lengths of the streams' banks would have to be deforested (Barton et al. 1985). Buffer strips are typically left along watercourses when forest management approved by the Ontario Ministry of Natural Resources or a registered professional forester is undertaken. These threats are likely to be realized only if extensive and unauthorized forest thinning takes place. Friis and Brett (2012) recommended, for streams supporting the Louisiana Waterthrush, that 75% of the stream length be maintained in natural vegetation, with a riparian buffer of at least 100 m. In West Virginia, forest removal due to shale gas development was detrimental. As a result of the development, forest cover declined from 95% to 91% over a 6-year period. Study streams had a mean of 23% of their length disturbed (range 0-67%). Territory density declined and territory length increased over time. Daily nest survival declined over time and all parasitism by cowbirds occurred in later years after disturbance. Nest survival averaged 37% in undisturbed areas and 31% in disturbed areas. Birds in disturbed areas fledged significantly fewer young. In addition to direct habitat change, streams in disturbed areas were affected by sedimentation. Nests were predominantly in forested habitat (94%) with 2.3% of the canopy disturbed. Disturbances related to shale gas development resulted in declines in its territory density, nest survival, nest productivity, and riparian habitat quality. Individuals breeding in disturbed areas potentially inhabited sink habitat. Declines occurred despite less than 5% forest cover loss in a predominantly forested area suggesting that factors other than forest cover also influenced demography (Frantz et al. 2018). In West Virginia, well pads, access roads, and pipelines in contiguous forest did not have any effects on this waterthrush (Farwell et al. 2019). Forest thinning in swamp habitats used by the Louisiana Waterthrush may be detrimental. Bushman and Therres (1988) reported a 50% decline due to selective logging that resulted in the understorey becoming too dense.

Mulvihill et al. (2008) studied the effects of stream acidification on the Louisiana Waterthrush in Pennsylvania. Although stream acidification is not an issue in Ontario, this research is important for 2 reasons. The first is that effects due to sedimentation and organic pollution that may result from urbanization, agricultural practices, or other disturbances will be similar to those resulting from acidification, but probably more severe. The second is that reductions in Louisiana Waterthrush populations in adjacent states due to stream acidification may reduce immigration from those areas to southern Ontario. Acidification had numerous effects in Pennsylvania. Although the mean abundance of macroinvertebrates was similar in acidified and circumneutral streams, their mean biomass was significantly lower and mayflies, a preferred food, all but disappeared in acidified streams. The average length of waterthrush territories was significantly longer on acidified (630 m) than circumneutral (370 m) streams and consequently breeding density was much lower on acidified streams. Extensive areas of habitat were unoccupied on acidified streams but occupancy gaps were rare on circumneutral streams. Significantly fewer males were paired on acidified (84%)

than circumneutral streams (92%). Acidified streams had a higher proportion of second-year birds and fewer of these birds returned to nest in subsequent years. Some birds moved from acidified to circumneutral streams. Acidified streams were occupied only as secondary or suboptimal habitat when high quality habitat was not available. Older and more experienced birds may exclude second-year birds from nesting along circumneutral streams. Pairs successfully raised young along acidified streams by decreasing density and foraging over a longer distance of stream.

Sedimentation may be the worst type of water pollution. It enriches the water and fills up the interstices among cobblestones and boulders and, in extreme cases, may bury coarser substrates. High sediment loads eliminate stoneflies and mayflies and other sensitive invertebrates. A significant limiting factor to the Louisiana Waterthrush in Ontario is fording of streams by off-road vehicles. This results in increased sedimentation which can affect food supplies. This is a growing problem on the Norfolk Sand Plain, which is where the largest population of this waterthrush occurs in Ontario (Friis and Brett 2012; McCracken 2006).

Urbanization within watersheds of streams that support the Louisiana Waterthrush may potentially to affect it, although the current threat level from this is low. Urbanization tends to result in delivery of sediments and organic nutrients to streams, which depress aquatic invertebrate populations. Urbanization often alters the hydrology of streams with resulting lower baseflow during dry periods and high peak flows during runoff events. This may cause premature drying of intermittent streams, stream bank erosion with subsequent sedimentation problems, and flooding. Flooding may result in the loss of nests either by their being washed out or by bank failure. Highly fluctuating water levels have adverse effects on aquatic invertebrates and may alternately flood or dry out waterthrush feeding areas (Eliason and Fall 1989; Friis and Brett 2012; Mattsson and Cooper 2007; Mattsson et al. 2020; McCracken 1991, 2006).

Friis and Brett (2012) concluded that irrigation or other water uses that reduced stream flows or drained swamps were a threat to the Louisiana Waterthrush.

Widespread use of neonicotinoid pesticides in southwestern Ontario agricultural lands is a threat. These persistent chemicals are especially toxic to mayflies and caddisflies which are important prey for the Louisiana Waterthrush (Heagy 2015).

A few localized threats to the Louisiana Waterthrush have occurred in Ontario. These include residential development close to its habitat; disturbance of nesting birds by fishermen, hikers, and dog-walkers along streams; and forest clearing for ski runs along the Niagara Escarpment (Heagy 2015).

Drought may have adverse effects on the Louisiana Waterthrush. Although a dry year was beneficial to it in Minnesota by exposing beaches suitable for foraging along a large river (Eliason and Fall 1989), it is not known to inhabit such areas in Ontario where it would benefit from lower water levels. Adverse effects due to drought have been observed at several sites in Norfolk County, which were abandoned following a succession of drought years (McCracken 1991, 2006).

In the Great Smoky Mountains, loss of riparian hemlocks due to the hemlock woolly adelgid did not affect Louisiana Waterthrush foraging habitat selection or adult survival rates. It selected nest sites in areas with more exposed live roots, but only where hemlocks were in poor condition. Nest

survival was lower where deciduous rather than coniferous species dominated the understorey, suggesting a potential long-term effect of hemlock decline (Bryant et al. 2020).

Eaton (1958) stated that late snowstorms appeared to have no effects upon the Louisiana Waterthrush in New York. Curry (2006) concluded that one seen on 6 April and the following 2 days in Hamilton probably perished in a late winter storm.

Price (2004) predicted that the range of the Louisiana Waterthrush might expand in southern Ontario if the average summer temperature increased by 2°C. McCracken (2006) and Friis and Brett (2012) pointed out that any northward range expansion due to climate change would likely be negated by decreased availability of water. Increased temperatures would probably contribute to lower groundwater levels and lower stream baseflows. It is more likely that the range and population of the Louisiana Waterthrush will contract due to climate changes.

Status

Until recently, the breeding distribution of the Louisiana Waterthrush was underestimated. Many breeding areas were overlooked until at least after the first atlas. Breeding was first confirmed in Aylmer in 1895 and at Rondeau in 1933. Baillie and Harrington (1937) stated that it occurred in small numbers north to Middlesex and Frontenac counties and that its only known nesting areas at that time were at Rondeau, where it was numerous, and in Middlesex and Wentworth counties. During the first atlas, breeding evidence was obtained in the Long Point area north to Cambridge, in the Bayfield River valley along Lake Huron, in ravines along the Niagara Escarpment in Grey County, and in the Kingston region. More intensive surveys after the first atlas found many more nesting in Haldimand, Norfolk, and Elgin counties. The first evidence of breeding in the Kingston area occurred in 1975 and it has bred there annually since 1980 (Austen et al. 1994; Eagles in Cadman et al. 1987; McCracken 1991). James (1991) considered it a rare and local breeder in the Carolinian Forest Region and occasional and rare in the Kingston area. McCracken (1991) stated that its centre of abundance was in the Norfolk Sand Plains, with secondary populations occurring locally along the Niagara Escarpment and in the Kingston area. The total Ontario population at that time was estimated at 150-313 pairs.

The second atlas confirmed that the breeding range of the Louisiana Waterthrush had not changed significantly since the first atlas, and the largest populations were concentrated in the same areas. It was documented occurring locally along portions of the Oak Ridges Moraine and in the Rideau Lakes area. There was no significant change in its probability of observation, and the population was believed to have remained stable at 105-195 breeding pairs since the first atlas. This population estimate is lower than the 1991 estimate, but is essentially the same because the earlier estimate did not account for intermittent use of habitat (McCracken 2006; McCracken in Cadman et al. 2007).

The breeding range of the Louisiana Waterthrush expanded northward through New England beginning in the 1920s. This was probably in response to reforestation of areas that were heavily lumbered in the late 1800s and early 1900s. It is unknown if this general increase occurred in Ontario because the species appears to have been largely overlooked in many areas until the late 1980s. The exception is the population at Kingston, which apparently did not become established until about 1975. In Elgin County, it occurred sparingly in 1891. By 2000, it was a very local summer breeder but

occurred wherever there was suitable habitat. This suggests that much of its habitat was lost in that county and that it is less common now than formerly. It was quite common north and northeast of Point Pelee in 1924 but is now virtually extirpated in Essex and Chatham-Kent. Peak numbers occurred in the Hamilton area in the late 1950s and 8 were present at Tiffany Falls in Ancaster in 1956. In Niagara Region, it formerly nested at Beamer's Falls in Grimsby, but breeding has not been confirmed there since 1960 and it was not recorded in Niagara at all during the second atlas. Despite these apparent declines in the 20th century, the Louisiana Waterthrush population appears to have been stable since the 1980s (Austen et al. 1994; Black and Roy 2010; Craig 1985; Curry 2006; Lancaster et al. 2004; Mattsson et al. 2020; McCracken 1991, 2006). The management plan objective for the Louisiana Waterthrush in Ontario is to maintain the current size and distribution of the population. It was acknowledged that population changes at the continental level could have significant effects on it in Ontario (Friis and Brett 2012).

The southwestern Ontario population is concentrated in the Norfolk Sand Plain. In 2014, it was estimated that this area supported 47-94 breeding pairs, about two thirds of the 2005 estimate of 81-133 pairs. The 2014 population estimate for south-central Ontario was 40-100 pairs, but new sites were found along the Niagara Escarpment. Probably fewer than 5 pairs nest in southeastern Ontario. The 2014 population level was similar to the 2005 estimate. Occupancy is intermittent at most Ontario sites (Heagy 2015).

The Louisiana Waterthrush is listed as threatened in Canada and Ontario. The Canadian population is estimated at 235-575 adults. The objective of the recovery strategy is to maintain or increase the size and distribution of its population in Canada. It is likely that maintaining the current population will require more than 235 adults (Brett 2023).

POSTFLEDGING PERIOD

By the second day after fledging, the young can fly about 15 m and can fly and perch skillfully 4 days after fledging. Fledglings begin feeding themselves when they have been out of the nest for approximately a week. At this time, their foraging methods are restricted to picking and they do not attempt leaf-pulling until 3 weeks postfledging. In New York, the young remained near the nest 2-3 days after fledging, where they perched in shrubbery. They occasionally moved out of the ravine into the adjacent oak forest, but this was exceptional. One brood of 4 was split between the parents with all remaining within 70 m of the nest and near the stream for the first 10 days after fledging. One young was seen 1 km from the nest being fed by an adult. One young left the nest on 12 June and was observed 4.8 km away on 19 July. Another fledged on 9 June and was 2.0 km away on 14 July. Fledglings may begin feeding themselves about a week after leaving the nest but may continue to be fed by adults until 4 weeks after fledging (Eaton 1958). One bird moved 1.5 km from the nest to an adjacent tributary 5.5 weeks after fledging (Mattsson et al. 2020).

Vitz and Rodewald (2006, 2007) captured both adults and juveniles in regenerating clear-cuts in Ohio during the postbreeding season. There was no indication that breeding had taken place in this habitat. Dense shrubby areas may be important to both adults and fledglings during the postfledging period. In a Missouri oak-pine-hickory forest, Porneluzi et al. (2014) captured 4 Louisiana Waterthrushes 2-15 years after it was clear-cut.

MIGRATION

The Louisiana Waterthrush migrates mostly, if not entirely, by night. Birds travel singly and usually appear in spring on a morning after a warm night with strong south winds. Females tend to arrive later than males in spring. Some arrive on the same day as males but others appear a week or more later. In New York, females arrived over a span of 9 days; males arrived over a 15-day period (Eaton 1958; Mattsson et al. 2020).

The Louisiana Waterthrush is one of the earliest warblers to arrive in the province. The average date of first arrival at Long Point is 20 April. In Elgin County, it arrives in the second or third week of April. In the Hamilton area, average spring arrival is in late April, with early birds in late March and migrants present until late May. In the Kingston area, it mostly arrives in late April, with earliest birds in mid-April (Curry 2006; Lancaster et al. 2004; McCracken 1991; Weir 2008).

Throughout its range, the Louisiana Waterthrush leaves its breeding range as early as July, but most leave in August and a few may linger into early October in the southern portion of its range. In Pennsylvania, double-brooded birds and their fledglings were the last to migrate, probably not leaving before the end of August. It defends a winter territory, so double-brooded birds may be at a disadvantage on the wintering grounds because of their late arrival (Mattsson et al. 2020; Mulvihill et al. 2009). Most Ontario birds have migrated by mid-August, with some remaining until early September (Curry 2006; McCracken 1991; Weir 2008).

Migration habitat is similar to that used during the breeding season, but the Louisiana Waterthrush may also occur near stagnant or open-water habitats and away from forested areas. It may forage in parks, gardens, and shrubby thickets where water is available. In Illinois, spring migrants were particularly abundant in rich bottomland forests, so these areas may be preferred habitat. During spring migration in North Carolina, it was observed only in beech and floodplain forests. It was not observed in pine-hardwoods, pine, oak-hickory, wet thicket, or dry thicket habitats. No particular selection for habitat was made within the general types of habitat that it used (Graber et al. 1983; Mattsson et al. 2020; Parnell 1969).

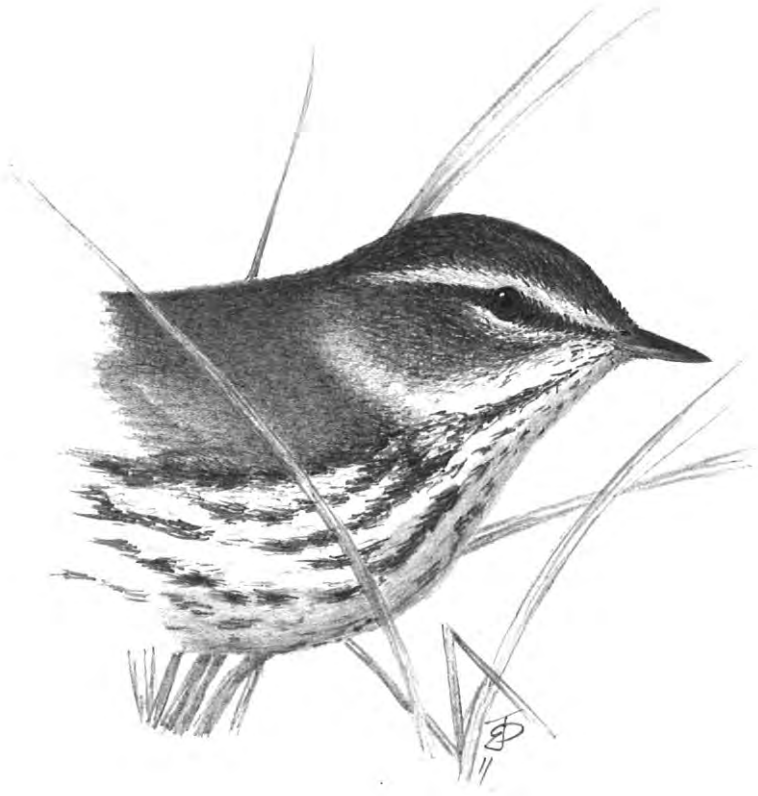
Parnell (1969) examined where the Louisiana Waterthrush spent its time during spring migration in North Carolina. Overall, 7.6% of observations were in the canopy, 31.7% in low trees, 15.8% in shrubs, and 44.8% on the ground. In the canopy, 2.3% of observations were in the inner crown and 5.3% were in the lower crown; it was not observed at the top of the crown or on tree boles. In low trees, 5.3% of observations were at the top of crowns, 5.3% in the inner crown, 21.1% in the lower crown, and 0% on tree boles. In shrubs, 2.6% of observations were at the top of the crown, 0% in the inner and lower crowns, 13.2% in dense thickets, and 0% in brush piles and grasses. On the ground, 8.3% of observations were in dense thickets, 0% in grasses, 20.8% at water's edge, and 8.3% in the open.

During migration, the Louisiana Waterthrush occasionally strikes tall buildings and communication towers. It also collides with windows and vehicles during migration (Mattsson et al. 2020). It was at high risk of colliding with buildings across the United States. At low-rise buildings, it was 46.4 times more likely to collide with a building than average for all species. It was not on the lists of the 20 most vulnerable species for striking 1-3-storey residences and high-rises (Loss et al. 2014).

The Louisiana Waterthrush is a rare migrant in Ontario. It occurs regularly in spring along the north shore of Lake Erie at Point Pelee, Rondeau, and Long Point, but is uncommon even at these migration concentration areas (James 1991; McCracken 1991, 2006).

Northern Waterthrush

Parkesia noveboracensis

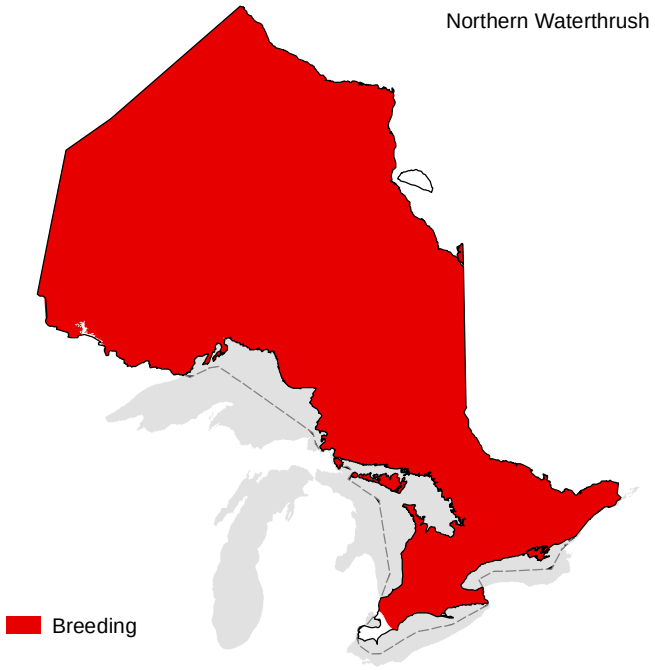


BREEDING SEASON

Habitat Requirements

In Ontario, the Northern Waterthrush has nested in moist or flooded forests (64.4% of nests), preferring mixed stands to deciduous and coniferous stands; in forested areas beside lakes, ponds, rivers, and streams (18.6%); at margins of marshes and beaver ponds (3.4%); in black spruce and sphagnum bogs (3.4%); in a dry forest (1.7%); and in unspecified woods (8.5%; Peck and James 1987). Its breeding habitat consists of mixed, deciduous, or coniferous forests; swamps; margins of isolated pools and ponds; and riparian edges. Trees within nesting habitat may be sparse and range in height from short to tall. It requires a dense shrub layer (James 1984b).

Although the Northern Waterthrush is often characterized as a forest bird associated with swamps, woodland ponds and vernal pools, or margins of forested lakes or watercourses, it may be locally common in shrub thickets. Along the western James Bay and southern Hudson Bay coasts, it was evenly distributed in willow thickets at edges of spruce woods. Most were observed in tall



willow thickets (Manning 1952). It occurred along the Brant River in willow thickets (Wilson and McRae 1993).

Near Pickle Lake in the Boreal Forest Region, the Northern Waterthrush occurred regularly in small numbers in shrubs at lake and river shorelines (James 1980). In the Pickle Lake, North Caribou Lake, and Little Sachigo Lake regions, highest densities were in deciduous shrubs followed by deciduous forest, mixed shrubs, coniferous shrubs, coniferous forest with understorey, and coniferous forest without understorey. It was absent in mixed forest, heath, and tundra (McLaren and McLaren 1981). Near Hearst, it occurred in clear-cuts 13-24 years old (Welsh and Fillman 1980). In the Clay Belt, it occurred mainly in wet habitats with poor to rich nutrient status. It occurred in black spruce, tamarack–white cedar, white birch–white spruce, and balsam poplar stands (Welsh and Lougheed 1996).

In Muskoka and Parry Sound districts, the Northern Waterthrush nested in alder thicket swamps, ash swamps, and undisturbed lakeshores (Mills 1981). In white pine shelterwood cuts in Algonquin Park, Kingsley and Nol (1999) reported it in 8.3% of 2-9-year-old cuts; in 0-18.2% of 10-16-year-old cuts; and in 20-21.4% of old cuts. In Algonquin Park, it nested along margins of lakes, streams, and flooded areas (MacLulich 1938). Also in Algonquin Park, it nested in black spruce and black spruce–white cedar stands. It was absent in wet or dry bogs, white birch–poplar, white birch–poplar–balsam fir–spruce, balsam fir–spruce, immature white pine, balsam fir–spruce-hardwoods, hardwood, and hemlock stands (Martin 1960).

In Durham Region in the Great Lakes–St. Lawrence Forest Region south of the Shield, the Northern Waterthrush nested in a young forest with an open canopy and much standing water, and in a sugar maple forest sloping down to a stream bordered by white cedar, balsam fir, and spruce with a dense undergrowth of raspberries and nightshade. Speirs and Orenstein (1975) considered it associated with balsam fir. It preferred wet forests at Presqu'ile (LaForest 1993).

Throughout its range, the Northern Waterthrush is strongly associated with the presence of water and dense shrub growth. It commonly nests in shrub thickets, treed swamps, treed bogs, and riparian forests. Occasionally it nests in upland forests along watercourses, but usually only in mountainous regions (Bent 1953; Brooks 1940; Chapman 1907; Harrison 1984; Whitaker and Eaton 2020).

Although the Northern Waterthrush is often considered an obligate forest species, it frequently nests in shrub thickets. It commonly nests in willows, dogwoods, and alders bordering rivers and lakes. Willow or alder thickets along watercourses are favoured habitat in Quebec. In British

Columbia, it prefers dogwood thickets that provide dense cover near water and frequently inhabits flooded vegetation, especially willow, trembling aspen, and alder mixed with spruce. Highest densities occur in alder-fern shrubbery and alder–skunk cabbage thickets. Near Fort Nelson, it occurs mainly in alders and willows along streams. In the Yukon, it is found in dense shrubbery along rivers, creeks, and sloughs, often at the edge of an area bordering open water. Highest densities in North Dakota occurred in willow shrub thickets. In Minnesota and Wisconsin, the primary habitats included alder thickets and sedge meadows that were regenerating with shrubs, especially dogwoods (Campbell et al. 2001; Faanes and Andrew 1983; Lemieux et al. in Gauthier and Aubry 1996; Manning and MacPherson 1952; Sinclair et al. 2003; Whitaker and Eaton 2020).

The Northern Waterthrush nests in a wide range of moist to wet forest types. These include stands dominated by balsam fir, white cedar, black or white spruce, trembling aspen, northern hardwoods, lowland hardwoods, tamarack, nutrient-poor jack pine, and red maple. It is characteristic of swamps and floodplain forests, and also of tundra with boreal forest near the northern extent of trees. It prefers forests with vernal or permanent pools of water or those that are along the bank of a river or lake. Nesting may also occur in forested habitat at edges of beaver ponds. Its abundance in forests is significantly correlated with the density of shrubs in the 0.3-1.0-m stratum. In 2 different Newfoundland studies, it occurred at higher densities in balsam fir stands with denser understorey. All 7 territories on the main island of Newfoundland contained open water, but only 1 of 7 on an adjacent island had open water (Campbell et al. 2001; Dawson 1979; Erskine 1977; Faanes and Andrew 1983; Golet et al. 2001; Kirk et al. 1996; La Rue et al. 1995; Morgan and Freedman 1986; Mossman 1988; Noon et al. 1979; Robbins et al. 1989; Samson 1979; Temple et al. 1979; Thompson et al. 1999; Vassallo and Rice 1982; Whitaker and Eaton 2020; Whitaker and Montevecchi 1997; Wiebe and Martin 1998). In Newfoundland, the climate provides unusual conditions and creates areas of nonriparian surface water in upland balsam fir stands. These areas support suitable habitat for abundant arthropods that provide suitable habitat for the Northern Waterthrush (Warkentin et al. 2003a).

Golet et al. (2001) and Freemark and Collins (1992) classified the Northern Waterthrush as a forest-interior species, but provided no supporting documentation. In southern Ontario, its abundance was significantly correlated with the amount of forest cover more than 100 m from edge (Austen et al. 2001). Most studies found that it is a riparian specialist that avoids forest interior. In Newfoundland, Whitaker and Montevecchi (1997, 1999) considered it a riparian habitat specialist. It was rarely seen away from water and travelled linearly along shorelines. It was rare in forest interior, with relative abundance of 8% in the interior compared with 85% in riparian habitat. In Quebec balsam fir and white cedar stands, La Rue et al. (1995) found it in 7 of 8 riparian plots and in no nonriparian plots. There was no difference in vegetation communities between riparian and nonriparian plots except for the presence of alder–reed canary grass wetlands in riparian habitat. In British Columbia, Wiebe and Martin (1998) studied riparian areas along second-order streams in mature to old-growth coniferous forests. Its presence was positively associated with riparian habitat. The percentage of birds seen in intervals from the willow or alder riparian habitat was: 0-50 m, 32.6%; 50-100 m, 18.6%; 100-150 m, 18.6%; 150-200 m, 10.5%; and 200-250 m, 19.8%. The distribution of birds differed significantly from random. It was recorded at least 250 m from a stream 2 km upstream from a lake, indicating that it may use a zone wider than the riparian vegetation itself. In Alaska, it

was largely restricted to the floodplain terrace landform (Handel et al. 2009). It is unlikely that the Northern Waterthrush can be classified as a forest edge or interior species. Its distribution within a forest is probably related more to the presence of water and dense shrub coverage than edge.

It is uncertain whether the Northern Waterthrush is an area-sensitive species. In southern Ontario, its abundance was significantly correlated with forest size, the amount of forest cover within 2 km, and the amount of regional forest cover, all suggesting that it is area-sensitive (Austen et al. 2001). In the mid-Atlantic states, Robbins et al. (1979) determined that its abundance was correlated with forest size and considered it area sensitive. Its maximum probability of occurrence occurred in forests larger than 3,000 ha, probability declined to 50% at 200 ha, and the 3 smallest woodlots in which it was observed at least twice were 187, 187, and 24.1 ha. In Rhode Island red maple swamps, it regularly occurred in swamps as small as 1 ha. This was not a good test of area sensitivity because the swamps were surrounded by upland forest. Its abundance was not related to forest size, probably because 60% of the landscape was forested (Golet et al. 2001). The Northern Waterthrush is not considered an area-sensitive species in Ontario. It was not identified as such by James (1984b) or Coleman et al. (2000).

Craig (1985) compared habitat use by Northern and Louisiana waterthrushes in Connecticut. The habitat consisted of rocky ravines containing watercourses, one of the less frequented habitats of the Northern Waterthrush. Although there was great overlap in the territories of the 2 species, Northern Waterthrush territories were much more densely vegetated; had more evergreen coverage in the form of mosses, shrubs, and trees; possessed typical swamp characteristics such as abundant hummocks, ferns, and alders; and had less fast-flowing water than Louisiana Waterthrush territories. Northern Waterthrush territories had significantly fewer forbs (12.5%) and significantly more ferns (31.9%) than those of the Louisiana Waterthrush (17.4% and 17.9%, respectively). Northern Waterthrush territories had significantly less fast-flowing water (3.8% compared with 23.7%) and more hummocks (45.8 compared with 30.9) than Louisiana Waterthrush territories. Northern Waterthrush territories had significantly higher total shrub density and higher densities of shrubs in the 1-2-m and 2-3-m strata than those of the Louisiana Waterthrush. Much of the difference was due to the presence of significantly more hemlock saplings in Northern Waterthrush territories. There were significantly more trees per ha (average 913, range 503-1,238) in Northern Waterthrush than Louisiana Waterthrush (average 666, range 470-948) territories, and Northern Waterthrush territories had a higher evergreen to deciduous ratio, higher density of hemlock, and a higher density of grey alder than Louisiana Waterthrush territories. Typical northern Connecticut habitats for the Northern Waterthrush were mixed deciduous-hemlock swamps traversed by meandering streams. In the south, it was found in pure deciduous or cedar swamps. In the mid-Atlantic states, abundance of the Northern Waterthrush was significantly correlated with percent canopy cover by conifers. It was negatively associated with slope, consistent with the fact that there is little fast-flowing water within its territories. Its abundance was positively correlated with foliage density between 0.3 and 1.0 m. It was negatively correlated with canopy closure suggesting that presence of dense shrubs is more important than tree coverage (Robbins et al. 1989).

Of 77 Ontario nests, 44.2% were in upturned roots of trees, 28.6% were among roots or in cavities near bases of standing trees and stumps, 13.0% were in depressions in earthen banks of streams and

rivers, 10.4% were in moss-covered hummocks and logs, 1.3% were under a log, 1.3% were under balsam fir branches, and 1.3% were in the side of a water-filled depression in a swamp. Nests were usually well concealed; 53.7% were either on the ground or in stream banks and 46.3% were elevated 0.2-1.2 m above water or occasionally above ground. One nest was reused the following year and another was situated just below a previous year's nest (Peck and James 1987). One nest in Sudbury District was in the side of an old beaver dam and hidden by grasses (Peck and James 1998a).

The nest is usually in complete shade and often not visible from above. Preferred nest sites are in cavities in root systems of wind-blown trees in forested swamps, under roots or other cover along stream banks, and on the ground in the base of a fern clump or in a cavity at the base of a tree or stump, or under logs, mosses, a clump of sod, driftwood along shorelines, or debris. Elevated nests are usually above water at heights as high as 80 cm, but usually less than 30 cm. Nests in upturned roots usually are directly over a small pool of water. One was on the ground and completely exposed, but there is usually cover over the nest with an opening to 1 side (Bent 1953; Campbell et al. 2001; Chapman 1907; Harrison 1984; Sinclair et al. 2003; Whitaker and Eaton 2020).

Territories are defended as soon as males arrive in spring, but territoriality ceases 3-4 days after the young leave the nest. In swamps, territories are often clumped in 1 area, usually in the thickest undergrowth, rather than being uniformly distributed. Even in large areas of apparently suitable habitat, territories are found near nest-support structures or cover such as roots of upended trees, stream banks, hollow stumps, or mossy logs. New York territories averaged 1.0 ha (range 0.8-1.5 ha). In Connecticut, the mean territory size was 0.47 ha; territory size may be halved if another territorial male arrives. In black spruce forests in Algonquin Park, territories extended from the ground to a height of 3 m, which corresponded to the top of the shrub layer and the bottom of the canopy. In mature balsam fir stands in Newfoundland, territory sizes at the 50% isopleth averaged 1.2 ha (range 0.1-4.6 ha). At the 70% isopleth, territories averaged 2.3 ha (range 0.1-8.2 ha), and territories averaged 4.3 ha (range 0.2-15.5 ha) at the 90% isopleth. Territory size was affected by the proportion of harvested versus naturally unforested land at the landscape scale and varied by greater than 2 orders of magnitude. Birds frequently foraged outside their territories and incorporated both natural and anthropogenic openings into their home ranges. They regularly flew directly across large lakes, peatlands, patches of harvested forest, and roads. Home range size at the 50% isopleth averaged 3.5 ha (range 0.8-10.6 ha). At the 70% isopleth, home ranges averaged 6.3 ha (range 1.6-19.5 ha), and home ranges averaged 13.3 ha (range 3.5-35.9 ha) at the 90% isopleth. Home range size was not affected by the amount of harvested versus naturally unforested habitat in the landscape (Craig 1984, 1985, 1987; Leonard et al. 2008; Lemieux et al. in Gauthier and Aubry 1996; Martin 1960; Whitaker and Eaton 2020).

Limited information is available on natal philopatry. In Newfoundland, 7 of 103 fledglings (6.8%) were resighted or recaptured in subsequent years. The median dispersal distance was 1,200 m (range 230-2,500 m; Whitaker and Eaton 2020).

In New York, 2 of 4 males returned to the same breeding site for 2 years. In Massachusetts, 67.8% and 71.4% of 2 groups of adults returned (Whitaker and Eaton 2020). In Newfoundland, 16.3% of adults returned, but these were mostly males due to their higher responsiveness to broadcast calls. The overall return rate was probably higher. Seventy-five percent of 20 adults were observed in 3 or

more years, which was likely more reflective of the return rate. Twenty-five percent of returning individuals were detected more than 1 km from their capture site, indicating some breeding season dispersal (Whitaker and Eaton 2020).

Limiting Factors

Eggs have been found in Ontario nests from mid-May until the second week of July, with most present in the last week of May and first week of June (Peck and James 1987). In Algonquin Park, eggs are present from late May to early June, nestlings occur in early June, and dependent fledglings have been observed from mid-June to early July (Tozer 2012).

One replacement nest was built in 3 days. One egg is laid per day and incubation is initiated after laying the third egg. The incubation period at 1 Ontario nest was not more than 14 days. Other authors reported incubation periods of 12 or 13 days. The young leave the nest before they can fly, at age of approximately 9 days (Harrison 1984; Peck and James 1987; Wander and Wander 1985; Whitaker and Eaton 2020).

The Northern Waterthrush raises a single brood per season. There are no records of second broods. Renesting commonly occurs if a nest is lost. Two Newfoundland birds started replacement nests 10-15 m from the original nest. In Ontario, clutches of 3-5 eggs have been reported (average 4.15 eggs, mode 4 eggs). Overall, clutches of 3-6 eggs have been reported, with most birds laying 4 or 5 eggs (Bent 1953; Campbell et al. 2001; Chapman 1907; Eaton 1995; Peck and James 1998a; Warkentin et al. 2003a).

The Northern Waterthrush first breeds when it is 1 year old and breeds thereafter. It is typically monogamous, but there is evidence for occasional polygyny. Two females with young in their nests were found in a male's territory in New York. In another case, 2 occupied nests were found under a stump with 1 nest close above the other (Eaton 1995). One male in Newfoundland was nonterritorial and did not appear to have a mate or nest (Leonard et al. 2008). Extra-pair copulations have not been confirmed. Males have been observed as far as 1 km from their territories, suggesting that they were seeking extra-pair copulations (Whitaker and Eaton 2014).

From spring arrival until the end of incubation, approximately 80% of foraging occurs in water. In aquatic habitat, the Northern Waterthrush alternately wades and walks along logs, on branches sloping down to the water, and at the water's edge, where it feeds on both submerged and floating organisms. It occasionally flutters over water to capture prey from the surface. Ground feeding includes capturing prey on mud, in leaf litter, on rocks, and on moss. When feeding on woody plants, it walks on stout branches and picks prey from the foliage and stems. The 2 major foraging methods are picking and leaf-pulling, which consists of pulling dead leaves from water or the litter with the bill and inspecting it for prey. These foraging techniques are used both on the ground and in water. It has been observed chasing but not catching adult mayflies and flies. In Connecticut, foraging substrates prior to leaf-out were 74.1% in water, 22.2% on the ground, 1.9% in foliage, and 1.9% in the air. After leaf-out, 38.3% of foraging occurred in water, 23.4% on the ground, 34.0% in foliage, and 4.3% in the air. The 2 waterthrush species foraged similarly prior to leaf-out, but the Northern Waterthrush used a wider range of substrates after leaf emergence. Both species commonly fed by picking and leaf-pulling prior to leaf-out, but picking was the dominant technique after leaves emerged. The Louisiana Waterthrush prefers prey larger than 13 mm; the Northern Waterthrush

prefers shorter prey items. Of 154 prey items, 35.1% were 7 mm or less, 38.3% were 7-13 mm, 22.1% were 13-19 mm, and 4.5% were longer than 19 mm (Craig 1984, 1987; Whitaker and Eaton 2020).

In Connecticut, the diet of both waterthrushes was highly aquatic with only 4.0% terrestrial prey items. The Northern Waterthrush most strongly preferred flies and strongly avoided isopods. Of prey items it caught, 54.7% were flies (mostly midges, but also mosquitoes), 11.0% were caddisflies, 13.6% were mayflies, 5.1% were oligochaetes, and 4.2% were isopods. In addition, it consumed dusky salamanders, adult moths, alderfly nymphs, crane fly larvae, ants, millipedes, centipedes, caterpillars, and snails (Craig 1984, 1987). Whitaker and Eaton (2020) summarized the diet of 25 birds during the breeding season in New York by volume and occurrence: fly adults and larvae, 50.5% and 48%; predaceous diving beetles, 7.5% and 8%; water scavenger beetles, 11.0% and 8%; ground beetles, 5% and 4%; weevils, 3% and 12%; caterpillars, 50% and 8%; stoneflies, 8.5% and 8%; unidentified insects, 51.9% and 88%; snails, 4% and 16%; and leeches, 2% and 4%. Other prey included crawling water beetles, springtails, true bugs, soft-winged bugs, leaf beetles, crane flies, fungus gnats, caterpillars, adult dragonflies, mayflies, alderfly nymphs, dobsonflies, isopods, centipedes, oligochaetes, water boatmen, damselflies, spiders, weevils, owlet moth caterpillars, slugs, and orthopterans. After leaf emergence, it may feed extensively on caterpillars. During migration, it has eaten small fish. During a spruce budworm outbreak in Quebec, it fed budworm larvae to its young (Bent 1953; Lemieux et al. in Gauthier and Aubry 1996; Warkentin et al. 2003a; Whitaker and Eaton 2020).

The Northern Waterthrush is a uncommon host of the Brown-headed Cowbird, partially because much of its breeding range is outside that of the cowbird's. It accepts cowbird eggs and both waterthrushes and cowbirds may fledge from parasitized nests. In Ontario, 11 of 94 nests (11.7%) were parasitized; 17% of 18 nests were parasitized in Quebec; in British Columbia, 0 of 17 nests were parasitized (Campbell et al. 2001; Lemieux et al. in Gauthier and Aubry 1996; Peck and James 1998a; Whitaker and Eaton 2020).

Much suitable habitat for the Northern Waterthrush must have been lost when European settlers cleared the land. Direct habitat loss is less of a threat now, but indirect losses of woodland pools and ponds due to agricultural drainage still occur. Wetlands may accumulate toxins, and the effects of these on it are unknown. Sedimentation and organic enrichment of streams has the potential to reduce its prey base (Eaton 1995). Near Montreal, it declined due to wetland drainage and channelization of watercourses. Increased cottaging on some lakes in southern Quebec has been detrimental (Lemieux et al. in Gauthier and Aubry 1996). Wintering habitat is threatened due to loss of mangrove forests (Whitaker and Eaton 2020).

Much work has been conducted on the effects of forest management on the Northern Waterthrush. In Newfoundland, Whitaker et al. (2008) compared survival rates in landscapes characterized by natural forest openings (mainly peatlands) or those created by clear-cuts. The annual survival rate was 36.5% in natural landscapes and 33.8% in cut landscapes. It was resilient to moderate amounts of clear-cutting. Also in Newfoundland, its occurrence was similar across different levels of forested cover within harvested landscapes, but not in natural landscapes. In harvested landscapes, it exhibited a constant occurrence of 30-35% in 10-100% forest cover. In natural landscapes, it was absent in areas with less than 10% forest cover, had an occurrence rate of

less than 10% in areas with 10-45% forest cover, and had 40% occurrence in 45-100% forest cover. Occurrence rates averaged 30% in cut landscapes, 34% in natural landscapes, and 32% overall. It was relatively insensitive to changes at the local (25 m) and neighbourhood (300 m) scales. Taylor and Krawchuk (2006) concluded that it could fulfill some of its resource needs in clear-cut portions of harvested landscapes but not in non-forested areas in natural landscapes, which consisted of bogs and rock barrens. Species packing may occur in harvested landscapes, whereby birds become more concentrated in residual uncut areas. Vanderwel et al. (2009) summarized studies that examined the effects of partial timber harvesting in the Boreal Forest Region. Its abundance did not change when 30%, 50%, or 70% of trees were removed. In Ontario in the Canadian Shield, there was no difference in its abundance in early and mid-successional clear-cuts compared with the same ages of forests after fire. Abundance was similar in early regenerating and mature stands, but significantly less in mid-successional than mature stands (Zimmerling et al. 2017).

Leonard et al. (2008) studied the effects of clear-cutting in the Newfoundland Boreal Forest Region on territory size of the Northern Waterthrush. There were more occupied territories in natural than harvested habitats. Only 2 settled in territories where gaps in woodland cover were due solely to harvesting. Territories were largest in the most heavily harvested landscapes. At the 70% isopleth, the mean territory size decreased from 3.9 to 0.8 ha as the proportion of unforested land in the landscape due to harvesting increased from 4% to 60%. Territory size increased where the proportion of harvested land was more than 60% to a maximum territory size of 6.5 ha. This represents territory shrinkage of 488% with increasing amounts of clear-cut openings up to a threshold near 60% of the landscape and subsequent territory expansion by 813% when more than 60% of the openings in the landscape were created by clear-cutting. The highly variable territory size may have been due to density and resource availability. In harvested areas, it tends to crowd into riparian buffer areas, thereby increasing density and decreasing territory size. At higher levels of harvest, foraging areas outside territories could be lost resulting in a requirement for larger territories to obtain adequate resources.

In Newfoundland, Whitaker and Montevecchi (1999) compared usage of undisturbed shorelines and those with retained 20-50-m riparian buffers adjacent to clear-cuts. There was no evidence that the Northern Waterthrush was less abundant in buffers than in undisturbed shorelines. They attributed this to the fact that it was associated only with the riparian habitat along shorelines and concluded that increasing the width of the buffer zone would not likely increase usage by waterthrushes.

Warkentin et al. (2003a) examined the effects of clear-cutting in Newfoundland on the Northern Waterthrush. They studied intact riparian and upland habitats and riparian and upland habitats adjacent to clear-cuts. Riparian habitat had consistently greater numbers and higher biomass of prey items even if aquatic organisms were not considered. Despite the variability in food supply, territory numbers in each of the 4 treatments was highly consistent year to year. Similar numbers of territories were present in intact riparian and upland habitats, but fewer Northern Waterthrushes occupied disturbed upland habitat and large numbers packed into disturbed riparian habitat. Birds in disturbed riparian habitats moved longer distances and more frequently than birds in the other 3 habitat types. Territory packing was still evident 5-10 years after clear-cutting, but did not appear to

have any effect on reproductive success. Crowding of disturbed riparian strips may lower foraging success and these retained habitats may not be viable over the long term.

Whitaker and Eaton (2020) suggested that aerial spraying for spruce budworms could reduce the biomass of prey available to Northern Waterthrushes, or kill birds if nonbiodegradable toxins were used. It has been found to carry high concentrations of blood methylmercury, presumably from foraging in contaminated water (Whitaker and Eaton 2020).

In Alberta, the Northern Waterthrush was significantly more abundant at seismic lines than in adjacent forest interior. It was significantly less abundant at pipelines than in adjacent forest interior, and there was no difference in its abundance at well pads and adjacent forest interior (Bayne et al. 2016).

The Northern Waterthrush may be vulnerable to the effects of climate change. In Quebec, it was associated with a low number of growing-degree temperatures (cooler sites), breeding season precipitation, and an early start to the growing season (DesGranges and LeBlanc 2012). Price (2004) predicted that the Northern Waterthrush might no longer breed in southern Ontario if the average summer temperature increased by 2°C. Increased summer temperatures are likely to result in increased evapotranspiration rates and loss of woodland vernal pools and ponds.

Status

McIlwraith (1894) stated that the Northern Waterthrush bred throughout the province and considered it as abundant as the Ovenbird. Manning (1952) reported that a survey completed in 1896 determined that it was very abundant all the way down the Moose River to Moosonee. Fleming (1907) concluded that it was possibly a rare summer resident in the Toronto area. Baillie and Harrington (1937) stated that it bred north to Lake of the Woods and James Bay and probably throughout the province. The first atlas confirmed that it was common and that its range covered the entire province except for the intensive agricultural areas of the southwest and much of Niagara Region and Haldimand County. Its abundance was highest in Peterborough and Haliburton counties, Nipissing District, and the Algonquin Park area (Eagles in Cadman et al. 1987). James (1991) concluded that it was a common summer resident throughout the province except in southern agricultural areas, where it was rare. In Elgin County, it was not known to be a breeder in 1891 or 1954, but was an extremely rare breeder in 2000 (Lancaster et al. 2004).

The second atlas indicated that there had been no change in the distribution of the Northern Waterthrush in Ontario since the first atlas. It was not found in some squares where it previously occurred in the vicinity of Sault Ste. Marie and Sudbury, and in some squares in southwestern Ontario. It was found in many new squares in the south on Manitoulin Island, south of the Bruce Peninsula, southwest of London, and east of Ottawa. Its probability of observation increased significantly province-wide since the first atlas. Increases occurred in all atlas regions and were significant in the Canadian Shield and Hudson Bay Lowland. Highest densities occurred in the Hudson Bay Lowland and the northwestern portion of the Boreal Forest Region. Densities in southern Ontario were much lower, with highest densities in this area occurring in the Kawartha Lakes area north to Algonquin Park and east to Perth County, along the Niagara Escarpment south to Halton Region, and in the Dundalk uplands (McLaren in Cadman et al. 2007).

Breeding Bird Survey results indicate that the Northern Waterthrush increased at an annual rate of 1.07% in Canada and decreased at an annual rate of 0.302% in Ontario 1970-2021. Trends for 2011-21 were an annual decrease of 3.26% in Canada and an annual increase of 0.97% in Ontario. All results were of medium reliability except that the short-term Canadian trend was of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Once young leave the nest, brood division occurs with each adult caring for half the brood. Fledglings hide under dense vegetation for 2-3 days after leaving the nest and can fly proficiently by the time they have been out of the nest for 8 days. Each adult feeds half the brood for 4-5 weeks after they fledge. One fledgling was completely independent 30 days after leaving the nest (Whitaker and Eaton 2020).

In Quebec, Major and Desrocher (2012) caught 2 Northern Waterthrushes in regenerating clear-cuts during the postfledging period. In Minnesota, Streby et al. (2011b) captured 5 adults and 13 juveniles in 2-10-year-old clear-cuts during the postfledging period. No waterthrushes were captured in this habitat during the breeding season. At least some juveniles and adults move to dense shrubbery in clear-cuts during the postfledging period. Although it prefers dense shrub cover year-round, it may move to upland sites devoid of water once the young are independent.

In Michigan, Akresh et al. (2009) studied avian usage of mature trembling aspen–large-toothed aspen stands during the postfledging period. The canopy composition of riparian and upland stands was similar, but riparian stands had a shrub layer of alders and honeysuckles. They captured 5 adults and 4 juveniles, all in riparian forests.

MIGRATION

The Northern Waterthrush migrates long distances nocturnally, probably in loosely associated homogenous flocks (Whitaker and Eaton 2020; Winker et al. 1992). Birds captured at Thunder Cape (83%) and Long Point (78%) were strongly represented by deuterium levels in the northern Boreal Forest Region and Hudson Bay Lowland in Ontario, the prairies west to southern British Columbia and north to the Yukon, Northwest Territories, and Nunavut. Forty-eight percent of birds captured at Long Point were representative of birds breeding in the Great Lakes–St. Lawrence and Boreal Forest regions in Ontario and Quebec. There is a strong southeastern migration in autumn and many Ontario and western Quebec breeders move southeastwards toward the Atlantic coast, bypassing Long Point to the north. It tends to move more north-south in spring than autumn and more directly to the breeding grounds (Dunn et al. 2006).

In Minnesota, there was sexual segregation in the spring but not in autumn, with males preceding females in spring. More stayed longer than 1 day in autumn than spring (Winker et al. 1992). In Maine, 2 spring birds stopped over for 6 days; 41 autumn migrants stopped over an average of 4.3 days (range 1-6 days; Morris et al. 1994).

The Northern Waterthrush is one of the earliest warblers to arrive in spring. In southern Ontario, it arrives at the end of April, with some arriving in early April. Most have left by the end of May, but spring migrants have been seen in early June (Black and Roy 2010; Curry 2006; LaForest 1993;

Lancaster et al. 2004; Weir 2008). In the southern Shield, average arrival is in the first week of May with the earliest records in late April (Mills 1981; Tozer 2012).

Autumn migration begins early, well before the end of July, soon after the young are independent (Bent 1953; Campbell et al. 2001; Harrison 1984). In the southern Shield, the Northern Waterthrush is one of the earliest birds to move south, with migrants observed from late July to mid-September (Mills 1981; Tozer 2012). In the south, significant southward movement occurs in July, although the main passage is in late August to mid-September (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

During migration, the Northern Waterthrush occurs in similar habitats to those that it uses during the breeding season. It is less selective in its habitat preferences during migration and may occur in sites that would not be used during the breeding season. These include mature upland forests, gardens and about dwellings, open muddy areas in pine barrens, oak meadows, dug-out ponds and water-filled ditches surrounded by shrubs, and freshly turned soil in a livestock corral. At Point Pelee in 1908, it occurred in several habitats including low, damp spots in woods, in upland walnut stands, in red cedar thickets, in brush piles, and in patches of herbaceous plants in cottonwoods (Bent 1953; Brush 1987; Campbell et al. 2001; Chapman 1907; Graber et al. 1983; Leighton et al. 2002; Sinclair et al. 2003; Whitaker and Eaton 2020). Migrants show a consistent preference for riparian thickets and swamps where they are usually found close to water. In Illinois, it shows a strong preference for bottomland forests during both spring and autumn migration. During spring migration in North Carolina, the average number of birds observed per hour was 0.69 in wet thicket, 0.21 in floodplain forest, and 0.04 in oak-hickory forest. It was not observed in pine-hardwoods forest, pine forest, beech forest, or dry thicket. During autumn in New Jersey, it occurs in shrubs along tidewater creeks and at rainwater or dried-up pools. In Minnesota in spring, there were higher capture rates in swamps and floodplains than in willows and upland habitat. In autumn, higher capture rates occurred in floodplains than willows and uplands, and it used swamps more than uplands. During spring migration in Wisconsin and Minnesota, it was observed significantly more in floodplain forests than in upland forests (Campbell et al. 2001; Chapman 1907; Graber et al. 1983; Kirsch et al. 2013; Leighton et al. 2002; Parnell 1969; Sinclair et al. 2003; Whitaker and Eaton 2020; Winker et al. 1992).

During spring migration in North Carolina, 4.2% of Northern Waterthrush observations were in the canopy, 20.9% in low trees, 37.5% in shrubs, and 37.4% on the ground. Of the canopy observations, all were in the inner crown with none at the top or lower crown or on the bole. In low trees, it was not observed at the top of the crown, 4.2% of observations were in the inner crown, 16.7% in the lower crown, and 0% on the bole. In shrubs, none were seen at the top or inner crowns, 4.2% of observations were in the lower crown, 16.6% in dense thicket, 12.5% in brush piles, and 4.2% in grasses. On the ground, 8.3% of observations were in dense thickets, 0% in grasses, 20.8% at water's edge, and 8.3% in open areas. It occurred at heights of 0-5.5 m (mean 1.2 m). It foraged on the ground and flew to low perches to sing (Parnell 1969).

During spring migration, some birds establish territories in swamps around shrubby edges of small ponds. These territories are defended and may prevent some individuals from finding satisfactory foraging areas. Birds defend a territory from 1 to 5-7 days, foraging and accumulating

enough fat to continue migrating. Individuals unable to establish a territory are forced to move on quickly. Migration feeding territories are 0.1-0.5 ha (Graber et al. 1983; Morse 1989; Whitaker and Eaton 2020).

A bird banded in Illinois on 9 September 1967 was recovered at the same location on 7 September 1969 (Graber et al. 1983). This suggests that some individuals may exhibit site fidelity during migration.

During migration, the Northern Waterthrush is frequently killed at television towers and other tall structures. Near Kingston, 189 were killed at the Lennox generating station chimneys 1972-82, including 80 on 6 September 1981 (Graber et al. 1983; Weir 2008; Whitaker and Eaton 2020). In the United States, it was particularly vulnerable to striking residences 1-3 stories tall and was 22.5 times more likely to suffer a collision than average for birds. It was not on the lists of the 20 most vulnerable species for striking low-rises or high-rises (Loss et al. 2014).

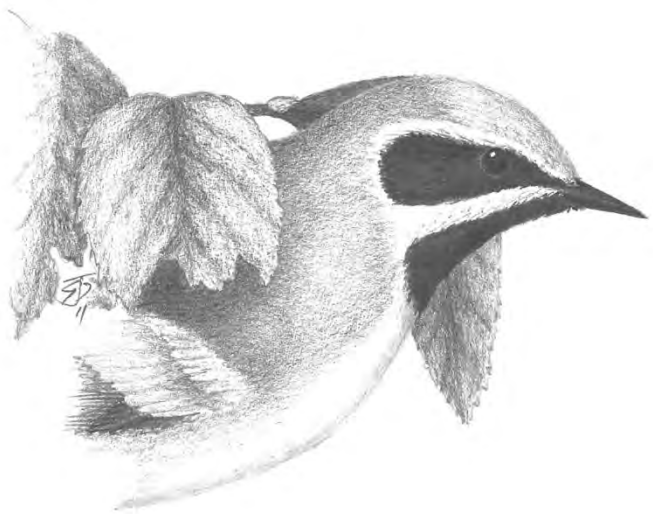
Seewagen (2013) examined the effect of mercury on autumn migrant Northern Waterthrushes in New York. Blood mercury levels averaged 0.42 ppm (range 0.09-2.08 ppm). Mercury did not appear to affect its foraging efficiency or other factors that reduced its stopover refueling rate. Most had blood mercury levels above the means reported from Northern Waterthrushes and numerous other long-distance passerines elsewhere in the eastern United States, but well below the level of 0.7 ppm that is used as an indicator of risk in passerines.

James (1991) considered the Northern Waterthrush a common migrant in Ontario. It is a common migrant at Point Pelee and Rondeau, but is rarely observed in Elgin County and seldom occurs during migration in Niagara Region (Black and Roy 2010; Lancaster et al. 2004).

The number of Northern Waterthrushes banded at Long Point 1961-88 declined significantly at a rate of 4.0% per year. Changes by periods were: 1961-70, −6.1%; 1970-79, −1.7%; and 1979-88, −10.0%. It was 1 of 4 neotropical migrants that exhibited a continuous decline (Hussell et al. 1992).

Golden-winged Warbler

Vermivora chrysoptera



BREEDING SEASON

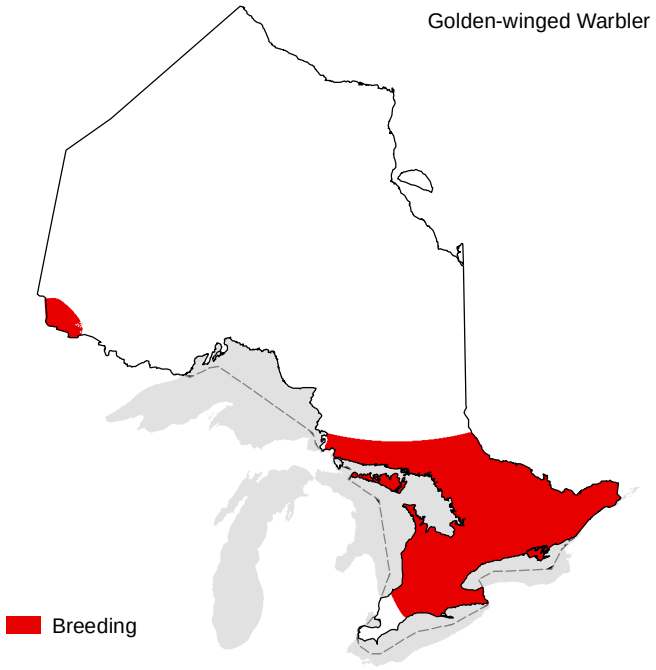
Habitat Requirements

In Ontario, the Golden-winged Warbler nests in fields of tall grasses and forbs overgrown with raspberries, shrubs, and saplings; in or at edges of open conifer plantations; in overgrown clearings and edges of deciduous and mixed woods; near roadsides and hedgerows; at edges of alder thicket swamps; and in an alder-willow-dogwood thicket swamp. Most territories were in dry habitat, but 3 of 33 nests (9.1%) were in wet areas (Peck and James 1987).

In the Canadian Shield in the Great Lakes–St. Lawrence Forest Region, the Golden-winged Warbler inhabits alder thickets, alder-spruce swamps, and tamarack bogs. Alder-spruce swamps appear are preferred habitat in Muskoka and Parry Sound districts (Fraser 2006; Mills 1981). Territories south of the Shield contain patches of herbaceous plants and shrubs with scattered trees, plus a forested edge that it uses for foraging and song perches. Most vegetation within territories is less than 3 m tall. Preferred areas include utility rights-of-way, shrubby field edges, recently logged areas, beaver meadows, and shrubby areas along streams (Fraser 2006; King et al. 2009; McIlwraith 1894; Weir 2008). Near Kingston, an open area maintained by late-summer cattle grazing that left more gradual edges to forests was the best habitat for the Golden-winged Warbler. Vegetation in most other areas in this region consisted either of tall, closely spaced trees or abrupt edges between meadows and forests. These habitats were suboptimal (King et al. 2009). In Durham Region, it nested

in a forest with an open canopy. There were some overgrown logging roads through it and much of the forest floor was under water. The lack of a canopy over much of the site resulted in a rank growth of ferns and raspberries (Speirs and Orenstein 1975).

Where the 2 species co-exist, the Golden-winged Warbler and Blue-winged Warbler readily hybridize. The F1 generation of hybrids comprises 2 hybrids known as Brewster's Warbler and Lawrence's Warbler. The hybrids are reproductively viable and mate with phenotypically pure Golden-winged or Blue-winged warblers and, less frequently, with other hybrids.



In agricultural landscapes, the Golden-winged Warbler nests predominantly in early successional habitats that include a mix of grasses, herbaceous plants, shrubs, scattered trees, and a forest edge. These include meadows, lightly grazed pastures, and utility rights-of-way passing through forested habitat. It occasionally used road rights-of-way, but the incidence of this is now rare. Abandoned farmland provides suitable habitat 10-35 years into succession. Younger areas do not support a sufficient density of trees and saplings to be attractive; older sites are too densely stocked with trees. In eastern Ontario, edge creation experiments documented that it will move into an area of suitable habitat within 3 years of its creation. Utility corridors may be suitable for longer periods because they are maintained to remain in early successional stages. The periodic maintenance results in a cycle of rights-of-way being unsuitable shortly after clearing and evolving into good habitat until they are cleared again. Rights-of-way that are 20 m or less in width are unoccupied unless there are other openings on either or both sides. Most occupied rights-of-way are 60 m or more wide. In more southern areas of its range, it has nested on open wooded dunes, in sandy savannahs where the dominant trees were bur oak and sassafras and there was dense shrub growth, on reclaimed surface mines, and in pine and oak barrens (Aldinger and Wood 2014; Buehler et al. 2007; Bulluck and Buehler 2008; Canterbury et al. 1993; Fraser 2006; Graber et al. 1983; Hands et al. 1989c; Kubel and Yahner 2008; Marsi 1980; Mossman et al. 1991). In West Virginia, numbers decreased in the shrub to forest stages. Highest densities occurred in the first stage of succession which included farms and recently abandoned farmland, reclaimed and abandoned surface mines, and open fields dominated by goldenrods and other weedy species. The next stage of succession supported lesser numbers. This habitat was shrubby with small shrubs and saplings plus goldenrods, and included species such as multiflora rose, blackberries, white pine, black locust, and staghorn sumac. The third stage of succession supported the lowest numbers. It was characterized by very shrubby habitat and trees 3-4.5 m tall, as well as Carolina rose and late-successional species such as maples (Canterbury et al. 1993).

Not only is the Golden-winged Warbler confined to a narrow successional range, it is highly specialized in its habitat requirements in meadows and thickets. Its requirement for few tall trees within its territory restricts it almost entirely to fields that were last farmed 10-35 years previously. Territories in this type of habitat have a consistent structure of a forested edge and an open patchwork of clumps of shrubs and short trees (usually under 6 m) within a mosaic of herbaceous vegetation. In New York, all 75 territories had a forested edge and territories extended 5-30 m into the forest. The minimum tree cover along a territory edge consisted of an old fence line with a dense row of trees and shrubs, with some 10-15 m tall. Some territories may contain large open spaces such as mowed or sprayed areas, bare soil, or marshy areas. Within the territory, there are few trees except for those in the forested border, and these are frequently used as singing perches. Too few or too many trees in the open portion of the territory result in it not being used. If an area is large enough to support many territories but there are no trees in the opening, territories are restricted to the treed edges. In 1 New York field, 35% of the habitat was open with tall grasses and scattered hawthorns and dogwoods, 45% was covered with dense shrubs 2-4 m tall, 15% was covered with trees as tall as 10 m, and 5% was wet and swampy. All New York upland nesting areas included patches of goldenrods, grasses, and patches of shrubs such as dogwoods, raspberries, poison ivy, and Asiatic bittersweet. In Kentucky, plant species characteristic of territories included orchard grass, green ash seedlings and saplings, and black locust saplings. Species indicative of sites supporting both the Golden-winged and Blue-winged warblers were bush-clovers, goldenrods, clematis vines, and blackberries. Results from many studies combined show a preference by the Golden-winged Warbler for low to moderate canopy cover (6-45%) and moderate (45-69%) shrub and herbaceous (48-73%) coverage (Buehler et al. 2007; Confer and Knapp 1977, 1979, 1981; Confer et al. 2003, 2010, 2020; Ficken and Ficken 1968a, 1968b; Frech and Confer 1987; Patton et al. 2010).

Within agricultural landscapes, the Golden-winged Warbler nests in habitats other than abandoned agricultural land. It nests within openings in forests where seepage areas prevent tree growth, and this is probably representative of habitat that was used before large-scale forest clearing occurred. It may also nest in shrubby growth along watercourses and has nested in abandoned gravel pits. In New York and Rhode Island, it commonly nests in treed swamps dominated by red maple or black ash. These wetlands had 60-80% canopy closure with a shrub layer consisting of spicebush, northern arrowwood, and wild raisin. Tussock sedge strongly dominated the ground layer and was the principal substrate for nests in the wetlands. Some wetlands contained dense patches of common reed that it avoided, although 1 nest was found in this habitat. Breeding in this type of habitat has not been confirmed in southern Ontario, but wetlands and beaver meadows may have been used historically. Wooded areas that are highly disturbed due to storms, fire, or excessive thinning may create temporary suitable habitat. Wide-scale disease or insect infestations of trees may create suitable habitat. In the mid-1940s, the Golden-winged Warbler was characteristic of decimated stands of American chestnut. Chestnut blight resulted in stands comprised of scattered dead chestnuts with a dense understorey of sprouting chestnut saplings. Young plantations may temporarily provide suitable habitat until the conifers become dominant. It formerly inhabited old orchards (Brooks 1940, 1947b; Confer and Knapp 1979; Confer et al. 2003, 2010, 2020; Golet et al. 2001; Hands et al. 1989c; Mossman and Hoffman 1989; Noon et al. 1979; Tyler in Bent 1953).

In forested landscapes, the Golden-winged Warbler commonly nests in wetlands or at open interfaces of forests and wetlands. It frequently nests in wetlands dominated by alders or willows and occasionally in tamarack bogs and swamps. It occasionally nests in forests. In central Minnesota, it historically nested in dense deciduous forests and may also nest in forested stands at elevations above 580 m. In North Carolina in 1886, it was characteristic of open oak woodlands where it occurred at elevations as high as 1,200 m. In Tennessee, it inhabited northern hardwoods and mesic oak-hickory stands less than 20 years old at elevations higher than 1,000 m. In Minnesota, average habitat characteristics of territories were 92.3% ground cover, 45.0% shrub cover, 31.4% canopy closure, 10.5 m canopy height, 10.4% coniferous cover, and number of trees of different size classes per 0.04 ha: smaller than 7.5 cm diameter at breast height (DBH), 3.2; 7.5-15 cm DBH, 5.7; 15.1-23 cm DBH, 4.6; 23.1-30 cm DBH, 2.7; 30.1-38 cm DBH, 1.0; 38.1-53 cm DBH, 0.5; 53.1-68 cm DBH, 0.3; and larger than 68.1 cm DBH, 0.1. It preferred deciduous edge vegetation and open areas with dense ground coverage and moderate shrub coverage. In Pennsylvania wetlands, its abundance was negatively correlated with canopy cover and positively correlated with the density of shrubs 1-2 m tall at the 100-m scale. At the landscape level, it was positively correlated with the amount of emergent wetland cover and percent wetland shrub edge (Collins et al. 1982; Confer et al. 2003, 2020; Hands et al. 1989c; Klaus and Buehler 2001; Martin et al. 2007; McNeil et al. 2018; Patton et al. 2010).

At the landscape level, abundance of the Golden-winged Warbler was strongly correlated with total forest cover, especially deciduous forest dominated by aspen. It was negatively associated with habitat edge density and patchy, perforated, and transitional forests. There was a lack of a positive association with edge and mesic forest conditions. It may achieve higher density in more forested situations in low-forest, high-edge landscapes. In high-forest, low-edge landscapes, highest density occurs where forest is less abundant and most fragmented by early successional patches. As forest cover increased in the landscape, the Golden-winged Warbler was more abundant as forest edge declined (Thogmartin 2010).

Crawford et al. (2016) examined landscape-level habitat and climate attributes of the Golden-winged Warbler at scales of 2.5 km and 500 m and compared them with those of the Blue-winged Warbler. They studied the Appalachian Mountain and Great Lakes populations, but did not include Ontario data in their analysis. In both areas combined at the 2.5-km scale, compared with the Blue-winged Warbler, Golden-winged Warblers were associated with higher elevations, cooler breeding season temperatures, and forests dominated by aspen. Golden-winged Warblers were found at an average elevation of 427 m (370 m for Blue-winged Warblers) and a mean maximum May temperature of 20.1°C (21.3°C for Blue-winged Warblers). Both species were found in roughly equal numbers in grassland mosaic landscapes (12.7% for the Golden-winged Warbler and 8.5% for the Blue-winged Warbler). Golden-winged Warblers were more than twice as likely to be found in woodland landscapes (20.2%) than Blue-winged Warblers (9.6%). The greatest extent of Golden-winged Warbler locations (39.5%) were associated with landscapes where trembling aspen was present compared with 7.0% for the Blue-winged Warbler. Fewer Golden-winged Warbler locations (4.5%) were associated with agricultural landscapes than Blue-winged Warbler locations (10.2%). At the 2.5-km scale in the Great Lakes population, Golden-winged Warblers were correlated with elevation, summer breeding temperature, land-cover type, and percent deciduous forest cover.

Golden-winged Warbler locations had a mean elevation of 335.2 m (240.9 m for the Blue-winged Warbler) and a minimum May temperature of 4.7°C (7.2°C for the Blue-winged Warbler). Fifty-eight percent of Golden-winged Warbler locations contained aspen compared with 26% for the Blue-winged Warbler; 16% of Golden-winged Warbler locations were associated with areas with no trees compared with 32% for the Blue-winged Warbler. Golden-winged Warblers occurred less in agricultural landscapes (6.8%) than Blue-winged Warblers (23.9%). Golden-winged Warblers preferred forests with an open or broken canopy with a greater percentage of locations in woodland landscapes (30.7%; 14.3% for Blue-winged Warblers). At the 500-m scale in the Great Lakes region, variables most strongly associated with the 2 species included percent deciduous forest, percent agriculture, and elevation. Both species were strongly associated with yellow birch–sugar maple forests, although the Golden-winged Warbler was also found in forests dominated by aspen-birch, jack pine, black spruce–tamarack, and swamp forests. The Blue-winged Warbler was also associated with beech–sugar maple–basswood forests and occurred in agricultural land types at lower elevations. In New York, the Golden-winged Warbler occurred more often in oak-pine and swamp forests than their availability; 10% of locations were associated with fallow pasture. In both the eastern and western portions of the Great Lakes range, it was most commonly associated with yellow birch–sugar maple forests. It occupied higher elevations (367 m) in Michigan, Minnesota, and Wisconsin than in New York (135 m), higher than for the Blue-winged Warbler (303 m and 154 m respectively). The Golden-winged Warbler was associated with a cool dry climate at elevations of 350-1,500 m and habitats comprised of at least 60% deciduous forest cover. In the Great Lakes area, its occurrence was best predicted by the distribution of aspen forest. At finer scales, it was negatively correlated with agriculture and human disturbances, which were more indicative of the presence of the Blue-winged Warbler.

In West Virginia, Aldinger et al. (2017) modelled Golden-winged Warbler density at 4 scales representing annual dispersal (5-km radius), extraterritorial movement (1.5-km radius), intraterritorial movement (100-m radius), and local resource utilization (11.3-m radius). The objective was to identify habitats that supported the highest densities at the various scales. In addition to the 4 scales, they sampled 4 habitats along a successional gradient including herbaceous areas, shrublands, young forests, and late succession forests. Five km was the longest between-season movement they recorded, 1.5 km was the maximum distance travelled by males within season, and 100 m corresponded with the territory size (2.4 ha) and matched their point count radius. At the 5-km scale, its density was negatively correlated with altitude. At the 1.5-km scale, density peaked at elevation 804 m, near the midpoint of elevations they sampled. At the 100-m scale, density was negatively associated with elevation and peaked at 540 m, the lowest elevation they sampled. These mid- to high-elevation landscapes may buffer Golden-winged Warbler populations from contact with the Blue-winged Warbler. At the 100-m scale, the amount of shrubland was important. The Golden-winged Warbler was not detected where shrubland cover was less than 11% but density did not reach higher than average levels until shrubland cover was greater than 52%; density was greatest where shrubland cover was 100%. Managing roughly circular or regularly shaped patches of contiguous shrubland cover of 9.0-12.6 ha surrounded by older-class forests may ensure that it uses the entire patch. Higher densities may be achieved within each patch by arranging multiple patches in a network with less than 2 km between patches. Irregularly shaped patches or patches with

embedded islands of trees may be preferred to create habitat. Densities were higher in shrublands than in young forests. Selective or diameter-limit harvesting of older forests usually does not remove enough tree cover to create suitable nesting habitat. The most important variables for high density included elevations of 602-1,006 m at the 1.5-km scale, elevations of 540-914 m at the 100-m scale, and shrubland cover of 52-100% at the 100-m scale.

Clear-cuts in New York did not provide habitat for the Golden-winged Warbler. Succession in clear-cuts did not provide the patchy distribution of vegetation that it prefers. The dense growth of saplings produced after clear-cutting was unsuitable habitat (Confer and Knapp 1981). In other areas, clear-cuts have provided suitable habitat and some of the highest densities ever recorded were in aspen clear-cuts in Wisconsin (Roth and Lutz 2004). In regenerating aspen clear-cuts in Minnesota, it used sites with residual trees unless the residual canopy exceeded 25% (Patton et al. 2010). In Tennessee, it used stands with a median age of 11 years (range 8-16 years) at 1 site and 10 years (range 3-13 years) at another site. Stand age and composition was critical in determining habitat suitability. Occupied sites had a lower basal area (BA) (10 compared with 40 m^2 ha) than unoccupied sites and were associated with unimproved logging roads. Occupied sites had lower sapling densities (4,445 compared with 5,271 stems per ha) and greater tree heights (11 m compared with 10 m) than unoccupied sites. There were no significant differences between occupied and random sites for other habitat characteristics such as percent grass cover, height of blackberries, elevation, slope, canopy cover variation, herbaceous cover variation, or aspect (Klaus and Buehler 2001). In Pennsylvania, clear-cuts in aspen and mixed oak stands created habitat for the Golden-winged Warbler. It was absent in uncut stands. Only 50% of the oak stands were cut but 75% of the aspen stands were cut. In oak stands, the dominant plant species were oak, red maple, grasses, and ferns, especially hay-scented fern. Dominant plants in aspen stands were aspen, oak, tartarian honeysuckle, grasses, and forbs, especially goldenrods. Almost all territories occurred in aspen clear-cuts, probably because of the higher cutting intensity and because it appears to prefer aspen regeneration (Kubel and Yahner 2008; Yahner 2003). It occurred in young, dense northern hardwoods occasionally interspersed with snags that regenerated shortly after clear-cutting in Wisconsin (Hoffman 1989a). Highest densities reported in North America occur in managed trembling aspen–large-toothed aspen–white birch stands in Wisconsin. Stands older than 25 years did not support the Golden-winged Warbler. It colonized newly created aspen clear-cuts in the first breeding season following harvest. It was not abundant during the seedling stage and persisted in low densities through the sapling and pole stages until 25 years after harvest. In older stands, it occurred largely in forest gaps, in areas of poor regeneration, along edges bordering shrub cover, and along utility and road rights-of-way. High abundance was correlated with the density of aspen suckers, which explained 60% of the variation in abundance. Shrub density explained an additional 17% of variation. Unlike territories on abandoned farmland, those in clear-cuts rarely contained patches of differing vegetation, with sites characterized by uniform regeneration. Territories were also not associated solely with forest edge and occurred in the middle of aspen stands. In other studies, the association demonstrated with edges may be simply because most shrublands are small and situated around the periphery of edges (Roth and Lutz 2004). Also in Wisconsin, it was most abundant in young aspen stands 1-4 years old and least abundant in ecotones between swamps and mature mixed upland forests. Intermediate numbers occurred in jack pine, swamp-upland

aspen ecotones, and shrub swamps. In harvested aspen stands, there was an increase in density from 1-2 years to 4-5 years, and a decline from 6-7 years to 9-10 years. Densities in age class 6-25 years were significantly lower than in 1-4-year-old stands. Aspen density was significantly correlated with its abundance and it was more than 2 times as abundant in young aspen stands as in other habitats. Conditions were most suitable when stands were 3-7 years old. One regenerating aspen stand on sandy soils did not attract the Golden-winged Warbler because it had fewer aspen stems and less woody and herbaceous cover at ground level (Martin et al. 2007). In the upper Midwest, alder wetlands and aspen clear-cuts were 2.7 and 1.5 times more likely to be occupied than other habitats that were sometimes used. Aspen had no significant effect on the probability of use suggesting that the vegetative structure created by clear-cuts was more important than the presence of aspen (Confer et al. 2020).

Peterson et al. (2016a) determined nesting success and fledgling survival rates at 2 sites in Minnesota and 1 in Manitoba, and modelled the effects of landscape-level habitat on full-season productivity. Productivity was 51% higher in upland than wetland habitats. At 1 site, succession of grassland to upland shrub cover was predicted to increase the area available for nesting and to increase productivity by 30%, despite a 12% decrease in the number of surviving fledglings. The models were sensitive to the size and landscape context of the proposed management and the site-specific configuration of the landscape. The relationship between edge and productivity varies substantially depending on landscape structure and composition and amount of edge. The amount of edge was positively related to full-season productivity until a threshold of approximately 0.5 km of shrubby edge within 50 m of any given point was attained. Increasing the amount of edge beyond this threshold decreased productivity. The edges they assessed were those between shrublands and forests and not smaller micro-edges within shrublands.

In Kentucky, the percent coverage by grasses was 42.2% where the Golden-winged Warbler occurred allopatrically and 35.7% where the Blue-winged Warbler was present. Canopy cover was 44.8% and 33.0% under these conditions, respectively. For Golden-winged Warbler management purposes, it was recommended that there be approximately 40% coverage by a mix of grasses and forbs, scattered mature trees with a BA of 2-8 m^2 per ha beyond the forest edge, aggregate sapling heights of as much as 45 m per 5 m^2, and approximately 20% shrub coverage (Patton et al. 2010). In Pennsylvania, vegetative structure differed between territories and unoccupied areas. Territories had a higher percent coverage of herbaceous cover (33% compared with 11%), fewer saplings, and more trees than unoccupied areas. Unoccupied areas had a higher percent coverage of blueberry (33% compared with 7%) and mountain laurel (29% compared with 2%) and a lower percent coverage by blackberry (0% compared with 39%) than territories. There was no difference in percent shrub coverage in territories and unoccupied areas. Black locust, chokecherry, pin cherry, black cherry, white pine, and red pine were indicators of territories. Sassafras, chestnut oak, and red oak were indicators of unoccupied areas. Territory placement and foraging locations were influenced by plant species composition and associated prey abundance. Woody plants that were indicators of territories had the highest abundance of caterpillars and were selectively foraged upon. In addition to the tree species, blackberry was an important habitat component. Plant species composition needs to be considered during management by preferentially maintaining or encouraging the

growth of black locust, pin cherry, white oak, and blackberry while discouraging sassafras, mountain laurel, and blueberry (Bellush et al. 2016).

In Pennsylvania and West Virginia, Frantz et al. (2016) compared the habitat characteristics of Golden-winged Warbler territories and home ranges. In Pennsylvania, there were significantly more saplings in home ranges than in territories. In West Virginia, there were significantly more trees in home ranges, and home ranges were significantly closer to a forest edge (14.3 m) than territories (44.8 m). Distance to shrubland averaged 45.9 m. Forest cover was important at the home-range scale, although actual visits to forests were rare (25 of 2,067 locations, 1.2%). Forest cover where individuals were observed was 20-110 years old and contained canopy gaps resulting in heterogeneous vegetative structure, with growths of shrubs, saplings, and herbaceous ground cover. Movements into forest may act as reconnaissance trips to identify areas suitable for raising fledglings. A male with fledglings progressively ventured further into closed-canopy forest away from his territory.

In West Virginia pastures, nests were significantly closer to the nearest shrub stem (87.0 cm) than random sites (149.5 cm). Within 11.3-m radius circles, the distance to forest edge was significantly less (28.9 m) at nests than at random sites (64.7%; Aldinger and Wood 2014). Therhune et al. (2016) studied nest-site habitat selection by the Golden-winged Warbler in the Appalachian (North Carolina, New York, Pennsylvania, Tennessee, and West Virginia) and Great Lakes (Minnesota and Wisconsin) populations. They compared habitat characteristics at nest sites to random plots 25-50 m away in the same territory. Consistent habitat characteristics used across its breeding distribution included patches of herbaceous cover, shrubs and saplings, and mature forest edges. Nests were associated with limited bare ground (0-10%), less than 55% grass cover, 40-80% herbaceous cover, and 15-35% woody cover. Nest sites contained less bare ground and greater woody cover than random sites. Nests in areas undergoing succession to forest cover had less grass than random sites. The opposite was true of nests in areas that originated from forest following timber harvest or fire. Blackberry cover was greater at nests in sites undergoing succession to forest than in random areas. It selected nest sites with vegetation density of 10-35%. Successful nests in forest-harvested areas had greater grass cover than unsuccessful nests. Average habitat characteristics at Tennessee nest sites in clear-cuts were: 889 saplings per ha (range 0-25,400), 38.8% canopy cover (range 5.0-73.8%), and 150 blackberry stems per ha (range 0-2,258). Nest sites had significantly lower sapling density and canopy cover than perch sites. Dominant plant species at Tennessee nests included bluestems, orchard grass, asters, goldenrods, and blackberry. Nest sites had more grass cover (52.3% compared with 39.3%) and forbs (49.3% compared with 39.9%) at the 1-m scale, fewer saplings (31.4% compared with 44.5%) at the 11.3-m scale, and less woody cover (34.5% compared with 47.2%) at the 1-m scale, than random sites (Aldinger and Wood 2014; Bulluck and Buehler 2008). At New York nests, there was an average of 127 trees with a DBH of less than 2.5 cm within 12.5 m, 190 shrubs within 80 m^2, 86% ground cover, and 56% grass coverage. The mean height of stems 1 m around the nest was 0.52 m (Confer et al. 2020).

Aldinger et al. (2015) examined microhabitat variables at 388 nests on 62 sites in 7 states and related these to daily nest survival rates. Percent grass cover affected daily survival rates, with rates constant up to 50% grass cover, after which survival rates declined. Daily survival rate declined to

88% at 90% grass cover. The Golden-winged Warbler preferred 5-50% grass cover within 1 m of the nest. Coverage by raspberries influenced survival rates, declining as coverage increased from 0-30% but then increasing steadily as coverage by raspberries increased. Survival rate at 50% raspberry coverage was similar to that at 0% and survival increased as raspberry coverage increased above 50%. Distance of nests to forest edge affected daily survival rate, declining from 0 m through 500 m then gradually increasing with increasing distance. The daily survival rate did not reach the level that it was at 0 m distant from forest edge until 900 m from forest. Management for percent grass cover had the most potential for creating or enhancing habitat; sedges or rushes could provide comparable coverage to grasses.

Bakermans et al. (2015) determined the effects of microhabitat features on the abundance of the Golden-winged Warbler in north-central Pennsylvania, northeastern Pennsylvania, and a south-central region that consisted of south-central Pennsylvania and western Maryland. Across all 3 regions in the 222 stands that they sampled, there were significant differences between stands where it was and was not detected. Significant differences between occupied and unoccupied stands occurred for size of clear-cut, years since harvest, perimeter-to-area ratio, percent forest cover within 1 km, percent urban cover within 1 km, and percent young forest cover within 1 km. Within the central Appalachian Mountains, abundance was best explained by the proportion of young forest within 1 km of a regenerating stand and size of the stand. Abundance was greatest between 5% and 15% young forest cover. Abundance was related to the total amount of forest but decreased with an increase in the size of the regenerating stand. Its abundance increased as herbaceous cover increased. The percent herbaceous coverage was 1.6 times greater in occupied stands (13.1%) than in unoccupied stands. Distance to a microedge, shrub cover, number of saplings per ha, and residual BA were also important, with greatest abundance at 7 m^2 per ha residual BA. Occupied stands had a mean BA of 6.3 m^2 per ha of residual trees compared with 8.3 m^2 per ha for unoccupied stands. In northeastern Pennsylvania, distance to the nearest regenerating stand was the most important factor determining abundance, with abundance decreasing with increasing distance to the nearest regenerating stand. Coverage by herbaceous species was also important. Other features contributing to its abundance in the northeast included residual BA, number of saplings per ha, shrub cover, and distance to a microedge. When creating habitat for the Golden-winged Warbler, managers should strive for 15% young forest within a heavily forested landscape (more than 70% forest cover) and regenerating stands should be clustered within 1-2 km of other young forests. Habitat for foraging, nesting, and territory delineation activities should be provided within regenerating stands. This can be accomplished by creating or maintaining patchy habitat that provides a mix of interspersed residual trees, saplings, forbs, grasses, and bare ground. Approximately 3-12 m^2 per ha of dominant or codominant crown-class trees should be maintained with at least 40% of these larger than 38 cm DBH.

In Pennsylvania, Leuenberger et al. (2017) characterized habitat features of 62 territories in a hardwood forest regenerating after a fire 19-20 years previously, and 28 territories in old-field habitat. Probability of occupancy in the regenerating forest increased with increasing coverage by raspberries. Occupancy rates of 95% were associated with 40% coverage by raspberries in 1 year and 20% coverage in another year. Maximum occupancy of the regenerating forest occurred with 0 BA in 1 year and 2-12 m^2 per ha in the other year. In the old field, occupancy was unrelated to

raspberry coverage and maximum occupancy occurred with a BA of 0-7 m^2 per ha. Probability of occupancy decreased as vegetation patchiness decreased regardless of territory type. Unoccupied patches had a BA greater than 12 m^2 per ha in both habitat types. Nests were in patchy areas where the average distance to a microedge was less than 2-3 m.

Two studies examined song perch characteristics of the Golden-winged Warbler. The North Carolina study (Rossell 2001) was conducted in a floodplain with a complex system of natural and disturbed wetlands and uplands. The Tennessee study (Klaus and Buehler 2001) was undertaken in a clear-cut. In North Carolina, 78% of song perches were in the upper 25% of the tree canopy. One of 87 perches was at the top of a tree and none were in the bottom 25% of the canopy. The remaining 21% of perches were evenly distributed between the second and third quartiles of the canopy. Ninety percent of song perches were in forest canopy trees compared with 33% of randomly selected potential perches. Perch trees were significantly closer to forest edge (0.6 m compared with 2.3 m) and water (29.3 m compared with 32.9 m) than randomly selected perches. Fifty-one percent of perches were within 15 m of water. There was no significant correlation between proximity to water and distance to a forested edge. Males selected an overwhelming majority of perches in the upper quarter of large trees on the edge of wooded areas. Perches were closer to water than expected and all but 1 bird had a perch 11 m or less from water. Males often sang above or adjacent to water. The ecological significance of water is uncertain. Areas near water may have a greater abundance and diversity of insects but it frequently nests where water is absent. In Tennessee clear-cuts, the average habitat characteristics around song perches were: 4,445 saplings per ha (range 0-32,258), 63.8% canopy cover (range 5.0-97.5%), and 44 blackberry stems per ha (range 0-600). There was a significant difference in habitat characteristics between perches and nest sites for sapling density and percent canopy cover. Nests were mostly in openings dominated by grasses and herbaceous species.

Some studies attempted to differentiate the habitat preferences of the Golden-winged and Blue-winged warblers based on moisture regime. These characterizations failed because the Golden-winged Warbler inhabits wetter areas than the Blue-winged Warbler in some regions and drier areas in other regions. The Golden-winged Warbler appears to be indifferent to soil moisture and nests in conditions from wet swamps with standing water to the driest hillsides (Canterbury et al. 1993; Confer and Knapp 1979, 1981; Ficken and Ficken 1968b; Hands et al. 1989c; Harrison 1984; Murray and Gill 1976).

Several studies compared the habitat preferences of the Golden-winged and Blue-winged warblers, particularly in agricultural landscapes. The Blue-winged Warbler nests in the same old-field habitats as the Golden-winged Warbler, and the territories of the 2 species frequently overlap. Ficken and Ficken (1968b) and Patton et al. (2010) found no significant differences in the old-field habitat used by the 2 species in New York and Kentucky. In New York, Confer and Knapp (1977, 1979, 1981) found no differences in the densities of herbaceous vegetation and shrubs in the territories of Golden-winged and Blue-winged warblers. There were significant differences in tree density, with the mean tree value for Golden-winged Warbler territories less than half that of Blue-winged Warbler territories. The variance of the tree value differed even more, with the Golden-winged Warbler variance less than 5% of that of the Blue-winged Warbler. Wood et al. (2016) compared the habitats

of Golden-winged Warblers in New York, where they are associated with the Blue-winged Warbler, with those in Pennsylvania where the Blue-winged Warbler is absent or rare, and the habitat of the hybrids. New York Golden-winged Warblers occupied structurally heterogeneous territories surrounded by homogeneously structured contiguous forests that were far from urban areas. Blue-winged Warblers exhibited opposite associations and hybrids' habitat associations were intermediate. Habitat associations of Golden-winged Warblers and cryptic hybrids were remarkably similar in Pennsylvania and New York. The Golden-winged Warbler declined in later successional stages in West Virginia. Areas characterized by very shrubby habitat with late-successional tree species such as maples had the lowest numbers of Golden-winged Warblers and highest numbers of Blue-winged Warblers. The Golden-winged Warbler was confined to old-field habitats that were abandoned 10-35 years ago. The Blue-winged Warbler inhabited these same fields, but also nested in young second-growth forest in areas abandoned 30-70 years ago. The Golden-winged Warbler is a habitat specialist whereas the Blue-winged Warbler is a comparative habitat generalist (Canterbury et al. 1993). There are 2 habitats used by the Golden-winged Warbler that are rarely used by the Blue-winged Warbler, and these may potentially provide sanctuary for isolated populations of the Golden-winged Warbler. The Golden-winged Warbler nests in treed and shrub swamps and these appear to be avoided or used very rarely by the Blue-winged Warbler, even when there is an adjacent population nesting in upland old fields. In New York, approximately 40% of Golden-winged Warblers nested in treed swamps. This habitat was rarely used by Blue-winged Warblers. The Golden-winged Warbler nests at higher elevations than the Blue-winged Warbler (Confer et al. 2010; Frech and Confer 1987; Patton et al. 2010).

Some studies suggested that the Golden-winged Warbler is area sensitive. In upland forest habitat in Wisconsin, it rarely or never occurs in patches smaller than 40 ha (Mossman and Hoffman 1989). In New York, it almost always occurred in large tracts of suitable habitat that were 10-50 ha, even though the territories occupied only a small proportion of the entire area. Many small areas that appear suitable are not used. The tendency for several birds to nest together in loose aggregations presents an additional habitat requirement. Nonetheless, Confer and Knapp (1981) found a single Golden-winged Warbler nesting in a small forest opening that corresponded to the size of its territory. Treed swamps in New York supported 1-3 pairs and these wetlands were only 0.5-5 ha (Confer et al. 2010). In Ontario, the Golden-winged Warbler is not considered area sensitive (Coleman et al. 2000). It is possible that it exhibits area sensitivity in some regions and not in others. It is also possible that not all habitat that is unoccupied is actually suitable given its exacting microhabitat requirements.

Most Ontario nests were on the ground, but 6 were 7.5-30.5 cm from the ground. They were concealed in clumps of tall grasses and other plants, especially goldenrods, and were often at the base of shrubs or tree seedlings. One nest was hidden in skunk cabbage leaves (Peck and James 1987, 1998a). A Hamilton nest was in a clump of showy lady's-slippers (Curry 2006).

Within old-field habitat, nests are usually at the periphery of the territory and near the interface of open and forested habitats. Nests are usually within the open habitat but close enough to the forest to be in the shade. Nests may also be in forests within 10 m of edge. They may also be along edges of logging roads, paths, or trails, in small woodland openings, or low areas where saturated

soils have retarded woody growth. In Minnesota and Manitoba, more than 95% of 226 nests were within 100 m of either side of an edge. One hundred West Virginia nests were supported by a total of 21 plant species, but 93% were in raspberries, goldenrods, or other woody-stemmed plants. Hawthorn was recorded most frequently as the nearest shrub stem. All nests were at a microedge between dense vegetation and an herbaceous opening such as fencerows, cattle trails, browse lines, and recently mowed strips. Successful nests had higher woody cover (16.6% compared with 12.6%) and less cover by raspberries (25.0% compared with 31.4%) than unsuccessful nests. Most nests are on the ground, often at the base of a large raspberry, sapling, or woody seedling stem. They are often in a clump or rosette of a herbaceous species, especially goldenrod and occasionally meadow-rue. They may be hidden by fern fronds or be deep in a clump of grasses or sedges. The nest is typically concealed from above by leaves or other vegetation. Some nests are above ground, often in a blackberry cane or rose bush. They are usually 0.3 m or less from the ground, but 1 Tennessee nest was 1 m up (Adkisson and Campbell 1977; Aldinger and Wood 2014; Bulluck and Buehler 2008; Chapman 1907; Confer et al. 2020; Ficken and Ficken 1968a, 1968b; Graber et al. 1983; Hands et al. 1989c; Klaus and Buehler 2001; Martin et al. 2007; Streby et al. 2014; Tyler in Bent 1953).

In Minnesota and Manitoba, Streby et al. (2014) studied the relationships between nest location relative to forest edge and fledgling survival. Nest success was lowest (10%) 100 m from forest edge in shrubland and highest (60%) 100 m from edge within forest. Fledgling survival was greatest (90%) 100 m from forest edge in shrubland and lowest (10%) 100 m from edge in forest. Early nest sites were in shrublands where fledgling survival was greater than nest success. Later nests were in forests where nesting success was greater than fledgling survival. This suggested that individuals risk early nest failure in exchange for greater fledgling survival. After early nests fail, they select sites where nests are likely to be more successful.

Males maintain a territory where they sing persistently before the arrival of females. Territories are maintained until the young fledge, and then territorial boundaries break down. Territory establishment may be somewhat irregular. In Michigan, 1 male sang regularly in 1 area 7-12 May, then disappeared and established another territory about 400 m away. Territory establishment continued through late May and early June. Late-arriving birds establish territories in peripheral areas or challenge existing territory holders. This may result in the compression of territories established by early arriving birds and a shifting of singing perches. Some birds had disjunct singing areas. Trespassing occurred on adjacent territories and birds were occasionally as far as 400 m from their territory. Territories usually do not overlap. If there is a small area of overlap, it is under dispute until territoriality wanes. In Kentucky, 4 of 25 territories (16%) overlapped by 0.7-17%. The Golden-winged Warbler may nest singly, but often occurs in loose aggregations of as many as 10 pairs, and an aggregation of 31 pairs occurred in Tennessee. Within these aggregations, territories are not densely packed and there may be undefended areas between territories. It is uncertain whether all suitable habitat is used. Nests of neighbours are frequently within 30 m of each other (Confer and Knapp 1977; Confer et al. 2020; Ficken and Ficken 1968a, 1968c; Fraser 2006; King et al. 2009; Klaus and Buehler 2001; Murray and Gill 1976; Patten et al. 2010).

The Golden-winged Warbler has a large territory size for a warbler. Extremes in territory sizes of 0.16-5.3 ha have been reported, but most are 1-2 ha. In Kentucky, the average territory size was 1.3

ha where the Blue-winged Warbler was present and 1.7 ha where it was absent. In Michigan, mean Golden-winged Warbler territory size was 1.9 ha (range 0.8-5.3 ha) at 1 site and 1.4 ha (range 0.4-3.2 ha) at another. New York territories were 0.4-0.8 ha. Birds nesting on utility rights-of-way in Pennsylvania had linear territories 100-175 m long that were 0.6-1.05 ha. Territories averaged 1.53 ha in a regenerating forest and 1.47 ha in old fields in Pennsylvania. In aspen clear-cuts in Wisconsin, mean territory sizes were 0.82 ha in seedlings, 0.28 in small saplings, 0.16 ha in large saplings, and 0.54 ha in pole-sized aspen. Territories were smaller than reported elsewhere, which may indicate high quality habitat. In the seedling stage, territory size may have been constrained by neighbours. In older stands, territories occurred in openings and were approximately the same size as the opening. Territory size may increase during the incubation period if the male attempts to court a second female (Confer and Knapp 1977; Ficken and Ficken 1968a; Fraser 2006; Graber et al. 1983; Hands et al. 1989c; Kubel and Yahner 2008; Leuenberger et al. 2017; Murray and Gill 1976; Patton et al. 2010; Roth and Lutz 2004). The large range in reported territory sizes may be related to the fact that it may frequent areas outside of the territory and have a larger home range. Frantz et al. (2016) used spot mapping and radiotelemetry to determine territory and home range sizes in Pennsylvania and West Virginia. Forty percent of radiotelemetry locations fell outside the mapped territory. In both states, the 100% minimum convex polygons were significantly larger for home ranges than for territories: a mean of 6.3 ha (range 1.4-19.8 ha) for home ranges and 1.7 ha (range 0.65-3.7 ha) for territories in Pennsylvania, and a mean of 11.8 ha (range 2.3-48.0 ha) for home ranges and 2.4 ha (range 0.80-4.8 ha) for territories in West Virginia. Using 50% minimum convex polygons, mean home ranges were also significantly larger: 0.5 ha (range 0.13-1.03 ha) for home ranges and 0.3 ha (range 0.12-0.69 ha) for territories in Pennsylvania and a mean of 0.6 ha (range 0.20-1.28 ha) for home ranges and 0.3 ha (range 0.13-0.63 ha) for territories in West Virginia. In Pennsylvania, home ranges overlapped an average of 2.1 territories (range 0-6) with an average overlap of 1.3 ha (range 0-4.53 ha). Territories overlapped an average of 0.7 territories (range 0-3) with an average overlap of 0.2 ha (range 0-0.54 ha). In West Virginia, home ranges overlapped an average of 2.4 territories (range 0-9) with a mean average of 2.6 ha (range 0-12.48 ha). Territories overlapped an average of 1.0 territory (range 0-2) with a mean average of 0.4 ha (range 0-1.18 ha). Most overlapping territories were those of Golden-winged Warblers (33 of 39 overlaps), but 1 overlap was with a Blue-winged Warbler and 5 were with hybrids. Home ranges determined by radiotelemetry were 3-4 times larger than spot-mapped territories. One Pennsylvania male travelled 1.6 km outside his territory in the afternoon, but was back the following morning. Territories may be larger in low-density populations. Spot-mapping was effective at determining 50% core areas, but underestimated 100% core areas. The high overlap in home ranges suggests that areas between territories are shared by neighbours and may provide undefended foraging areas. Three males foraged within a 10-m radius with no aggressive interactions. Territories had little overlap but home ranges overlapped extensively. Because of the larger home ranges, locations where singing males are detected may be only loosely associated with the breeding territories. Streby et al. (2012) used spot-mapping and radiotelemetry to determine home ranges and territories in Minnesota. Home ranges determined by spot mapping averaged 0.16 ha compared with 0.45 ha for those determined by radiotelemetry. Home ranges contained more mature forest (37%) than territories determined either by radiotelemetry (22%) or spot-mapping (5%). Seventy-five percent of afternoon perches were in mature forest and birds rarely returned to their territories during that period. Zero of 28 spot-mapped territories overlapped, 2

territories of radiotracked males overlapped by 5%, and home ranges of radiotracked birds included the entirety or a portion of 4-7 other territories.

Where the Blue-winged Warbler is present, there may be a brief period when these species are aggressive toward each other. This occurs for a few days when at least one and often both males become paired. The territories of the 2 species overlap widely and they generally ignore each other after the initial brief period of interspecific aggression. Where territories of the 2 species overlap, birds tend to occupy the same areas at different times. Both species may sing near each other simultaneously, but they tend to use different singing perches (Confer and Knapp 1977; Confer et al. 2003; Ficken and Ficken 1968a, 1968b, 1968c, 1968d; Frech and Confer 1987; Murray and Gill 1976; Patten et al. 2010).

Both the Golden-winged and Blue-winged warblers have 2 song types. Type 1 is for mate attraction and species recognition, Type 2 is for territorial defence during aggressive interactions. The Type 2 song of both species is virtually identical. Hybrids may sing the song of either species, both species have been known to sing the other species' Type 1 song, and rarely Golden-winged and Blue-winged warblers sing both species' song. The postures and displays associated with territorial defence are similar in the 2 species and their hybrids. The flexibility in song choice creates opportunities for hybridization and determines which individuals a male will defend his territory against. Birds with similar songs and plumages have non-overlapping territories; birds with different songs and plumages have overlapping territories. Brewster's Warblers with similar songs had non-overlapping territories and 1 Lawrence's Warbler with a Blue-winged Warbler song had a territory that overlapped extensively with that of a Blue-winged Warbler (Ficken and Ficken 1968a, 1968c, 1968d; Harper et al. 2010; Murray and Gill 1976).

Natal philopatry rates are low with the highest reported rates from the Kingston area. Sixteen of 368 nestlings (4.3%) returned to the natal area and some nested as close as 500 m to their natal site. Of the 16 returning young, 11 were males and 5 were females. In 1 Michigan study area, 0 of 51 nestlings and 2 fledglings returned and 0 of 88 young returned in another Michigan study. In West Virginia, 3% of young returned. In New Jersey, 1 young returned (Confer et al. 2020; Fraser 2006; Hands et al. 1989c).

Adult site fidelity rates are high in Ontario and some other locations. Near Kingston, 50-88% of adult males and 33-53% of adult females returned. During a 3-year study, 5 males and 6 females nested in 2 years and 3 males were present in all 3 years (Fraser 2006; McKinnon and Robertson 2008; Vallender et al. 2007b). In other areas, both males and females returned to the same area for as long as 7 years. In Michigan, 50% of adult males and 10% of adult females returned the year after they were banded. In total, 24 of 63 of adults (38%) returned. In New York, return rates in various studies were 30 of 63 adult males (48%), 31 of 81 adult males (38%), and 30% of adults. Only 16% of adults returned in West Virginia. Brewster's Warblers have similar return rates (Carter 1944; Confer and Knapp 1979; Confer and Larkin 1998; Confer et al. 2010, 2020; Fraser 2006; Hands et al. 1989c). In Tennessee and Minnesota, Peterson et al. (2015) banded adult Golden-winged Warblers and installed geolocators on a subsample of them. In Tennessee, 47% with geolocators returned compared with 42% of control birds. In Minnesota, 45% of birds in both groups returned. Geolocators weighing 0.45-0.51 g did not affect return rates.

Limiting Factors

Eggs have been found in Ontario nests from mid-May until the third week of July, with most present from the last week of May until the third week of June (Peck and James 1987). Near Kingston, the mean date of nest initiation for 86 nests was 23 May (Bulluck et al. 2013).

Pair formation begins immediately after the females arrive. Early arriving females wait 1-2 days before starting to build the nest. Late-arriving females may initiate nest building the day of arrival. Cold weather may delay nest building by as long as 10 days. Nest building usually takes 2-3 days but may rarely be completed in a single day. Egg laying is often initiated the day after the nest is completed but may be delayed during wet springs. During warm, dry springs, the interval between nest completion and egg laying was 1-4 days (mode 1 day). During a warm, wet spring, the interval was 4-6 days (mode 5 days). Usually 1 egg is laid daily but occasionally a day may be skipped. Incubation may begin in the afternoon that the penultimate egg is laid. The eggs usually hatch in 10-11 days, but occasionally in 12 days. The incubation period of 1 Ontario nest was at least 12 days. The nestling period is 8-10 days and young typically leave the nest within 24 hours of each other, rarely over 2 days (Buehler et al. 2007; Chapman 1907; Confer et al. 2020; Ficken and Ficken 1968c; Hands et al. 1989c; Klaus and Buehler 2001; Peck and James 1987; Tyler in Bent 1953).

One brood is raised annually; there are no records of attempted second broods. Renesting is common in Ontario, but rare in Manitoba where birds arrive on the breeding grounds as much as 2 weeks later than in Ontario. Clutches of 3-5 eggs have been reported in Ontario (average 4.17 eggs). Near Kingston, the average clutch size of first nests was 5.0 eggs for Golden-winged Warblers and 4.8 eggs for hybrids in 1 study and 5.06 and 5.00 eggs respectively, in another study. Another study near Kingston examined 86 nests and reported clutches of 2-6 eggs (average 4.95 eggs). Mean clutch sizes were 4.30 and 4.51 eggs in 2 Tennessee studies, 5.2 eggs in Michigan, and 4.39 eggs in New York. Clutch size declines with the season and replacement clutches are smaller than first clutches. Overall, clutches of 3-7 eggs have been reported, but 4-6 eggs is the normal clutch size with 5-egg clutches most frequent. In New York, clutch size increased with the amount of herbaceous cover within the territory (Bulluck and Buehler 2008; Bulluck et al. 2013; Chapman 1907; Confer et al. 2003, 2020; Fraser 2006; Hands et al. 1989c; Klaus and Buehler 2001; Peck and James 1987; Reed et al. 2007; Tyler in Bent 1953; Vallender et al. 2007b, 2012).

The age at first breeding is 1 year and birds breed annually thereafter. The mating system is typically monogamous, but polygyny rarely occurs. Confer et al. (2003) reported 3 bigamous males. In New Hampshire, 2 nests were 32 m apart and within a single male's territory, suggesting polygyny. In New York, 2 of 61 territorial males (3.3%) fed young at 2 nests, indicating polygyny. In a Kentucky population, the sex ratio was male-biased so that only 67% of males were able to attract a mate. Such highly skewed sex ratios have not been reported elsewhere. The pair bond typically lasts only a single breeding season, but remating of pairs in subsequent years has been reported in Ontario. In 3 cases, the same birds paired in consecutive years and in 1 case the same birds paired in 2001 and 2003. A high rate of extra-pair copulation occurs. Near Kingston, 30 of 54 broods (55.5%) contained at least 1 extra-pair young and all young were extra-pair in some broods. Of 240 nestlings, 75 (31.8%) were extra-pair. In 21 cases (72%), the extra-pair sire was the closest male to the breeding territory. Most broods had only a single extra-pair sire, but 5 broods had 2 and 2 broods had 3. More

broods than expected contained only within-pair or extra-pair young and fewer than expected contained both within-pair and extra-pair young. Another study near Kingston found at least 1 extra-pair young in 13 of 17 nests (76%) and 24 of 62 nestlings (39%) were extra-pair. Females may gain genetic diversity or superior male genes or both for their offspring by mating with multiple males. This may hasten the rate of genetic introgression (Carter 1944; Confer et al. 2003, 2020; Ficken and Ficken 1968d; Fraser 2006; Harper et al. 2010; Reed et al. 2007; Vallender et al. 2007b).

The Golden-winged Warbler feeds by gleaning, hovering, and hanging upside down and probing into a bud, flower, or curled leaf. In May in New York, 84% of foraging was by probing, 6% by gleaning, 1% by hovering, and 9% by hanging. During June and early July, it fed mostly in flowers and occasionally gleaned caterpillars from leaves. The primary trees used for foraging were apple, black cherry, and hawthorn. Some feeding was done near the ground by clinging to small herbaceous species. Fifty-eight percent of foraging occurred in the upper quarter of trees, 27% in the third quarter from the ground, 15% in the second quarter, and 0% in the bottom quarter. It fed only in the peripheral portions of trees and shrubs. There were no significant differences in the foraging methods, rates, and locations of the Golden-winged, Blue-winged, and Brewster's warblers. Ficken and Ficken (1968b) concluded that it was doubtful that the Golden-winged and Blue-winged warblers could coexist because of their similar ecological requirements. Bellush et al. (2016) studied tree and shrub species that were used for foraging by the Golden-winged Warbler. Of 7 tree species used at least twice for foraging, it foraged more on black locust and pin cherry than black cherry. It foraged more on white oak than sassafras and sweet birch compared with their respective availabilities. Only 4 shrub species occurred within territories, but no foraging was observed on blueberry or sweet fern. It selectively foraged on blackberry compared with mountain laurel. Among trees, black locust, pin cherry, and black cherry had the highest caterpillar abundance; sassafras, sweet birch, and white pine had the lowest. Blackberry and sweet fern had similar caterpillar abundances that were higher than for mountain laurel and blueberry.

In Minnesota, 94% of food items fed to nestlings were caterpillars (mostly of leafroller moths); they were also fed spiders. Adult Golden-winged Warblers eat predominantly leafroller moths and their larvae, other moths and caterpillars, moth pupae, other winged insects, and spiders and spider egg sacs. It occasionally extracts spittlebug larvae from their cocoons while foraging close to the ground. It rarely eats flying insects or nectar. It is uncertain if it actually consumes nectar. It is most likely capturing insects when it feeds in flowers (Confer et al. 2020; Fraser 2006; Hands et al. 1989c; Reed et al. 2007; Streby et al. 2014; Tyler in Bent 1953).

Parasitism by the Brown-headed Cowbird is one of the 3 main threats to the Golden-winged Warbler, although it is not nearly as significant a limiting factor as the other threats. If other factors are suitable, it is usually able to overcome the effects of parasitism. Where Golden-winged Warbler recruitment and replacement rates are nearly equal, parasitism may be the additional factor that leads to its decline. In Ontario, 13 of 33 nests (39.4%) were parasitized, but only 3.8% of nests near Kingston were parasitized. Parasitism rates are around 30% in New York and Michigan. It was estimated that this rate of parasitism results in a 17% decline in its reproductive productivity. In New York, 68% of unparasitized nests fledged warblers compared with 32% of parasitized nests. In Tennessee, 0 of 23 nests were parasitized and 0 of 100 West Virginia nests were parasitized. An

examination of nests over much of the eastern United States revealed almost identical parasitism rates of Golden-winged Warbler nests (11 of 113 nests, 9.7%) and Blue-winged Warbler nests (20 of 232 nests, 8.6%). Parasitized nests of the 2 species reached the nestling stage with equal frequency: 15.3% for the Golden-winged Warbler and 19.1% for the Blue-winged Warbler. The proportion of nests that were abandoned due to parasitism was identical at 14.3% for both species. In New York, parasitism rates increased with increasing herbaceous cover in territories, although clutch size also increased. Parasitism occurred in 47% of nests with above average herbaceous cover compared with 18% of nests with below average herbaceous cover (Aldinger and Wood 2014; Buehler et al. 2007; Coker and Confer 1990; Confer et al. 2003, 2010, 2020; Fraser 2006; Klaus and Buehler 2001; Hands et al. 1989c; Peck and James 1998a).

Habitat loss is a major threat to the Golden-winged Warbler throughout its range. The early successional habitat that it uses is ephemeral and becomes unsuitable as soon as grassy and herbaceous cover is replaced by shrubs and saplings. In the 1840s, millions of hectares of farmland were abandoned creating large expanses of suitable habitat. Most of this habitat has since been lost due to natural succession, tree planting, further clearing for agriculture, and conversion to residential areas. Fire suppression inhibits creation of habitat through natural processes. In some areas, it nests in swamps and these are threatened due to drainage, agriculture, and invasion by common reed. This invasive plant replaces tussock sedge and other native wetland plants, rendering the habitat unsuitable for nesting. Active habitat management by humans is required for it to persist in much of its range (Buehler et al. 2007; Canterbury et al. 1993; Confer 2006; Confer and Knapp 1979, 1981; Confer et al. 2003, 2020; Fraser 2006; Klaus and Buehler 2001; Kubel and Yahner 2008; McCracken 1994; Roth and Lutz 2004).

The other major threat to the Golden-winged Warbler is hybridization with the Blue-winged Warbler. This is a significant threat wherever the 2 species are sympatric, and this now includes almost the entire Golden-winged Warbler's range except for portions of Manitoba and some high altitude areas. Once the 2 species come in contact, there are 5 predictable stages of population dynamics: mostly Golden-winged Warblers with few Blue-winged Warblers and hybrids; balanced populations of Golden-winged and Blue-winged warblers with some Brewster's Warblers; mostly Blue-winged Warblers with few pure Golden-winged Warblers and many Brewster's Warblers, and the first appearance of Lawrence's Warbler; introgressed Blue-winged Warblers with few hybrids and no Golden-winged Warblers; and introgressed Blue-winged Warblers and Lawrence's Warblers. This entire evolution may take place over 50 years but may be completed in as few as 4-5 years. This has happened everywhere the 2 species are sympatric except for a population in the Hudson Highlands of New York where the 2 species have coexisted for over a century. The Golden-winged and Blue-winged warblers are sister species that diverged approximately 1.5 million years ago. Historically, they were geographically separated, with the Blue-winged Warbler originally occurring only west of the Appalachian Mountains. Extensive forest clearing in the early to mid-1800s allowed the Blue-winged Warbler to expand eastward into the range of the Golden-winged Warbler, and both species have been expanding northward as well. Hybrids were first reported in 1874 when Brewster's and Lawrence's warblers were described as full species. There are numerous similarities in the biology of the 2 species that facilitate hybridization. There is great genetic similarity in the species which helps explain why they hybridize so readily and why hybrids appear to have high fitness. The 2 species

occupy identical habitat, although the Blue-winged Warbler uses a wider range of habitat, and the territories of the species may overlap or be adjacent to each other. The songs of the 2 species are very similar and each may occasionally sing the other's song. The courtship displays and sexual reactions of the species are similar. Sex ratios of one of the species may be temporarily biased due to differential timing of spring arrival of the species or sexes, or when 1 species is locally rare and this promotes hybridization due to lack of conspecific mates (Bledsoe 1985; Buehler et al. 2007; Canterbury et al. 1993; Confer 2006; Confer and Knapp 1977; Confer and Tupper 2000; Ficken and Ficken 1968b, 1968c, 1968d; Fraser 2006; Frech and Confer 1987; Gill 1980, 1987, 2004; Harper et al. 2010; King et al. 2009; Patton et al. 2010; Vallender et al. 2007a, 2009).

The mechanisms by which hybridization results in the local extirpation of the Golden-winged Warbler were the subject of many studies, but much is yet to be learned. Interspecific mating of the 2 species is uncommon, but mating of pure species and hybrids is common. Male Golden-winged Warblers dilute their genes by mating with hybrids more frequently than male Blue-winged Warblers do, although the reverse may be true where the Blue-winged Warbler is rare. Male Blue-winged Warblers pursue female Golden-winged Warblers at a higher frequency than male Golden-winged Warblers pursue female Blue-winged Warblers resulting in asymmetry in the transfer of genes. These factors favour introgression of ancestral Blue-winged Warbler into Golden-winged Warbler phenotypes. It was originally thought that the gene flow was unidirectional from the Blue-winged Warbler to the Golden-winged Warbler, resulting in genetic swamping of the Golden-winged Warbler. More recent research demonstrated that gene flow is bidirectional and that the genetic compliment of the Blue-winged Warbler also becomes introgressed. There appears to be a mosaic of pure and mixed populations throughout the sympatric range of these species, with varying amounts of introgression. The rate of introgression depends upon the length of contact of the 2 species and their relative population sizes. The long-term persistence of the Golden-winged Warbler in 1 area of New York may be because introgression may not have been enough to swamp the local population, or this population might be continually augmented by immigration. Genetic swamping of the Golden-winged Warbler is hastened through extra-pair copulations that result in broods of mixed parentage and genetic compliments. Several studies concluded that male hybrids are at a disadvantage in obtaining a mate, probably due to lack of the facial patterns that may be important in attracting a female. Some studies determined that facial patterns are important in attracting females. Others have found that facial patterns are unimportant. Ontario studies demonstrated that hybrid males were as likely to attract a mate as males of either of the 2 species. There was no difference in clutch size, food-provisioning rates, or fledgling success of nests with male hybrids or males of pure species. Earlier studies were based on smaller sample sizes, but it is possible that there is regional variation in mating success of hybrid males based upon local population structures. Once mated, hybrids are likely to be as successful as males of either species (Buehler et al. 2007; Confer 2006; Dabrowski et al. 2006; Ficken and Ficken 1968d; Fraser 2006; Gill 1980, 2004; Leichty and Grier 2006; Parker 1951; Reed et al. 2007; Shapiro et al. 2004; Vallender et al. 2007b, 2009). Wood et al. (2016) determined that the habitat preferences of hybrids were intermediate between those of the Golden-winged and Blue-winged warblers. Even populations that are isolated from Blue-winged Warblers contain cryptic hybrids that appear to be pure Golden-winged Warblers. The pattern of habitat occupancy by these hybrids may promote contact with

Golden-winged Warblers and thus facilitate genetic introgression even where the Blue-winged Warbler is absent.

The rate of genetic introgression in the Golden-winged Warbler is alarming. Most studies estimate the proportion of pure Golden-winged Warblers and hybrids in populations by plumage characteristics. Short (1963) examined 1,028 museum specimens and concluded that 312 of 431 definite hybrids (72.3%) would be identified as a pure species in the field. Vallender et al. (2007a) analyzed the genetic make-up of Golden-winged Warblers from Manitoba, Kentucky, Tennessee, and Ontario and found that almost a third of phenotypically pure individuals had experienced cryptic past hybridization. The number of pure populations is probably much smaller than field studies indicate. Genetic analyses conducted in 9 states and 3 provinces revealed that all populations except those in Manitoba and Quebec showed some level of introgression. No introgression was found in populations from southern Ontario near Long Point or Quebec, but it was concluded that this was likely due to small sample sizes rather than actual absence of introgression. At Rainy River, 7.1% of birds were introgressed and 22.2% of Barrie birds were introgressed or were clear Brewster's Warblers. Manitoba appears to support the only pure populations of the Golden-winged Warbler, but this province supports less than 1% of the global population. Samples from southern Ontario had the highest rates of introgression at 43%. The Kingston population was allopatric until the Blue-winged Warbler was first observed in the late 1980s. By 2004, 17% of the breeding population was comprised of hybrid phenotypes although Blue-winged Warbler occurrence remained low at 1%. The most common route of introgression at Kingston was mating by advancing male Blue-winged Warblers with females of the established Golden-winged Warbler population. The continued advancement of Blue-winged Warblers and hybrids into the current breeding range will perpetuate declines in Golden-winged Warbler populations. As of 2007, approximately 33% of the Kingston Golden-winged Warbler population was introgressed despite the relatively short contact period and low incidence of observed hybridization. There are varying opinions on the future of the Golden-winged Warbler, but all concur that it looks bleak. One prediction is that the Golden-winged Warbler will be very rare by the end of the 21st century, persisting in early stage successional habitats at high elevations and latitudes, and perhaps in swamps. There are signs of co-existing populations in southern New York, Michigan, and West Virginia that suggest that the Golden-winged Warbler will likely escape total replacement by the Blue-winged Warbler. A second opinion suggests that complete genetic swamping of the Golden-winged Warbler is not a foregone conclusion. This is due to site-specific differences in patterns of introgression. The third opinion is that the only currently genetically pure populations are in Manitoba and that it is likely that Blue-winged Warbler genes will eventually become prevalent even in these populations. By 2010-12, 8 of 128 Golden-winged Warblers (6.3%) in Manitoba had DNA mismatches indicating that introgression is proceeding rapidly there. In this event, the Golden-winged Warbler may become genetically extinct. All these predictions may be correct. It is possible that isolated populations of birds will persist that have plumage characteristics typical of pure Golden-winged Warblers, but that all populations will exhibit some introgression and genetically pure populations will become extinct (Confer et al. 2010; Dabrowski et al. 2005; Fraser 2006; Gill 1980, 2004; Reed et al. 2007; Vallender et al. 2007a, 2007b, 2009, 2012; Vallender and Bull 2016).

It was originally thought that the Blue-winged Warbler had a competitive advantage over the Golden-winged Warbler and that interspecific competition was a factor in the decline of the Golden-winged Warbler. Blue-winged Warbler males regularly harass Golden-winged Warbler males in West Virginia and Michigan. Golden-winged Warblers nesting close to Blue-winged Warblers in New York laid smaller clutches than those without a Blue-winged Warbler neighbour. In New York, however, Golden-winged Warblers were dominant in more than half the interactions with Blue-winged Warblers. Intense aggression appeared to occur only in relation to nest defence or mate guarding. Experiments involving removal of adjacent Blue-winged Warblers determined that Golden-winged Warblers did not expand their territories. Blue-winged Warblers do not drive Golden-winged Warblers into inferior habitat and interference competition is not a cause of Golden-winged Warbler decline. There are single records of the male of each species feeding the young of a pair of the other species and, in both cases, aggression was directed toward the intervening male. In 1 case, the intruding Blue-winged Warbler male was dominant to the Golden-winged Warbler male (Adkisson and Campbell 1977; Coker and Confer 1990; Confer and Larkin 1998; Confer et al. 2003, 2020; Gill 1980, 2004; Rayner 1988c).

The habitat selected by the Golden-winged Warbler for nesting may affect reproductive success. In West Virginia, 86% of nests in early stages of succession were successful compared with 33-52% in areas of dense shrub and sapling growth. Nest success declined with increasing shrub and sapling growth in New York. In Tennessee, nest success increased with increasing shrub cover and decreased with sapling density. Daily survival rates of nests decreased as daily minimum temperatures increased, possibly because higher temperature may increase activities of predators such as snakes. In Pennsylvania, nest predation rates were significantly lower in clear-cuts than along utility rights-of-way. Clear-cuts had a greater interspersion of shrubs and herbs; rights-of-way were abrupt edges. In New York, nest success was 65% in swamps and 37% in upland habitat, which supported a high density of chipmunks and snakes (Bulluck and Buehler 2008; Canterbury et al. 1993; Confer et al. 2003, 2010; Kubel and Yahner 2008).

Vallender et al. (2012) sampled Golden-winged Warblers in Manitoba, Ontario, and Quebec to determine the prevalence of blood parasites in them. These are intercellular sporozoans that complete part of their life cycles within circulating red blood cells in birds. Infections are chronic and tend to resurface during periods of stress, particularly during the breeding season. None of the birds sampled showed clinical signs of illness. The rates of infection were 0% in Quebec and at Barrie, 7.1% at Rainy River, and 30% in Manitoba. The infection rates were considered an underestimate. The higher rate of infection in Manitoba is of conservation concern because infections may reduce fitness. In Manitoba, birds with more grassland or marsh cover within 200 m were more likely to be infected with blood parasites (Enslow et al. 2023).

The Golden-winged Warbler readily deserts its nest if disturbed while building it. Even nests with incomplete clutches may be abandoned. Once incubation starts, females often stay on a nest despite considerable disturbance (Confer et al. 2020). In Minnesota, young that were forced to fledge experienced a higher survival rate than those that fledged naturally. Premature fledging did not adversely affect survival rates and the ability to fledge early may be a predictor of higher probability of fledgling survival (Streby et al. 2013).

In Virginia, Albrecht-Mallinger and Bulluck (2016) broadcast calls of the Golden-winged Warbler to determine if this method could be used to attract breeding males to a site. Males did not respond strongly to conspecific attraction in a low-density and highly fragmented system. Male increases near treatment areas resulted in a decline in previously occupied areas. Other studies in dense and less-fragmented populations have demonstrated conspecific attraction.

In Pennsylvania, a severe hailstorm produced 2.5-cm hail and caused the failure of 8 of 9 nests (88.9%). Seven of the 8 nests contained damaged eggs and all nests sustained damage. Two females were found dead within 0.5 m of their nests. The storm may have had greater effects than what was observed because little territorial or renesting activity occurred in the following weeks. Climate change has the potential to increase the frequency of damaging severe storms (Fiss et al. 2019).

The potential effects of climate change on the Golden-winged Warbler are uncertain. Price (2004) predicted that its range in southern Ontario might contract if the average summer temperature increased by 2°C. Thogmartin (2010) noted that moths and their larvae are a favoured food and that there is evidence that moths are responding to climate warming. This may result in a gradient in food abundance that at some point may become asynchronous with Golden-winged Warbler habitat as the climate changes. Confer et al. (2020) stated that it had experienced major range changes in the last century and that it uses a wide range of altitudes. They concluded that it may be adaptable to a wide range of temperatures.

Status

Prior to European settlement, the Golden-winged Warbler was probably present in very low numbers in the extreme south, which would have been at the northern extent of its range. The first record for the province was from Hamilton in 1860. At the end of the 19th century, it occurred regularly at London and had been recorded at Port Rowan and Dunnville in addition to Hamilton. Middlesex County was one of its early strongholds, with the first nests found there in 1912 and 1914. It was fairly common there and in Norfolk County in the 1930s. In the Hamilton area, it was documented in 1929 and every year thereafter, with breeding first occurring in 1935. By the 1950s, its breeding range had extended northward by 250 km to include the Region of York and Peterborough and Simcoe counties. In the early 1960s, the breeding range included Kingston, the Bruce Peninsula, and southern Muskoka District and the range continued to expand northward to Parry Sound, Manitoulin Island, and near Sudbury. By 1980, there was evidence of its becoming established in the Rainy River area. During the first atlas, there was a population at Rainy River and it occurred throughout south of a line from Sault Ste. Marie to North Bay, except in Essex County. The stronghold of the species was in a broad band along the southern edge of the Canadian Shield. Distribution in much of the southwest that was its former stronghold was spotty by then. Its centre of abundance had shifted considerably northward (Baillie and Harrington 1937; Curry 2006; McCracken 1994; McIlwraith 1894; Mills in Cadman et al. 1987). James (1991) considered the Golden-winged Warbler an uncommon to locally common resident in the south.

In the 1990s, there was no evidence that overall numbers of the Golden-winged Warbler were declining and they may have been increasing. It has exhibited a pattern of extending its range northward and abandoning areas further south where it was formerly common. This pattern has been continuing for about 1.5 centuries (King et al. 2009; McCracken 1994). The evidence of

withdrawal from the southern portion of the province was evident well before the first atlas. Breeding numbers in the Hamilton area peaked in the 1960s and Curry (2006) predicted that it might not be long before the Golden-winged Warbler disappeared as a breeding species near Hamilton. In Elgin County, it was a common breeder in 1891, a regular but not common breeder in 1954, and possibly extirpated as a breeder in 2000 (Lancaster et al. 2004). McCracken (1994) predicted that it would be largely extirpated from many areas south of Toronto by the end of the 20th century, and this prediction was correct.

The second atlas demonstrated that there had been no change in the overall distribution of the Golden-winged Warbler since the first atlas. It was not found in many squares where it was present during the first atlas. It declined in all atlas regions except in the Rainy River area, and declines were significant in the Carolinian Forest Region and the Great Lakes–St. Lawrence Forest Region in the Shield. It was most abundant along the southern edge of the Shield, especially near Georgian Bay and north of Kingston on the Frontenac Axis. Smaller areas of high density occurred east of Sudbury, east of Algonquin Park, and near Gravenhurst (Vallender in Cadman et al. 2007).

Preliminary results of the third atlas indicate a further decline in the Ontario Golden-winged Warbler population. There were few records in the southwest and the population in the Parry Sound area and east of Algonquin Park almost disappeared completely. The population in the Rainy River area increased from being in 5 squares in the second atlas to 28 squares by 2024 (Cadman 2024).

Both hybrids are rare in Ontario. The Brewster's Warbler is found most often around the southern Niagara Escarpment, on the Oak Ridges Moraine, along the southern edge of the Shield, and in the Long Point area. The Lawrence's Warbler was found in only 5 locations during the second atlas, mostly in or just north of the Carolinian Forest Region but one was found in southeastern Ontario (King et al. 2009; Vallender and Leckie in Cadman et al. 2007).

No northward expansion of the Golden-winged Warbler's range occurred between the first and second atlases. Further northward expansion may be inhibited by lack of suitable habitat. The Boreal Forest Region, with its dominance by spruce and fir, is marginal habitat at best for it (Buehler et al. 2007; King et al. 2009). The lack of northward range expansion coupled with declines in the south is likely to result in precipitous declines in the Ontario population.

Golden-winged Warbler populations have not been stable for at least the past 150 years. Population trends are characterized by localized expansion, establishment of regional populations of moderate abundance, and subsequent declines. The population expanded its range northward while contracting southward, disappearing in more southerly areas where it was formerly fairly common. The northward range expansion appears to have stalled now that populations have reached the southern edge of the Boreal Forest Region. Until the 1990s, it may have been increasing in Ontario, but it is now declining significantly. Breeding Bird Survey (BBS) data for 1998-2007 suggested a decline of 4.4% per year in Ontario and 11.3% per year in the Great Lakes–St. Lawrence Forest Region in the Shield. The rate of decline in Ontario is increasing and was as high as 14.4% per year 1992-2002. Although the rates of decline in Ontario are alarming, they are not as pronounced as declines in the United States. It is declining at rates greater than for most other North American passerine species (Confer 2006; Confer et al. 2020; Fraser 2006). Rosenberg et al. (2016) mapped the range of the Golden-winged Warbler during 1880-1920, 1980, and 2013. Its range shifted northward

until the 1980s, with limited expansion to the north since then except in Manitoba. Its range was originally contiguous through the Appalachians and the Great Lakes region. Due to its disappearance in many Great Lakes states, the Appalachian and Great Lakes populations are now isolated from each other. In the Appalachians, it is becoming restricted to high-elevation sites where the Blue-winged Warbler is absent.

Bulluck et al. (2013) used adult survival and fledging success rates to estimate population trends of the Golden-winged Warbler near Kingston. They concluded that this population was declining rapidly at a rate of 24% per year, a higher rate of decline than BBS data indicated (8.01% per year for the entire province). The number of birds remained fairly constant at the Kingston site, suggesting that this high-quality habitat receives immigrants on a regular basis. Based on the Golden-winged Warbler Atlas Project and eBird results, the 2013 range in southern Ontario contracted to exclude most of the area west of Hamilton and areas north to central Bruce and Grey counties. In these areas, it has largely been replaced by the Blue-winged Warbler and hybrids (Rosenberg et al. 2016).

BBS data indicate that the Golden-winged Warbler increased at annual rates of 0.561% in Canada and 0.436% in Ontario 1970-2021. Trends for 2011-21 were an annual increase of 0.1% in Canada and an annual decrease of 1.36% in Ontario. The long-term trends were of medium reliability; the short-term trends were of low reliability (A.C. Smith et al. 2023).

The Golden-winged Warbler is designated threatened in Canada and special concern in Ontario. The population and distribution objectives identified in the recovery strategy are to maintain self-sustaining populations in Manitoba, Ontario, and Quebec while maintaining, at a minimum, the current population of approximately 35,000 pairs (Friis et al. 2016).

POSTFLEDGING PERIOD

During the postfledging period, adults and juveniles may occur both in open successional habitat and in forests. Dense vegetation in these areas, particularly forest edges, may provide important foraging opportunities and possibly cover from predators. In northern Minnesota, broods were observed in the interior of forests. In Michigan, 8 juveniles but no adults were captured in mature riparian trembling aspen forests with an understorey of alder and honeysuckle. No Golden-winged Warblers were captured in mature upland trembling aspen–large-toothed aspen forests with minimal understorey. In clear-cuts in Minnesota, 30 were caught in mist nets during the breeding season. During the postfledging period, 53 adults and 108 juveniles were caught in the same location. In other areas, adults with broods have been observed in dense thickets of dogwoods and alders. In Minnesota and Manitoba, adults usually moved their fledglings into forest within 10 days of leaving a nest in open habitat, or kept them near the nest if it was in forest (Akresh et al. 2009; Hands et al. 1989c; Patton et al. 2010; Streby et al. 2011b, 2014).

In Minnesota, fledglings were 8-66 m (average 26 m) distant from their nests within 24 hours. Thirteen percent of fledglings were outside their natal territory by this time. Five days after fledging, young were 25-346 m (average 156 m) from the nest and within 10 days they were 126-510 m (average 252 m) from the nest. This suggested that 85% and 100% of fledglings were outside their natal territory within 5 and 10 days, respectively (Streby and Andersen 2013a). In Pennsylvania 1-5 days postfledging, sub-broods made average daily movements of 38.7 m (range 5.3-127.5 m) and 44.9 m (range 3.0-104.7 m) at 2 sites. During days 6-28, sub-broods made average daily movements

of 155.9 m (range 61.1-322.8 m) and 156.7 m (range 56.9-369.1 m). One to 5 days after fledging, sub-broods averaged 92.5 m (range 6.1-278.9 m) and 106.0 m (range 4.1-266.1 m) from the nest. Average distances from the nest 6-28 days postfledging were 749.3 m (range 207.4-2,042.8 m) and 694.3 m (range 38.9-3,600.2 m; Fiss et al. 2020).

Brood division occurs, with the male and female each caring exclusively for individual fledglings. In Minnesota and Manitoba, 98.5% of broods were divided with equal parental care whereby the male and female cared for similar numbers of young. Both sexes were equally likely to care for male or female offspring. Both male- and female-reared sub-broods moved similar distances from the nest in the early postfledging period. In the last 5 days of the postfledging period, female-reared sub-broods were 461 m from the nest and 354 m from the natal patch edge; sub-broods reared by males were 164 m from the nest and 108 m from the natal patch. Male-reared sub-broods appeared to change directions in a manner that kept them closer to the nest. Female-reared broods exhibited a period of directional movement 8-10 days postfledging that took them further from the nest. Following 10 days postfledging, sub-broods cared by both sexes made movements more than 90° in direction in successive days, keeping them in appropriate brood-rearing habitat (Peterson et al. 2016b, 2022).

In Minnesota and Michigan, male- and female-reared sub-broods used areas with similar vegetation characteristics (vertical cover, shrubland, lateral vegetation density, and forest strata) throughout the postfledging period. Vegetation characteristics of sites used by sub-broods changed with time. From fledging to independence, the percentage of vertical cover in inhabited areas increased from 40% to 60%, nonshrub forest use increased from 45% to 85%, the frequency of fledglings perched on the ground decreased from 35% on day 1 to 0% by day 13, and the frequency of use of the midstorey increased from 0% to 15%. Lateral vegetation density of fledgling locations remained constant at 65% and understorey use remained constant at 60%. There was no difference in survival rates of fledglings raised by males and females. Managing for postfledging cover types as far as 700 m from a managed shrubland would provide postfledging habitat for 95% of the broods that were studied. Many unoccupied areas that appear to be suitable breeding territories may not be surrounded by adequate postfledging habitat at a scale used by females to rear their broods (Peterson et al. 2016b, 2022). In Pennsylvania, sub-broods selected for even-aged stands harvested less than 10 years previously over all other cover types 1-5 days postfledging and avoided edges between early successional and mature forests. At 6-28 days postfledging, sub-broods selected the same forests plus those harvested 10-25 years previously with trees less than 15 cm DBH. At 1 site, they also selected upland shrubland (Fiss et al. 2020). In Pennsylvania, fledglings consistently selected for greater lateral and overhead vegetation density and lower basal area than available in stands. Nests were associated with abundant herbaceous vegetation, but fledglings preferred areas with greater structural complexity provided by taller woody plants. Herbaceous cover at nests averaged greater than 40% but fledglings used areas with less than 30% herbaceous cover in all stands. Sapling height averaged 2 m at nests and more than 3 m at fledgling locations, especially in mature and forested wetlands where sapling heights averaged more than 4 m. In even-aged stands harvested less than 10 years previously stocked with trees less than 15 cm DBH, fledglings strongly selected for increased cover by raspberries. Raspberry coverage greater than 80% was associated

with greater than 70% probability of use; coverage less than 25% was associated with less than 60% probability of use (Fiss et al. 2021).

In Pennsylvania, polygynous and monogamous males moved fledglings under their care in different manners. One nest was attended by a female Golden-winged Warbler and a male Brewster's Warbler. The fledglings remained within 40 m of the nest for the first 2 days; brood division occurred on the third day. The male and female travelled in different directions with their fledglings, with the female entering a nearby closed-canopy forest and the male remaining in the timber harvest area where the nest was located. On day 4 after fledging, the male led the young 166 m to a nest attended by a female Brewster's Warbler. Over the next 12 days, the male regularly fed his fledgling, the second female, and her nestlings, with the fledglings remaining within 36 m of the second female's nest. The first female and her fledglings remained an average of 275 m from the second female's nest during this period. After the second female's nest failed, the male moved away from it. His movements were then unbiased by its location. Both adults led their sub-broods away from the natal nest, but the female led her sub-brood 30% further than the male. The female and her sub-brood moved an average of 122 m per day compared with 86 m per day for the male sub-brood. The next year, the same male was monogamously mated to a female Golden-winged Warbler. In that year, he moved his sub-brood into the adjacent closed-canopy forest, similar to what his mate of the previous year did. In the second year, he moved his sub-brood an average of 160 m per day compared with 86 m the previous year. Results suggested that polygynous males may constrain their postfledging movements by approximately 50% when they are attending a second nest (McNeil et al. 2019).

Streby et al. (2016) studied survival rates of Golden-winged Warbler fledglings in relation to habitat in Minnesota and Manitoba. Forty-eight percent of fledglings were depredated before they became independent of their parents at age 25 days; 75% of predation occurred in the first 3 days after fledging and 86% occurred in the first 8 days. Fledgling survival was greatest from nests in forests, lowest from nests in shrublands, and intermediate from nests closest to forest-shrubland edge. Fledgling survival was least in shrublands and greatest in forests for the first 8 days after which fledgling survival was generally high. The probability of a fledgling surviving to day 25 was 84% in sapling-dominated clear-cuts, 75% in mature forests, 46% in wetland shrublands, and 40% in shrub-dominated clear-cuts. In the first 8 days after fledging, young selected for mature forests and sapling-dominated clear-cuts over all other cover types, selected against roads and grasslands, and used shrub-dominated clear-cuts, wetland shrublands, firebreaks, and forested wetlands in accordance with their availability. Older fledglings selected for mature forests over all other cover types and for shrub-dominated clear-cuts over all other cover types except mature forests. They selected against roads and grasslands and used wetland shrublands, firebreaks, and forested wetlands in accordance with availability. First-day movements of fledglings from shrubland nests were oriented toward shrubland-forest edges but first-day movements from forest nests were not oriented toward shrubland-forest edges. The best predictor of survival was location of the nest relative to a forest-shrubland edge. Fledgling survival is strongly influenced by nest-site choice, which may explain why the Golden-winged Warbler rarely nests in areas that maximize nest success. Adults direct or lead their fledglings to forest cover, or keep them in forest cover, regardless of the location of the nest. Crossing roads had no significant effects on fledgling survival because they

crossed roads quickly by flying. Young fledglings use shrubs and understorey trees while their parents forage elsewhere, often more than 300 m distant. Early postfledging habitat might be limited in landscapes with primarily closed-canopy forests with limited shrub and sapling growth. Two potential management strategies include forest canopy thinning to promote shrub and sapling growth and maintaining close associations between shrublands and sapling-dominated regenerating stands through rotational harvest.

MIGRATION

Judging by kills at television towers, migration may be nocturnal. Males migrate first in spring and arrive on the breeding grounds 2-7 days before females (Confer et al. 2020). The differential in timing of migration by the sexes may be greater in Ontario. Males appear in early May in the province, with peak numbers in mid-May; some arrive at the end of April. Females arrive 1-2 weeks later (Fraser 2006; King et al. 2009). In the southern Shield, spring migrants occur from mid-May to early June (Mills 1981; Tozer 2012).

Autumn migration in the southern Shield extends from mid-August to early September, with some remaining until early October (Tozer 2012). In the south, migration peaks in late August and early September, with stragglers until early October (Fraser 2006; Weir 2008).

During migration, the Golden-winged Warbler is much less exacting in its habitat requirements than during the breeding season. In addition to thickets, it may occur in open woodlands and closed-canopy forests. During migration in Michigan, it occurred in the forested strip nearest a river in a large riparian woodland, but was absent in the next 2 wetland bands distant from the river and in the outer band of upland forest. During spring migration in Wisconsin and Minnesota, it was equally abundant in floodplain and upland forests. In Algonquin Park, migrants usually occur in alder swales, in swamps, and along shrubby edges of forests. During the breeding season, it avoids conifers, but may forage in white pine during migration (Chapman 1907; Fraser 2006; Inman et al. 2002; Kirsch et al. 2013; Tozer 2012; Tyler in Bent 1953).

Ficken and Ficken (1974) considered the Golden-winged Warbler a social mimic of the Black-capped Chickadee during migration. The 2 species have similar plumages, both often forage by hanging upside down, and both forage on buds in spring. Although only 5% of warblers present during 1 spring migration were Golden-winged Warblers, 50% of warblers seen within 5 m of a chickadee were that species. Interactions between the 2 species involved close approaches and following with little sign of aggression. Both species may benefit by this close association. The warbler may benefit by following the chickadee because it is a resident species that presumably knows the best foraging areas and might also be aware of predators. The chickadee gains access to buds opened by the warbler, which may not prey on all the available insects because it is rapidly displaced by the chickadee.

The Golden-winged Warbler occasionally strikes television towers and other tall structures during migration. Ten were killed at the Lennox generating station chimneys near Kingston on 4 and 7 September 1984. Over an 11-year period, 52 deaths were reported at a Florida television tower. Although numbers of mortalities during migration appear low, they are disproportionately high given its low population. At regularly monitored communications towers, 542 mortalities were reported at 15 of 47 surveyed sites. This mortality rate was exceptionally high compared with other

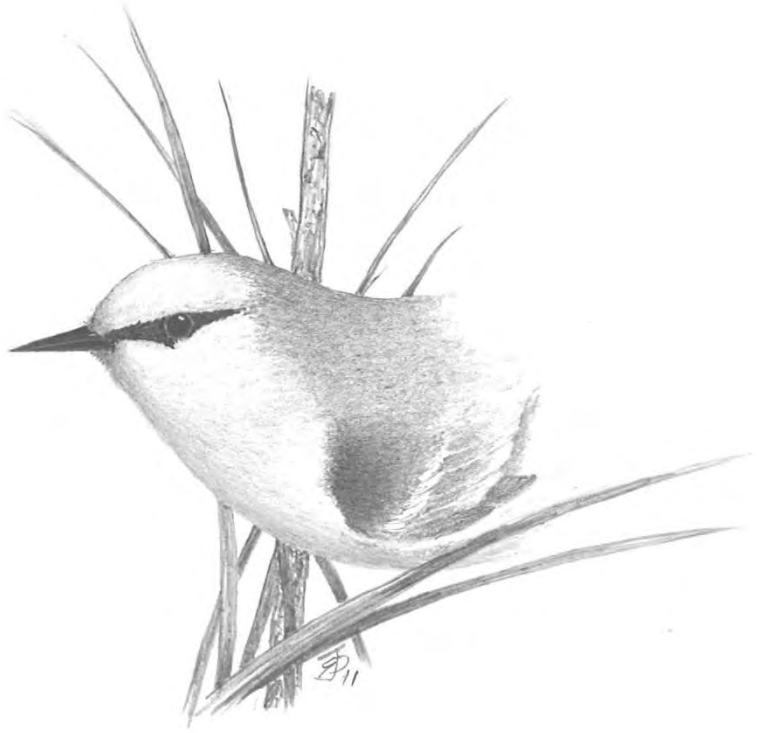
species that are orders of magnitude more abundant but that had only slightly higher mortality (Confer et al. 2020; Hands et al. 1989c; Weir 2008). Loss et al. (2014) examined bird collisions with buildings in the United States. The Golden-winged Warbler was 35.3% more vulnerable to colliding with buildings than birds on average, regardless of the type of building. At low-rise buildings, it was the most vulnerable species, being 141.7 times more likely to strike a building than average. At high-rise buildings, it was 23.1 times more likely to suffer collisions than birds on average. It was not on the list of the top 20 most vulnerable species for striking residences 1-3 stories tall.

James (1991) considered the Golden-winged Warbler a rare migrant in the province and all books summarizing regional populations concurred.

Long Point Bird Observatory data from 1960 to 1989 indicated that the number of Golden-winged Warblers captured increased during this period, but the ratio of Golden-winged to Blue-winged warblers decreased. The number of Golden-winged Warblers captured 1960-69 was 13, 18 were caught 1970-79, and 37 were caught 1980-89. The ratio of Golden-winged Warblers to Blue-winged Warblers captured was 2.6:1 in 1960-69, 1.4:1 in 1970-79, and 0.5:1 in 1980-89 (McCracken 1994).

Blue-winged Warbler

Vermivora cyanoptera



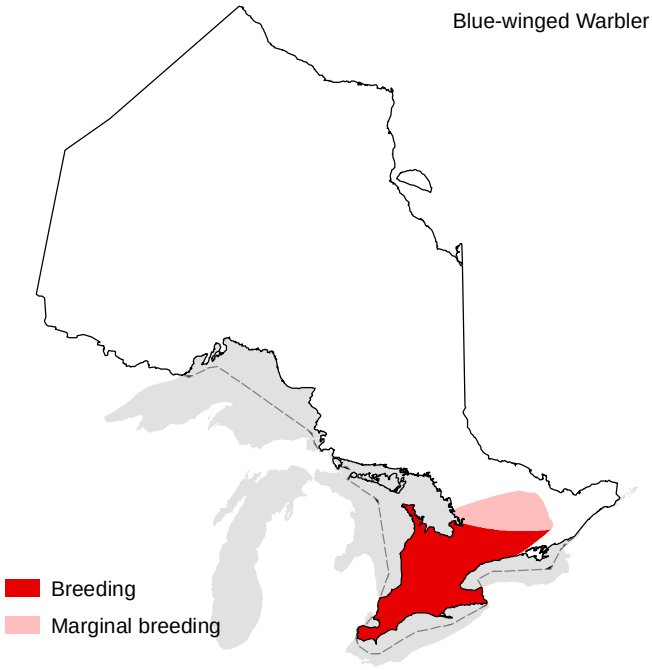
BREEDING SEASON

Habitat Requirements

In Ontario, the Blue-winged Warbler has nested near edges of mixed and deciduous woods, or in open, treed habitats. These areas were vegetated with grasses or mixed grasses and sedges and were overgrown with shrubs and small trees such as hawthorns, apples, and planted conifers. Three of 7 nests were near wet areas (Peck and James 1987). In Elgin County, nesting occurred in a semi-circular opening on the edge of mixed deciduous woods (Rayner 1988c). Near Kingston, it nested in an old field where early succession was maintained by late-summer grazing by cattle (King et al. 2009).

The most common nesting habitat for the Blue-winged Warbler is old fields and pastures with some shrub and tree growth. Utility rights-of-way may provide suitable habitat. Optimum habitat consists of clumps of vegetation, with patches of grasses and herbaceous plants, shrubs, and trees less than 10 m in height. Old-field areas that it inhabits typically are bordered on one or more sides by deciduous forest. It uses trees within and at territory edges as singing perches and for foraging. It also nests in young second-growth forests; on sand dunes; in shrub thicket swamps; in red maple swamps with 60-80% canopy closure and an understorey of spicebush, northern arrowwood, and

tussock sedge; in oak-hickory clear-cuts 2-10 years old; in young pine plantations; in oak savannahs; in pine barrens, particularly pine stands with a dense understorey of oaks; along shrubby margins of watercourses; and occasionally in forest interior (Bent 1953; Bielefeldt and Rosenfield 1994; Brooks 1940; Brush 1987; Chapman 1907; Confer 2006; Confer and Knapp 1981; Confer et al. 2010; Ficken and Ficken 1968a, 1968b, 1968d; Gill et al. 2020; Golet et al. 2001; Graber et al. 1983; Harrison 1984; Lehnen and Rodewald 2009a; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991; Patton et al. 2010; Rich et al. 1994).



Old fields that the Blue-winged Warbler uses tend to have a mix of grasses and herbaceous species, shrubs, and trees growing in a patchy distribution. In 2 New York study areas, grass and forb coverage was 10% and 21%, shrub coverage was 15% and 25%, and coverage by trees shorter than 5 m was 33% and 23%. In West Virginia, highest site occupancy occurred at 50-100% shrubland cover within 100 m. Occupancy was negatively correlated with basal area, decreasing by 93% as basal area within 100 m increased from 0 to 30 m^2 per ha. In Connecticut, it preferred clear-cuts with dense shrubs 0.5-1.5 m tall, a canopy height less than 7 m, and territories close to road or utility rights-of-way. In West Virginia, 33% of territories were covered by dense herbaceous cover; trees covered only 10% of territories. One New York breeding site was characterized by 35% open habitat dominated by tall grasses with scattered hawthorns and dogwoods, 45% was covered with dense shrubby growth 2-4 m tall, and 15% was covered with taller trees (10 m) with an understorey of shrubs. In Kentucky, occupied habitat consisted of patches of herbaceous plants, shrubs, and saplings, with grass cover averaging 34.6%. Plant species characteristic of territories included bush-clovers, goldenrods, clematis, and blackberries. In Indiana oak savannah-type habitats, its density was negatively correlated with tree height. Highest densities occurred at tree heights of 4 m and dropped off to almost 0 at 10 m. Average habitat around nest sites consisted of 100 trees less than 10 cm diameter at breast height (DBH) within 12.5 m of the nest in Michigan, 112 trees of similar size in West Virginia, and 105 in Ohio. The number of shrubs in 80 m^2 transects within 12.5 m of nests averaged 190 in Michigan, 205 in West Virginia, and 198 in Ohio. On West Virginia reclaimed surface mines, it was most abundant in areas planted to shrublands and was next abundant in grassland habitats. It occurred at low densities in remnant and intact forests (Confer and Knapp 1977; Gill et al. 2020; Grundel and Pavlovic 2007a; Margeneau et al. 2019; Oliver et al. 2023; Patton et al. 2010). In Pennsylvania, core home ranges had greater grass cover (68.5% compared with 58.6%) and goldenrod cover (43.9% compared with 27.3%) than total home ranges. Total home ranges had

greater overhead cover (74.1% compared with 61.9%) and leaf litter cover (51.9% compared with 32.2%) than core home ranges. There were no differences in coverage by forbs, ferns, and raspberries in core and total home ranges. Core home ranges had greater average shrub density (9,872 compared with 7,106 stems per ha), lower average sapling density (5,114 compared with 6,052 stems per ha), lower snag density (31 compared with 39 per ha), and lower basal area (6.8 compared with 13.6 m^2 per ha) than total home ranges. The average DBH did not differ between core and total home ranges. Core and total home ranges all contained forest, shrubland, and ecotones. Core home ranges had less forest cover (24.8%) than total home ranges (43.9%). There were no differences in core and total home ranges for ecotone cover (22.4% and 16.8%, respectively) and shrubland cover (52.9% and 39%, respectively). In core home ranges, males used shrublands and ecotones relative to their abundance and selected against forest cover. In total home ranges, males used shrublands relative to their abundance, selected for ecotones, and selected against forest cover. Habitat management based solely on vegetation within core areas could overlook important habitat components that the Blue-winged Warbler selected in total home ranges. Core home ranges were mostly shrubland with a patchy mosaic of vegetation 1-5 m tall. Total home ranges were more forested, with greater overhead cover, basal area, tree density, and tree height (Fuoco et al. 2024).

In old-field habitats, there is little difference in the habitat preferences of the Blue-winged Warbler and the Golden-winged Warbler and the 2 species frequently have overlapping territories. Some studies failed to find any differences in habitat between the 2 species. The greatest difference appears to be in the amount of tree cover in the territories of the 2 species. Cover by herbaceous species and grasses tends to be lower in Blue-winged than Golden-winged warbler habitat and there is considerably more tree cover within Blue-winged Warbler territories. In New York, the mean tree value for Blue-winged Warbler territories was more than twice that of Golden-winged Warbler territories. The variances for tree value differed even more, with the Golden-winged Warbler value less than 5% that of the Blue-winged Warbler. The range of tree values in Blue-winged Warbler territories (2-54) encompassed the entire range for Golden-winged Warbler territories (3-12). Blue-winged Warbler territories had considerable tree growth (30%); Golden-winged Warblers were confined to more open areas with 10% or less tree cover. The Golden-winged Warbler was restricted to areas that were 10-35 years into succession after cropland abandonment. The Blue-winged Warbler occupied these same fields as well as areas 60-70 years into succession. The Blue-winged Warbler is a habitat generalist and the Golden-winged Warbler is a specialist. In New Jersey, the Blue-winged Warbler occurred in fields 10, 20, and 40 years old, but disappeared once the fields became overgrown with trees at age 50 years. In high elevation areas, the Golden-winged Warbler may prefer areas that support heavier tree growth than the Blue-winged Warbler. The 2 species may be separated elevationally, with the Blue-winged Warbler restricted to areas below 530 m and the Golden-winged Warbler occurring at much higher elevations. In Kentucky, however, the Blue-winged Warbler nested at an elevation of 738 m (Confer and Knapp 1977, 1979, 1981; Confer et al. 2003; Gill et al. 2020; Parkes 1951; Patton et al. 2010; Suthers 1988).

Some authors concluded that the Blue-winged Warbler and Golden-winged Warbler are separated by their differing preferences for moisture regime. It was generally thought that, in the east, the Blue-winged Warbler preferred low, wet areas and the Golden-winged Warbler occurred in drier, upland areas. The reverse appeared to be true in the west and reversal of these apparent

habitat preferences was occasionally recorded in the east. Of 29 New York Blue-winged Warbler territories, 26 were wet and contained standing water or a stream. In a later year when the Golden-winged Warbler was absent, the Blue-winged Warbler occupied most of the drier areas where Golden-winged Warblers formerly held territories. It has since been concluded that the Blue-winged Warbler occupies both wet and dry sites independent of the presence or absence of water. In West Virginia, unmated males defended territories in wetter areas than mated males (Ficken and Ficken 1968b; Gill et al. 2020; Short 1963).

Crawford et al. (2016) examined landscape-level habitat and climate attributes of the Blue-winged Warbler at scales of 2.5 km and 500 m and compared them with those of the Golden-winged Warbler. Their study included the area of the Appalachian Mountains and Great Lakes populations of the Golden-winged Warbler, excluding Ontario. In both areas combined at the 2.5-km scale, compared with Golden-winged Warblers, Blue-winged Warblers were associated with lower elevations, warmer breeding season temperatures, and less use of aspen forests. The Blue-winged Warbler was found at an average elevation of 370 m (427 m for Golden-winged Warblers) and a mean maximum May temperature of 21.3°C (20.1°C for the Golden-winged Warbler). Both species were found in roughly equal numbers in grassland mosaic landscapes (8.5% for Blue-winged Warbler and 12.7% for Golden-winged Warblers). Blue-winged Warblers were less than half as likely to be found in woodland landscapes (9.6%) than Golden-winged Warblers (20.2%). The Blue-winged Warbler probability of occurrence was 7.0% in landscapes where trembling aspen was present compared with 39.5% for the Golden-winged Warbler. More Blue-winged Warbler locations (10.1%) were associated with agricultural landscapes than Golden-winged Warbler locations (4.5%). At the 2.5-km scale in the Great Lakes population, Blue-winged and Golden-winged warblers differed in their preferences for elevation, summer breeding temperature, land use, and percent deciduous forest cover. Blue-winged Warbler locations had a mean elevation of 240.9 m (335.2 m for Golden-winged Warbler) and a minimum May temperature of 7.2°C (4.7°C for Golden-winged Warblers). Twenty-six percent of Blue-winged Warbler locations contained aspen compared with 58% for Golden-winged Warblers; 32% of Blue-winged Warbler locations were associated with areas with no trees compared with 16% for Golden-winged Warblers. Blue-winged Warblers occurred more in agricultural landscapes (23.9%) than Golden-winged Warblers (6.8%). Blue-winged Warblers preferred grassland landscapes (34.6% of locations, 15.5% for Golden-winged Warblers) compared with forests with an open or broken canopy (14.3%, 30.7% for Golden-winged Warblers). At the 500-m scale in the Great Lakes region, variables most strongly associated with the 2 species included percent deciduous forest, percent agriculture, and elevation. Both species were strongly associated with yellow birch–sugar maple forests, although Blue-winged Warblers were also found in beech–sugar maple–basswood forests and in agricultural land types at lower elevations. The Golden-winged Warbler was also associated with forests dominated by aspen-birch, jack pine, black spruce–tamarack, and swamp forests. The Blue-winged Warbler occupied higher elevations (303 m) in Michigan, Minnesota, and Wisconsin than in New York (154 m), lower than for the Golden-winged Warbler (367 and 135 m respectively). At finer scales, the Blue-winged Warbler was positively associated with agriculture and human disturbance. The Golden-winged Warbler was negatively associated with these features and positively associated with the distribution of aspen forest.

Cunningham and Johnson (2019) determined that the Blue-winged Warbler preferred areas that were 2-58% forested in New York.

In southern Ontario woodlands, abundance of the Blue-winged Warbler was positively correlated with the amount of forest cover 100 m or more from edge and the amount of forest cover within 2 km. It was negatively correlated with woodlot size and the amount of regional forest cover. These relationships were not significant (Austen et al. 2001). In New Jersey forests, it was equally likely to be detected at forest edges with unpaved roads 8 m wide, paved roads 16 m wide, and power-line rights-of-way 23 m wide. There was no difference in its abundance at forest edge and in forest interior (Rich et al. 1994).

In shrublands in Ohio, Rodewald and Vitz (2005) netted birds 20, 50, and 80 m from mature forest edge. Adult Blue-winged Warblers appeared to avoid the forest edge and were 2.3 times more abundant 80 m from edge than 20 m from edge. Results were less conclusive for juveniles, which were 1.7 times more abundant at 50 m and 1.4 times as abundant at 80 m as they were 20 m from forest edge.

Confer and Knapp (1981) suggested that the Blue-winged Warbler may be area sensitive in New York, where it was found only in tracts of old fields that were 10-50 ha. There is no evidence of area sensitivity from any other areas, and it was specifically noted that it was not area sensitive in Connecticut. In New Jersey, it nested in fields that were 1.8, 2.3, and 6.5 ha. In Ohio, it nested in clear-cuts as small as 4 ha and patch size was not a good predictor of annual survival or juvenile recruitment. There was no evidence of area sensitivity. Another Ohio study found no differences in its abundance in small (4-8 ha) and large (13-16 ha) clear-cuts. In Rhode Island, it nested in red maple swamps that were less than 1 ha in area, although these were surrounded by upland forests that potentially provided additional habitat (Gill et al. 2020; Golet et al. 2001; Lehnen and Rodewald 2009a; Rodewald and Vitz 2005; Suthers 1988).

Ontario nests were on the ground among grasses. One was adjacent to goldenrod stalks, one was in a clump of goldenrods, and another was at the base of a small dead sapling (Peck and James 1987). A nest in Elgin County was 2 m from the edge of an open area and was surrounded by several saplings. The dead top of a bracken fern rested across the nest and concealed it (Rayner 1988c).

Most nests outside Ontario were at edges of old fields near a deciduous forest, often close enough that the adjacent trees shaded the nest. Nests have also been found at the edge of and in the interior of upland deciduous forests and in deciduous treed swamps. Nests may be along deer trails. Most nests are on the ground but they may be as high as 30 cm from the ground in blackberries or sturdy herbaceous species. Most frequently, nests are well hidden within a clump of goldenrods or at the base of a goldenrod or raspberry plant. They are typically attached to upright stems of a clump of forbs or grasses. One nest was buried in a clump of skunk cabbage in a wet swamp. Most are well concealed by grasses, herbaceous material, or ferns. One in a mixed-wood forest was between the exposed roots of a decaying stump and concealed by ferns (Bent 1953; Chapman 1907; Ficken and Ficken 1968a, 1968b; Gill et al. 2020; Harrison 1984; Murray and Gill 1976; Patton et al. 2010; Short 1964).

The Blue-winged Warbler may nest in loose colonies that contain as many as 10 breeding pairs, but it is not a true colonially nesting species. It frequently nests solitarily as well. During the first week after arrival, males sing infrequently and respond poorly to playback, but restrict their movements to the area that later becomes their territory. During this period, they occupy an area of 1-8 ha. Some birds establish territories in areas other than where they first settled. One bird moved 180 m. Territory establishment continues through late May into early June. Later arrivals either establish territories in peripheral, unoccupied areas or challenge a territory holder and claim a portion of his territory. Males confine most, if not all, of their activities to their territory but some infrequently trespass on their neighbour's territory. In old-field habitat, most territory boundaries are defined by a row of trees or an edge. One New York bird had a territory that was bisected by a strip of trees. Territorial disputes are usually confined to a narrow boundary between territories. Territories of Blue-winged and Golden-winged warblers frequently overlap. Territorial aggression between the 2 species occurs only briefly in the spring, only when one or both males are mated and before they settle into their final territories. Once the breeding season is underway, the 2 species largely ignore each other, although they tend to use different singing perches within shared areas. Hybrids may sing the song of either the Blue-winged or Golden-winged warbler, and these may either be attacked or ignored depending upon which song they sing. Birds with similar songs or plumages have non-overlapping territories. Birds with different songs or plumages may have territories that overlap. The Blue-winged Warbler has a large territory size for a warbler. The smallest territories of less than 0.4 to 0.8 ha were reported in New York, but this was an unbanded population and some individuals may have been mistaken as 2 birds. Another New York study reported territory sizes of 1.0-2.0 ha (average 1.3 ha). In Michigan, territories ranged from 0.4 to 3.0 ha (average 1.8 and 2.0 ha) at 2 sites. In northeastern Ohio, territory size averaged 1.1 ha (range 0.3-5.0 ha). Territories were larger in years of lower density. In Pennsylvania, the median 50% core home range size was 2.9 ha (range 0.6-16.5 ha) and the median 95% total home range size was 12.9 ha (range 2.3-90.6 ha). Six of 27 core home ranges (22%) and 16 of 27 total home ranges (59%) overlapped (Confer 2006; Confer and Knapp 1977; Confer and Larkin 1998; Confer et al. 2003; Ficken and Ficken 1968a, 1968c, 1968d; Fuoco et al. 2024; Gill et al. 2020; Meyerriecks and Baird 1968; Murray and Gill 1976; Patton et al. 2010; Short 1963).

Natal philopatry rates for the Blue-winged Warbler are variable. In Ohio, 11 of 353 (3.4%) juveniles were encountered as adults and 8 (2.3% or 72.7% of returning birds) returned to the natal site (Lehnen and Rodewald 2009b). In New Jersey, 19 of 216 young (8.8%) returned and 3 returned in multiple years (Suthers 1988). Zero of 35 juveniles in Michigan and 0 of 41 in West Virginia and another Ohio area returned (Gill et al. 2020).

Adult site fidelity rates vary and may be lower where the range is expanding northward. Some males returned to the same area for as many as 4 years. At 2 Michigan study areas, 5 of 10 males returned at 1 site, but one established a territory 9.6 km from where it was banded. One of 5 returned at the other site. In Ohio, 62 of 323 adults (19.2%) were re-encountered and 61 (98.4%) returned to the same site. Other adult return rates include 16 of 51 (31.4%) in West Virginia, 10 of 17 (58.8%) in Michigan, and 8 of 18 (44.4%) in New York. Numbers of birds returning for the second year were 11 of 23 (47.8%) in Michigan, 12 of 51 (23.5%) in West Virginia, and 6 of 10 (60.0%) in Ohio. Numbers returning for the third year were 5 of 17 (29.4%) in Michigan and 7 of 17 (41.2%) in West Virginia. Return rates of adult females were 10% in Michigan, 14.3% in West Virginia, and 65.8% in Ohio. A

Michigan male moved 9.6 km between successive breeding seasons and 2 in West Virginia moved 12 km. Birds do not necessarily move to larger habitat patches but may be forced to move if natural succession of habitat becomes too advanced (Gill et al. 2020; Lehnen and Rodewald 2009b; Murray and Gill 1976).

Limiting Factors

Eggs have been reported in Ontario nests from the last week of May until mid-August, with most present from mid-June to early July (Peck and James 1987). Pair formation begins shortly after the arrival of females, often within 12 hours. Nest building starts soon after pair formation, often on the same day for late-arriving females. Early females may wait 1 or 2 days before initiating nest building. It usually takes 2-4 days to build the nest, occasionally 5 days, and rarely as long as 12 days during cold, wet weather. Egg laying usually starts the day after the nest is completed but longer intervals occur during inclement weather. The interval between nest completion and initiation of egg laying is 1-4 days during dry, warm springs (mode 1 day); as long as 5 days during wet, warm springs; and 8 days during wet, cool springs. One egg is laid per day. Incubation begins with the laying of either the penultimate or last egg. The incubation period is 10-12 days. The young leave the nest when they are 8-10 days old. Usually all young leave the nest within an hour but fledging may rarely extend over a 2-day period (Bent 1953; Chapman 1907; Ficken and Ficken 1968a, 1968c; Gill et al. 2020; Harrison 1984).

The Blue-winged Warbler raises a single brood per year but replacement clutches are common if the first one is lost. Nests are not known to be reused. Clutches of 2-6 eggs were documented in Ontario. Throughout its range, clutches of 2-7 eggs were reported, but mostly 4 or 5 eggs. Clutches of 2, 3, and 7 eggs are rare. The mean clutch size is 4.55 eggs and 3.65 eggs for clutches containing cowbird eggs. Replacement clutches may be smaller with only 2 or 3 eggs. These later nests are also subject to higher rates of cowbird parasitism (Bent 1953; Chapman 1907; Gill et al. 2020; Peck and James 1987).

The age at first breeding is 1 year. The Blue-winged Warbler is typically monogamous, but may occasionally be polygynous. No studies have been done on extra-pair copulation, but this is probably prevalent and may promote introgression with the Golden-winged Warbler (Gill et al. 2020).

In May in New York, 98% of feeding was by probing which consisted of inserting the bill into a bud, cluster of leaves, flower, or curled leaf, then opening it slightly to spread the vegetation. An additional 2% of foraging was by gleaning. Birds were not observed hovering or hanging upside down to feed during that month. In July, foraging consisted of 27% probing, 31% gleaning, 5% hovering, and 36% hanging upside down. During 1 day in late July, 2 birds foraged entirely by probing in curled dead leaves. Birds foraged 47.7% of the time in the top quarter of the tree, 53% in the second quarter from the top, 9% in the second quarter from the bottom, and 0% in the bottom quarter. The main trees used for foraging were apple, hawthorn, and black cherry. Some feeding was done near the ground by clinging to small herbaceous species. Most foraging was done near the tops of trees and shrubs and only in the peripheral portions of woody vegetation. The Blue-winged Warbler had a tendency to forage lower than the Golden-winged Warbler, but not significantly. The similarity in foraging methods and locations by the 2 species suggests that they

are eating the same food items. It is doubtful that the 2 species can remain sympatric because of their similar ecological requirements (Ficken and Ficken 1968b).

In West Virginia, young were fed mostly caterpillars and this has been observed elsewhere; small flying insects may also be fed to nestlings. Adults eat predominantly caterpillars, small crickets and grasshoppers, and spiders. Beetles, moths, ants, flies, small locusts, and spittlebug larvae may be consumed. The diet is probably very similar to that of the Golden-winged Warbler and it is likely that most of the caterpillars eaten are those of leafroller moths (Chapman 1907; Ficken and Ficken 1968b; Gill et al. 2020).

The Blue-winged Warbler is commonly parasitized by the Brown-headed Cowbird. Coker and Confer (1990) examined nest records over a wide geographic area and 20 of 232 nests (8.6%) were parasitized. Nine of 47 parasitized nests (19.1%) reached the nestling stage; 2 of 14 parasitized nests (14.3%) were abandoned. Parasitism rates are higher in fragmented than intact landscapes. In highly fragmented habitats in Ohio, 8 of 12 nests (66.7%) were parasitized. In intact habitats in West Virginia, only 1 of 212 nests (0.5%) was parasitized. Reproductive success decreased by as much as 67% in the fragmented Ohio habitats, although both warblers and cowbirds may fledge from a nest (Gill et al. 2020). In New York, 2 of 9 nests (22.2%) were parasitized (Hahn and Hatfield 1995). In Ontario, 2 of 6 nests (33.3%) were parasitized and 1 nest contained only cowbird eggs (Peck and James 1987).

Throughout most of its range, habitat loss is a significant limiting factor for the Blue-winged Warbler. Populations have a history of waxing and waning in response to the availability of early successional habitat. This type of habitat is declining over much of its range due to urbanization, decreased abandonment of farmland, and natural succession. The effects of habitat loss have not yet been manifested in Ontario because it is still expanding northwards. Once it becomes established throughout southern Ontario to the southern edge of the Canadian Shield, it is likely that it will start to experience population declines due to habitat loss. Although the Blue-winged Warbler is a habitat generalist compared with the Golden-winged Warbler, it is still reliant predominantly on ephemeral habitat. Its preferred habitat is the type of habitat that is most likely to be converted to other uses (Confer and Tupper 2000; Gill et al. 2020; McCracken 1994; Morse 1989; Shapiro et al. 2004).

The Blue-winged Warbler and Golden-winged Warbler regularly hybridize wherever they co-exist. They produce 2 recognizable forms of hybrids known as Brewster's Warblers and Lawrence's Warblers and backcrossing between the species and hybrids occurs frequently. There are a number of factors that facilitate hybridization of the 2 species. They are genetically very similar and no more different in their level of enzyme differentiation than morphologically indistinguishable populations of passerine birds. The 2 species occupy the same habitat types and their territories may be adjacent to each other or overlap. Their songs are similar and individuals of 1 species may sing the other's song. The courtship displays and sexual reactions of the 2 species are similar and they are attracted to each other sexually. Males of both species readily mate with hybrid females, thus increasing the incidence of genetic introgression. Both species are shifting their ranges northward and hybridization may be encouraged when 1 species is rare compared with the other and has difficulty finding a conspecific mate. Birds that arrive late in spring may also not be available to find a suitable mate. Most hybrid pairings consist of a pure male pairing with a hybrid female, with pairs of 2 hybrids

or the 2 pure species uncommon. The 2 species may be too similar ecologically to co-exist (Confer 2006; Confer and Larkin 1998; Ficken and Ficken 1968c, 1968d; Gill 1987; Morse 1989; Parkes 1951; Vallender et al. 2007b).

The Blue-winged and Golden-winged warblers are sister species that separated 1.5 million years ago. Historically, they were geographically separated with the Blue-winged Warbler occurring mainly west of the Appalachian Mountains where it nested along the prairie-forest ecotone. Large-scale forest clearing by European settlers followed by anthropogenic shrub growth allowed it to expand its range eastward and northward, thus coming into contact with the Golden-winged Warbler. Once sympatry occurs, the Blue-winged Warbler typically replaces the Golden-winged Warbler within 50 years, but occasionally in as few as 4 years. There is a population in New York, however, where the 2 species have co-existed for over a century. There are 5 stages in the replacement of the Golden-winged Warbler by the Blue-winged Warbler: a population that is predominantly Golden-winged Warblers with few Blue-winged Warblers and hybrids; equal numbers of Golden-winged and Blue-winged warblers with some Brewster's Warblers; mostly Blue-winged Warblers with few Golden-winged Warblers, with a broad range of hybrids and the first appearance of the Lawrence's Warbler; a conspicuously introgressed Blue-winged Warbler population with few hybrids and no Golden-winged Warblers; and a Blue-winged Warbler population with some variation in wing-bar colouration and the occasional Lawrence's Warbler (Confer 2006; Confer and Tupper 2000; Gill 1980).

Although much has been written about how detrimental hybridization is to the Golden-winged Warbler, it also adversely affects the Blue-winged Warbler through genetic introgression and reduction in the number of pure Blue-winged Warblers. The rate of introgression is greater than originally thought, with early determinations being based upon visual inspections in the field. Short (1963) examined a large number of Blue-winged Warbler, Golden-winged Warbler, and hybrid museum specimens and concluded that 312 of the 431 specimens (72.4%) that he considered hybrids would have been identified as pure species in the field. Introgression had occurred in a Long Island population of Blue-winged Warblers that was allopatric. By analyzing mitochondrial DNA, Vallender et al. (2007b) found that some hybrids were morphologically indistinguishable from one of the parental species, but contained genes from both parental taxa. In Pennsylvania, gene flow as a result of hybridization was unidirectional from the Blue-winged Warbler to the Golden-winged Warbler, resulting in the genetic swamping of the Golden-winged Warbler and eventual replacement of it by the Blue-winged Warbler. Studies of other populations have demonstrated that hybridization is more often bidirectional so that both species are compromised by introgression. Patterns of introgression vary geographically depending upon the relative abundance of the species and hybrids and the historical context of interactions between the species (Dabrowski et al. 2005; Gill 2004; Shapiro et al. 2004; Vallender et al. 2009b).

Vallender et al. (2009b) examined 145 Blue-winged Warblers that appeared to be pure based upon plumage characteristics. They were collected from 7 states and 2 provinces (8 birds from Ontario and 1 from Quebec). Fourteen (9.6%) had a mismatch between their pheonotype and their mitochondrial DNA, which was higher than for the Golden-winged Warbler at 8.0%. The Ontario samples showed the highest level of introgression at 45%. Of the 8 Ontario birds, 4 had ancestral

Blue-winged Warbler DNA and 4 had ancestral Golden-winged Warbler DNA. There was no sign of introgression in Kentucky. Dabrowski et al. (2005) analyzed the genetic makeup of birds in this complex from Ontario and New York. In Ontario, all Brewster's Warblers had ancestral Golden-winged Warbler DNA. Lawrence's Warblers had equal numbers of ancestral Golden-winged and Blue-winged warbler haplotypes. Introgression was rare at Kingston and the most common route of introgression was mating by advancing male Blue-winged Warblers with females of the established Golden-winged Warbler population. In New York, 13 of 15 Blue-winged Warblers (86.7%) had ancestral Blue-winged Warbler DNA and the others had ancestral Golden-winged Warbler DNA. Vallender et al. (2007b) examined samples from Ontario and Kentucky. One apparent Blue-winged Warbler could not be assigned to either ancestral population, suggesting that it was a hybrid. Another Blue-winged Warbler had ancestral Blue-winged Warbler DNA. One of 49 Golden-winged Warblers (2.0%) had ancestral Blue-winged Warbler DNA, 9 of 10 Brewster's Warblers had ancestral Golden-winged Warbler DNA and the other had ancestral Blue-winged Warbler DNA. Four 4 Lawrence's Warblers were equally split between ancestral Golden-winged and Blue-winged warbler DNA. All 12 Blue-winged Warbler samples from Kentucky had ancestral Blue-winged Warbler DNA. Shapiro et al. (2004) examined specimens from Missouri, Ohio, and West Virginia. All Blue-winged Warblers from Missouri and Ohio were pure, and these populations are allopatric. In West Virginia, 15.3% Blue-winged Warblers had Golden-winged Warbler DNA; 12.4% Golden-winged Warblers had Blue-winged Warbler DNA; of 9 Brewster's Warblers, 4 had Blue-winged Warbler DNA and 5 had Golden-winged Warbler DNA; and of 4 Lawrence's Warblers, 3 had Blue-winged Warbler DNA and 1 had Golden-winged Warbler DNA. In New York, the hybridization rate for pure Blue-winged Warblers (4.8%) was less than for the Golden-winged Warbler (8.1%), but not significantly (Confer and Larkin 1998). This study relied on plumage characteristics rather than genetic analyses.

Farwell et al. (2019) studied the effects of shale gas infrastructure (well pads, access roads, and pipelines) on the Blue-winged Warbler in contiguous forest in West Virginia. It exhibited no significant response to these features.

Price (2004) predicted that the Blue-winged Warbler might become extirpated in southern Ontario if the average summer temperature increased by 2°C.

Status

The Blue-winged Warbler is a recent addition to Ontario's avifauna. The first record was one collected at Point Pelee in the autumn of 1908. The primary route of colonization appears to have been through the Niagara Peninsula. The first record for the Hamilton area was in 1937 and it began to be seen regularly there in the mid-1950s. Prior to 1950, there were only a handful of records for the entire province. The first nest was found at Ancaster on 3 July 1956 and a week later another nest was found at Milton Heights. By 1961, 5 nests had been documented in the Hamilton area and one had been found at Glen Morris in Brant County. Many early nests had mixed pairings of Blue-winged Warblers and Golden-winged Warblers. The Blue-winged Warbler was a rare breeder in the province in the 1960s, but had been recorded during the breeding season in Middlesex County, at Toronto, in Caledonia, in Durham Region, and at Kitchener. In the Kingston area, the first record was in 1957 but it did not appear as a regular migrant at Prince Edward Point until 1970. By 1979, it had increased so much in parts of the south, such as in the Kitchener area, that it was more abundant than the Golden-winged Warbler. At this time, it occurred during the breeding season north to Kingston and the Oshawa-Scugog area, and vagrants were appearing in Wellington County. By

the 1980s, it was fairly common in Haldimand, Norfolk, Middlesex, and Oxford counties and occurred in even greater numbers in the southwest. Its distribution at that time was from Pelee Island to the Bruce Peninsula east to Gravenhurst and Brockville. In the 1980s, the Blue-winged Warbler was more abundant than the Golden-winged Warbler in Waterloo Region and the counties of Oxford, Haldimand, and Norfolk. The first nesting record for Elgin County was not until 1985, although the first observation there was in 1963. In the Kingston area, the average number of summer sightings was 0.8 in 1981-90, 1.6 in 1991-2000, and 4.8 in 2001-05. Near Chaffey's Locks north of Kingston, it likely arrived in very low numbers in the late 1980s, but was not confirmed breeding until 2005. In the Hamilton area, highest populations occur in Flamborough Township. There is considerable shrubby and early successional habitat there due to the presence of alvars (Baillie 1963, 1967; Curry 2006; King et al. 2009; Lancaster et al. 2004; McCracken 1994; Rayner 1988c; Weir 2008). James (1991) considered it rare to locally uncommon in the south north to Georgian Bay and Kingston.

The second atlas indicated that the range of the Blue-winged Warbler had expanded somewhat to the northeast in areas such as the Oak Ridges Moraine between Orangeville and Trenton and southern portions of Hastings, Lennox, Addington, and Frontenac counties. There were scattered observations in the southern Canadian Shield in Muskoka, Haliburton, and Renfrew. Within southwestern Ontario, there was considerable infilling of its range and it was widely distributed in the Carolinian Forest Region. Its probability of observation increased significantly province-wide and in all atlas regions where it occurred. It was most abundant in the Norfolk Sand Plain, particularly in Norfolk County (Vallender in Cadman et al. 2007).

The continental population of the Blue-winged Warbler started to increase around the 1900s in response to creation of shrublands following forest clearing by European settlers. Forest clearing allowed it to expand its range northeastward. This expansion is still occurring, although it is nearing the limit of suitable habitat at the southern edge of the Boreal Forest Region. The typical scenario is that it increases its population northeastward, but declines in more southerly areas where it was formerly common. Once an area becomes saturated with Blue-winged Warblers, populations tend to decline due to natural succession and habitat loss. Breeding Bird Survey (BBS) data from 1966 to 1993 indicated that the overall population was stable (Confer and Tupper 2000; Gill et al. 2020; Morse 1989). BBS results indicate that it increased at annual rates of 3.48% in Canada and Ontario 1970-2021 and 0.548% 2011-21. All results were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

The brood is divided by the adults. The female takes care of 1-2 fledglings if that is all that is produced and the male cares for any additional young. The parents may move the young out of the male's territory or remain within it for 2-5 days. Fledglings remain motionless in shrubby thickets waiting for the adults to bring food. The 2 family groups remain close to each other for a few days after fledging, often within 100 m (Gill et al. 2020).

In Ohio hardwood clear-cuts, Vitz and Rodewald (2006) mist-netted 118 adults and 209 juveniles during the postfledging period. It was the most abundant species that they captured. Netting was not conducted during the breeding season so it was uncertain if these were local breeding birds or if they had moved in from other areas.

In Missouri, Porneluzi et al. (2014) netted during the postfledging period 2-15 years following a clear-cut in an oak-pine-hickory forest. The Blue-winged Warbler was the seventh most abundant early

successional species captured. Peak numbers occurred 2-3 years after cutting with few present 10 years or more after harvesting.

MIGRATION

The frequent mortalities at communication towers and tall buildings indicate that nocturnal migration occurs.Males usually arrive on the breeding grounds 2-9 days before females. At a Michigan breeding area, males continued to arrive during the entire month of May, but some late arrivals may have moved in from surrounding areas rather than having just returned from migration (Ficken and Ficken 1968c; Gill et al. 2020; Murray and Gill 1976). In southern Ontario, spring migrants arrive mostly in the last week of April or first week of May. Birds continue to move through until the end of May (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

Throughout its range, the Blue-winged Warbler may begin autumn migration in late July (Gill et al. 2020). In southern Ontario, autumn migration normally extends from late August until mid-September. A few birds remain until late September or rarely into November (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

During migration, the Blue-winged Warbler prefers early successional habitat and open forests, similar to the breeding season, but it may also be found in denser forests. In Illinois, spring migrants were most abundant in forest-edge habitat, but also occurred in mature upland and lowland forests. In Texas, migrants occur in scrub forests, thorn forests, and lowland riparian forests. During spring migration in Pennsylvania, significantly more detections per 100 m of transect occurred in shrub habitat (0.42) than in forest (0.02). The capture rate per 1,000 hours of netting was significantly higher in shrubs (8.6) than in forest (0.6); 146 Blue-winged Warblers were captured in shrubs compared with 8 in forests. During spring migration in Ohio, there was no difference in its abundance in upland and riparian forests. During spring migration in Minnesota and Wisconsin, it was significantly more abundant in upland forests than in floodplain forests (Gill et al. 2020; Graber et al. 1983; Kirsch et al. 2013; Rodewald and Matthews 2005; Smith and Hatch 2008).

Prolonged winter weather during spring migration may kill some migrants. The Blue-winged Warbler is frequently killed by striking buildings and communication towers during migration. This rarely occurs within the breeding range, but is more prevalent in the south (Gill et al. 2020).

In Pennsylvania, an outbreak of the viburnum leaf beetle resulted in almost complete mortality of southern arrowwood, formerly the third most abundant shrub species. Prior to the infestation, spring migrating Blue-winged Warblers gained significant mass after sunrise, but no weight gains occurred after the infestation (Smith and Hatch 2017).

The Blue-winged Warbler is a rare migrant in Ontario (James 1991), but its numbers are increasing. At the Long Point Bird Observatory, 5 were banded 1960-69, 13 in 1970-79, and 81 in 1980-89. The ratios of Blue-winged Warblers to Golden-winged Warblers during these periods were 0.38:1, 0.71:1, and 2.0:1, respectively (McCracken 1994). In Niagara Region, the number counted during spring migration increased significantly from 1966-75 to 1977-2006 (Black and Roy 2010). At Presqu'ile, there were only 5 records of the Blue-winged Warbler from 1960 to 1979. Numbers increased dramatically during spring migration in 1983 after which it occurred regularly, but in low numbers (LaForest 1993). In the Kingston area, an average of 2.1 birds were observed in spring 1971-80 compared with 5.5 1981-90, 7.4 1991-2000, and 8.3 2001-08 (Weir 2008).

Black-and-white Warbler

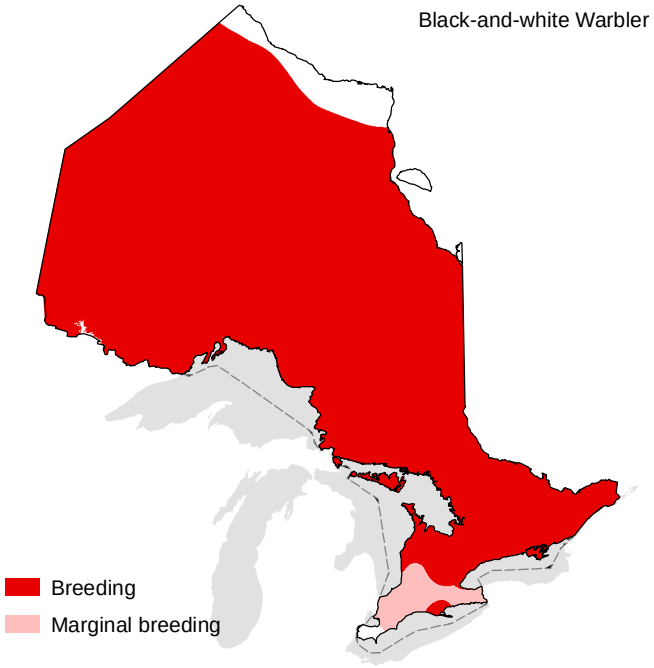
Mniotilta varia

BREEDING SEASON

Habitat Requirements

In Ontario, the Black-and-white Warbler has nested in mixed (37.0% of nests), coniferous (7.4%), deciduous (3.7%), and unspecified (44.4%) woods; in a black spruce bog (3.7%); and in an alder swamp (3.7%). Eleven nests were at edges of woodlands or clearings, or were near roads or fencerows. Eight were in wet habitats with the remainder in dry or unspecified habitats (Peck and James 1987). James (1984b) concluded that it was tolerant of a wide range of forest conditions. It nests mostly in mixed or deciduous forests and less frequently in coniferous forests. It requires a dense understorey of deciduous shrubs in open forests, edges, or openings. It shows no preference for tree height, and may nest in wet riparian forests and swamps as well as dry upland forests.

In the Hudson Bay Lowland, the Black-and-white Warbler nested in lichen-rich spruce forests along streams (Wilson and McRae 1993).



In the northwest portion of the Boreal Forest Region, it was most abundant in mixed and deciduous scrub. It was much less abundant in deciduous forest and present in low density in mixed forest and coniferous forest with a woody understorey. It was absent in coniferous scrub, coniferous forest without an understorey, and in heath and tundra habitats (McLaren and McLaren 1981). In the Boreal Forest Region of Ontario, it was associated with immature to younger hardwoods that were more open in character, and with high disturbance and edge levels (Rempel 2007; Rempel et al. 2007). Welsh (1993) considered it a mid-successional species. It was most abundant in 12-year-old clear-cuts, occurred in cuts as young as 5 years and declined in abundance from 12 to 33 years. It also occurred in stands 150-200 years old, but at lower density than in 12-year-old stands. Near Hearst, it was much more abundant in mixed stands where it occurred in clear-cuts 3-24 years old (the entire range of ages of stands sampled) and in an uncut upland stand. There was little difference in its abundance among stands from 5 years of age to unharvested mixed stands. In lowland conifers, it was present in 9- and 24-year-old clear-cuts but absent in other-aged clear-cuts and in uncut stands (Welsh and Fillman 1980). Near White River in jack pine stands, it was most abundant in stands that had been cut 8-10 years previously. It was not significantly more abundant in this age class and was not an indicator species for any age class of forest (Venier and Pearce 2005). In the Clay Belt, it was most abundant in trembling aspen and balsam poplar stands, but was also common in white cedar–tamarack stands, uncommon in balsam fir–white spruce–jack pine stands, and least abundant in black spruce stands. It occurred mostly in wet stands rich in nutrients, but it was present in stands that represented the full spectrum of nutrient levels and moisture regime (Welsh and Lougheed 1996).

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Black-and-white Warbler regularly nests in mature and old-growth white pine stands. It is more abundant in old-growth than mature stands. Its abundance in white pine stands was significantly associated with the basal area (BA) of deciduous species and age of the stand (Kirk et al. 2012). Near Gogama, it rarely nested in jack pine stands. One pair nested in a uniform stand of young jack pines 8-10 m tall where there was dense ground cover of blueberries and sheep laurel with a sparse growth of taller deciduous shrubs. It was usually associated with the deciduous component of mixed forests, where it was uncommon. It was found mostly in stands approximately 20 years old or at edges of taller woods where tall shrubs covered most of the ground below or among taller deciduous trees (James and Peck 1995a). In Quetico Park, it occurred only in early successional stands resulting from fire 1-23 years previously. It was not observed in stands 67-370 years old (Apfelbaum and Haney 1995).

Near Parry Sound, it nested in open jack pine stands mixed with deciduous species, reaching its highest density in stands 10-15 m tall (James 1979a). In Algonquin Park, Martin (1960) recorded it in black spruce, black spruce–white cedar, white birch–poplar, balsam fir–spruce, white birch–poplar–balsam fir–spruce, and hemlock stands. He did not observe it in bogs or immature white pine stands. In white birch–poplar stands, it was active from the ground to a height of 9 m which was just below the top of the canopy. In black spruce–white cedar, its activities extended from the ground to 11.9 m, which was just below the top of the cedars but about 10 m below the top of the spruce canopy. In balsam fir–spruce stands, it was active from the ground to the tree tops. In hemlock stands, it was active from the ground to a height of 6 m, about 3 m below the bottom of the canopy. It was not considered characteristic of any habitat type. In white pine stands in Algonquin Park, Kingsley and Nol (1999) found it in all age classes including 2-9-year-old cuts, 10-16-year-old cuts, and uncut stands. Also in Algonquin Park, it strongly favoured mature forests over early successional habitats and the presence of large trees was critical (Tozer 2012). Near Sault Ste. Marie, it was most abundant in areas of advanced regeneration of shrubs in gaps created by selection thinning (Holmes and Pitt 2007). In the southern portion of the Shield, it was associated with high tree density (the highest of all species studied), a high amount of understorey woody vegetation, and moderate to high canopy volumes. Habitat that it occupied was typical of areas that had been cleared and allowed to regenerate to an early successional stage. It was considered a species of deciduous forest, but was associated with high conifer composition (Clark et al. 1983).

In the off-Shield portion of the Great Lakes–St. Lawrence Forest Region in Durham Region, Speirs and Orenstein (1975) considered the Black-and-white Warbler associated with white cedar. They documented it in wet, open stands with heavy growths of raspberries, in a black spruce bog with an adjacent red maple–poplar swamp, in a mature white cedar–elm swamp, and an open riparian stand of white cedar, balsam fir, and spruce. Near Kingston, McLeish and Robertson (1997) concluded that upland white cedar stands could provide high quality habitat for it.

In Elgin County in the Carolinian Forest Region, the Black-and-white Warbler nested at the bottom of a steep ravine forested with hemlock and sugar maple (Lancaster et al. 2009). In Brant County, it nested in an upland trembling aspen–ash forest in an area dominated by aspens (personal observation).

At the landscape level, the Black-and-white Warbler preferred areas that were 59-75% forested in North Dakota; no areas had greater than 75% forest cover (Cunningham and Johnson 2019).

In the Yukon, the Black-and-white Warbler nests most frequently in riparian balsam poplar forests containing white spruce as a secondary species. Suitable stands have abundant tall shrubs and forest floor litter. It also occurs in mixed and structurally complex habitats at edges of white spruce forests and in deciduous forests dominated by tall alders (Sinclair et al. 2003). In British Columbia, breeding habitat consists mainly of deciduous thickets in wet areas or along margins of water. Along rivers, it preferred alder-willow patches in spruce or spruce–trembling aspen stands in very moist areas. It frequently inhabited alder and willow patches in moist, middle-aged trembling aspen stands with white birch present. It nests in a variety of forest types including mixed stands of white spruce, trembling aspen, balsam poplar, and white birch; pure trembling aspen and balsam poplar stands; and in black spruce bogs. It appears to prefer riparian areas along lakes, beaver ponds,

streams, and bogs appear (Campbell et al. 2001). In Alberta, it preferred dense aspen and other deciduous stands where it occurred in the lower strata. In northcentral Alberta, breeding habitat included fragmented and contiguous mixed-wood stands dominated by trembling aspen, with high densities of willow in the understorey (Schieck et al. 1995). In Saskatchewan, the Black-and-white Warbler was associated mostly with deciduous or mixed forests, but also occurred in black spruce and species-poor jack pine stands. It occurred around the midpoint on the moisture regime and stand nutrient level (Kirk et al. 1996). In Quebec, it breeds in stands of varying ages but prefers those growing in moist areas. It also nests in alder and willow thickets. It is most frequent in deciduous and mixed stands and decreases with increasing conifers. In the Boreal Forest Region of Quebec, it mostly occurs in stands dominated by trembling aspen and white birch. It often breeds among saplings at edges of damp wooded areas, regenerating clear-cuts, and roadsides. It also nests in balsam fir–red maple, white birch–gray birch, and sugar maple–yellow birch stands (Villard in Gauthier and Aubry 1996). In New Brunswick and Nova Scotia, it is a common breeder in northern hardwood stands, but avoids spruce plantations and coniferous forests. In unharvested hardwood stands, it was one of the dominant species (Freedman and Johnson 1999; Freedman et al. 1981). In Newfoundland, the Black-and-white Warbler regularly nests in balsam fir stands, where it is a habitat generalist (Thompson et al. 1999; Whitaker and Montevecchi 1997, 1999). In the Boreal Forest Region, it is one of the dominant species in deciduous forests, particularly in aspen and birch stands. It also occurs in mixed stands and in lower densities in stands dominated by balsam fir, white pine, red pine, and hemlock-pine. Within hemlock-pine associations, it is restricted to areas that support deciduous trees (Erskine 1977).

Considerable information is available on the Black-and-white Warbler's habitat requirements and preferences in the United States. In Illinois, the only breeding populations were in upland forests although it had been reported breeding in scrub forests, on sand dunes, and in bottomland forests (Graber et al. 1983). In Mississippi, a pair nested in the corner of a regenerating clear-cut bordered by a pine-oak forest. The birds confined their activity to an area 25-50 m from the forest in thick but patchy growth 1-3-m tall of oaks, pines, sweetgum, red maple, sassafras, and blackberries (Chandler et al. 1994b). In Vermont, territories included both forested habitat and clear-cuts, with 1 territory being predominantly in a clear-cut (Lent and Capen 1995). In Vermont, mean habitat values were 44.1% ground cover, 11.1% ground cover by slash, 70.5% canopy closure, 15.5 m canopy height, 9.9 m canopy depth, 12.8 m^2 BA of deciduous trees, 6.1 m^2 BA of coniferous trees, 10.5 cm diameter at breast height (DBH) for deciduous trees, and 8.5 cm DBH for coniferous trees. It was associated with intermediate canopy closure and dense understorey. It was associated with pole-sized hardwoods with canopy closure of 55-80%, high understorey density, and a mean DBH of 8-15 cm (Thompson and Capen 1988). In Maine and New Hampshire, it was most abundant in white pine stands (which included numerous small deciduous trees), followed by stands dominated by hemlock, balsam fir, northern hardwoods, swamp hardwoods, aspen, spruce-fir, and white birch. Its abundance was positively correlated with canopy closure, the number of coniferous trees larger than 10 cm DBH, and the total foliage volume of deciduous trees 2-10 cm DBH. It was negatively correlated with total foliage volume of deciduous trees larger than 10 cm DBH (DeGraaf et al. 1998). Collins (1983a) compared the habitat of Black-and-white Warblers nesting in Minnesota and Maine. In Minnesota, it occupied habitat characterized by 70% or more ground cover and moderate canopy cover. In

Maine, its habitat was characterized by high percent canopy cover, variable coniferous cover, and many trees in the smaller size classes. Birds may have been selecting the most optimal habitat at each site. In Wisconsin and New Jersey, it is an uncommon to common breeder in pine and oak barrens. In New Jersey barrens, it is most common in pitch pine swamps and also in upland oak and pine forests with a dense understorey of oak (Brush 1987; Mossman et al. 1991). Brooks (1940) reported that it was a characteristic breeding species in American chestnut thickets and other shrubby growth containing scattered dead chestnuts in the Allegheny Mountains. In Minnesota, it occurred in aspen-birch stands or edges of deciduous forests where it was associated with increasing numbers of larger trees, more medium-sized deciduous trees, fewer large conifers, and less ground cover. Its habitat was characterized as second growth and forest edges with a high percentage of shrub coverage. It was a shrub–forest edge species (Collins et al. 1982). In clear-cuts in spruce–balsam fir forests in Maine, the Black-and-white Warbler was absent in young cuts 1-2 years old and in the oldest seral stage which consisted of a dense coniferous overstorey with an open forest floor. It was a dominant species in the third seral stage. This stage was characterized by deciduous regeneration taller than 2 m with a well-developed but slower growing coniferous regeneration layer. This occurred 7-12 years after cutting once regeneration had begun to shade out the raspberries. It was less common in the earlier stage of regeneration, which consisted of dense raspberries and regenerating hardwoods, and also in the later stage which was characterized by increased density of hardwood regeneration taller than 4.5 m, trees with a DBH of 10-15 cm, and reduced slash and raspberries (Titterington et al. 1979). In Pennsylvania, it nested on power-line rights-of-way through oak forests, but did not nest within the forest. It nested among oaks and red maples bordering the forest. It was adapted to early successional habitat and was one of the more common breeding species on the right-of-way (Yahner et al. 2002). In Wisconsin, the Black-and-white Warbler is uncommon in northern mesic forests where it occurs in pole-size and saw-timber-size deciduous forests as well as mixed and coniferous forests. On forested islands in Wisconsin, it was most abundant in white birch–red oak, silver maple–yellow birch, white birch–yellow birch–white cedar, and aspen stands. It was rare in hemlock–yellow birch stands and absent in pine stands. Its density increased with increasing density of woody understorey, particularly deciduous species. In Wisconsin, it nests among dense saplings in clear-cuts where there are nearby mature conifers (Beals 1960; Hoffman 1989a; Mossman and Hoffman 1989). In Maryland, it occurs in young, medium-aged, and mature deciduous and mixed forests, but is most abundant in pole-sized stands. It prefers closed-canopy forests, but will tolerate openings. The BA of inhabited stands varies from low to high, but a well-developed woody understorey is present (Bushman and Therres 1988). In North Dakota, it is restricted primarily to drier upland forests and reaches its highest density in mature trembling aspen stands. It is characteristic of semi-open upland forests comprised of immature and second-growth trees (Faanes and Andrew 1983). In Texas pine and pine-hardwood forests, its abundance was positively correlated with vegetation height; number of tree and shrub species; percent canopy closure; foliage density at 3 m, 7-10 m, and above 20 m; percent coverage by hardwoods 5-6 m and larger than 32 cm DBH; and number of tree stems larger than 32 cm DBH. It was negatively correlated with percent coverage by pines 5-16 cm DBH. It was in a guild that inhabited mature pine-hardwood forests. It was associated predominantly with hardwoods; the other species in the guild were associated mostly with pines (Conner et al. 1983). In the northeastern United States, it nests in red maple swamps, oak-pine forests, early successional and mature upland hardwoods,

poplar-birch forests, pine forests, upland spruce–balsam fir forests, lowland conifers (black spruce, tamarack, and white cedar), mixed forests (where it may be associated with yellow birch and sugar maple), and in small openings and forest edges (Back 1979; Capen 1979; Chapman 1907; Crawford and Titterington 1979; Dawson 1979; Golet et al. 2001; Harrison 1984; Morse 1989; Noon et al. 1979; Rich et al. 1994; Taylor and Taylor 1979; Temple et al. 1979). Niemi and Pfannmuller (1979) considered it to be in a guild of species in the northeastern United States that was abundant in disturbed shrub habitats and mature upland deciduous forests; very common in aspen regeneration, mature upland conifers, and alders; and uncommon in young plantations, recent clear-cuts, and mature lowland conifers. Kricher (2020) stated that it breeds in mature second-growth deciduous and mixed forests, with a strong preference for deciduous stands. It may have a preference for swampy forests. It does not breed as commonly in balsam fir and spruce stands, but may be increasing in these forest types in the Boreal Forest Region. In 1 study, it showed a strong preference for mature forests over early successional habitat. In the northeastern and northcentral United States, it selected forests with more tall trees and more open understorey than in its more northern breeding range. In Pennsylvania, more territories were present in mature than successional trembling aspen and oak forests, but its abundance was correlated with the density of understorey trees and shrubs, indicative of successional habitats. It occurred predominantly in the lower midstorey, but was present in all strata, including the ground.

The Black-and-white Warbler may nest in forests of all age classes, but tends to prefer younger stands and sites dominated by early successional species such as aspen. It occasionally nests in shrub thickets and cuts and burns dominated by deciduous saplings. In the Boreal Forest Region of Ontario, the amount of forest older than 80 years represented 36% of variation in its abundance at the 50-ha scale and 55% of variation at the 5,000-ha scale. It was negatively correlated with older forests (Rempel 2007). In forests dominated by black spruce, balsam fir, and aspen near Manitouwadge, it was most abundant in stands 1-21 years old. It was present in intermediate-aged stands (24-36 years) and mature stands (60-223 years) but at lower densities of 91.3% and 45.7% of those in young stands, respectively (Venier et al. 2009). In Saskatchewan, it was associated mostly with young stands, appearing in stands as young as 15-20 years old (Kirk et al. 1996). In Alberta trembling aspen forests, it was significantly more abundant in young than mature or old-growth stands (Schieck et al. 1995). In hemlock–white pine–hardwood stands in Pennsylvania, it occurred in 9.1% of old-growth forests, 42.8% of forests statewide, and 50.1% of forests in the Appalachian Plateau. It was significantly negatively correlated with old-growth forest (Haney 1999). In the northern United States, it was detected more frequently in disturbed and successional habitats in upland hardwoods than in mature, undisturbed habitats. In northeastern aspen-birch stands and pine forests, it is absent in the seedling and early sapling stages and first occurs in pole-sized stands. In mixed-wood forests, it was associated with late seral stages rather than mature stands (Back 1979; Capen 1979; Noon et al. 1979; Temple et al. 1979). In New York, the Black-and-white Warbler was absent in 1979-80 in a forest where it had been present 30 years previously. Litwin and Smith (1992) attributed its local extirpation to natural succession. Between surveys, the forest gaps filled in and the dense, extensive woody understorey became open with the exception of occasional patches of shrubs. In Newfoundland balsam fir stands, it was more abundant in uncut forests than those that had been cut 40 or 60 years previously. Mature stands had a lower density of small trees and more

shrubs than 40-year-old stands, but were not significantly different from 60-year-old stands for these parameters (Thompson et al. 1999). In a Connecticut woodlot over a 59-year period, there was a progressive shift to larger trees, a sparser shrub layer, and a less diverse tree canopy dominated more by oaks and maples. It declined in the woodlot but populations remained stable in the state. The decline was probably due to maturation of the forest and decline of the shrub layer (Buchanan et al. 2016).

The Black-and-white Warbler is an area-sensitive species in Ontario and most other locations. Its degree of sensitivity varies geographically and with the amount of forest cover in the local landscape. In southern Ontario, its abundance was correlated with the amount of forest 100 m or more from edge, woodland size, amount of forest cover within 2 km, and regional forest cover. The only significant relationship was the amount of forest cover within 2 km (Austen et al. 2001). James (1984b) concluded that the Black-and-white Warbler required in excess of 100 ha of forest or continuous forest to maintain a viable population in Ontario. In the Ottawa area, it occurred in 36% of 45 forests ranging in size from 2.8 to 57.5 ha (median 20.1 ha). A further study was done in 50 mature deciduous woodlots 3.0-129.8 ha (median 11.8 ha). There were local extinctions from year to year within individual woodlots. Its abundance was positively correlated with forest size and negatively correlated with distance to the nearest forest occupied by the species (Villard et al. 1995). That the degree of area sensitivity exhibited by the Black-and-white Warbler varies with distance to the nearest occupied forest and the amount of forest cover within 2 km is reflected in its distribution in southern Ontario. In Niagara Region, southwest of London, and the agricultural landscapes of southern Huron and Perth counties where woodlots are smaller and scattered, there are few Black-and-white Warblers. North of a line roughly from Goderich to the northern extent of Toronto, it is present in almost every atlas square (McLaren in Cadman et al. 2007). Based on information collected predominantly in Maryland, Robbins (1979) suggested that 300 ha was the minimum forest size capable of sustaining a viable population. Further work completed by Robbins et al. (1989) found that its abundance was significantly correlated with forest size, the amount of forest cover within 2 km, mean canopy height, and number of trees larger than 3 cm DBH, but it was negatively correlated with canopy cover. Its highest probability of observation occurred in forests larger than 3,000 ha, the probability was reduced to 50% at 220 ha, and the 3 smallest woodlands it was observed in at least twice were 493, 208, and 208 ha. The authors concluded that it required 220 ha of forest to maintain a viable population. Bushman and Therres (1988) reported that it occurred only in forests larger than 4,000 ha in western Maryland. Other Maryland studies found it in woodlots as small as 14 ha and suggested a minimum forest size requirement of 70 ha. It has been reported in woodlots as small as 7 ha in New Jersey. In Maryland, its abundance was positively correlated with forest size and negatively correlated with woodlot isolation and the total BA of trees (Lynch 1987). In aspen woodlands in North Dakota, Grant and Berkey (1999) considered it area sensitive. Its abundance was correlated with forest size and the number of oak trees. Its probabilities of observation were 17% at 10 ha, 39% at 100 ha, and 60% at 1,000 ha. It was not observed in 1.0-ha woodlots. In red maple swamps in Rhode Island, the Black-and-white Warbler was equally abundant in forests smaller than 1 ha, 1-5 ha, 6-10 ha, and larger than 10 ha. These swamps were surrounded by upland forests and may not have been good indicators of its area sensitivity (Golet et al. 2001). In Wisconsin, Beals (1960) studied the avifauna on islands of differing sizes. He identified species that were restricted to larger

islands, but did not include the Black-and-white Warbler on this list. In Saskatchewan, it was randomly distributed within fragmented landscapes. There were no significant relationships between its abundance and forest size or amount of forest cover within 5 km (Hobson and Bayne 2000). In Alberta over a 2-year period, it was found in 4 forest fragments that were 2, 50, 107, and 140 ha. Four unoccupied fragments were 4, 6, 9, and 32 ha. All woodlots were dominated by trembling aspen older than 80 years, and the landscape was approximately 30% forested with the remainder being pasture or cropland (Sodhi and Paszkowski 1997).

Golet et al. (2001) and Freemark and Collins (1992) considered the Black-and-white Warbler a forest-interior species, but did not provide any supporting evidence. In New Jersey, Rich et al. (1994) found that it was consistently more abundant in forest interior than forest edge. Most other studies that examined its distribution in relation to edge found that it is more abundant near edge than in forest interior. In Tennessee, territories were aligned parallel to a hydro corridor through forest. Highest density occurred 20 m from forest edge, declined to 0 at 120 m from edge, increased at 160 m, declined to almost 0 at 200 m, and increased again around 240 m from edge. Core areas of territories adjacent to the corridor appeared to be shifted toward the edge. The density of territories near the edge was not significantly greater than in forest interior (Kroodsma 1984). In Newfoundland, it occurred in riparian balsam fir stands adjacent to lakes and rivers but was absent in forest interior (Whitaker and Montevecchi 1997, 1999). Many studies classified it as an edge species. It is likely that it shows no strong preference for edge or forest interior but selects areas throughout the forest that have the required density of shrubs and saplings in the understorey.

In Ontario, 73.9% of nests were on the ground and the remainder were 0.2-1.8 m from the ground. Nests on the ground were at the base of a tree or stump, commonly among roots (65.5% of ground nests); beside or under logs (13.8%); under shrubs, ferns, and overhead tree branches (13.8%); under dead branches and leaves (3.4%); and in a mossy hummock (3.4%). Elevated nests were in stump cavities, one of which had been excavated by a Pileated Woodpecker (41.7% of elevated nests); in upturned roots (33.3%); in a rock crevice (8.3%); between 3 adjacent white cedar trunks (8.3%); and in a mossy bank (8.3%). Nests were concealed by overhanging grasses or branches, beneath shrubs, or under roofs of dead deciduous leaves (Peck and James 1987). In Algonquin Park, 1 nest was 1.5 m from the ground in an old Pileated Woodpecker feeding excavation (Tozer 2012).

Most nests reported throughout the Black-and-white Warbler's range were on the ground, often at the base of a tree or shrub. It often selects hillsides, ravines, and swampy areas for the nest site. Nests may be under logs, among tree roots, or sheltered by overhanging branches or stones. Ground nests are typically in a small depression among dead leaves that are occasionally arranged to form a partial canopy. Elevated nests are most frequently on the top of stumps in leaf-filled cavities; occasionally nests may be among roots of upturned trees. An early report from Louisiana that nests are usually in a small hole in a tree was considered questionable. Given that a similar nest has been found in Algonquin Park, this early record cannot be discounted, although nests in tree cavities are likely rare. In addition, 1 nest was found in the cavity of a pine tree created when it was struck by lightning. An unusual nest was in the drain of a house (Byers 1950; Chapman 1907; Kricher 2020; Mousley 1916a; Sinclair et al. 2003; Smith 1934; Tyler in Bent 1953).

The Black-and-white Warbler is aggressively territorial, attacking conspecifics as well as other warblers and species that wander into its territory. Territoriality persists late into the summer, long after other warbler species have ceased territorial defence. Intrusions into other territories are rare. Near Quebec City, there was no evidence of clumping of territories. It appeared to be strongly associated with habitat features within its territory, and these may have determined occupancy patterns. In Algonquin Park, the average size of territories was 0.52 ha (range 0.02-2.8 ha). Quebec territories averaged 0.43 ha (range 0.35-0.63 ha). Territories in Alberta forest fragments ranged from 0.9 to 6.6 ha (Bourque and Desrocher 2006; Kricher 2020; Martin 1960; Morse 1989; Villard in Gauthier and Aubry 1996).

No information is available on natal philopatry, but it is probably very low. Some adults return to the same area to breed in subsequent years, but the percentage of birds that do so is unknown (Kricher 2020).

Limiting Factors

Eggs have been reported in Ontario nests from late May to late July, but most are present from the first to third weeks of June (Peck and James 1998a). In Algonquin Park, nests are under construction from mid- to late May, eggs are present from late May to late July but mainly in June, nestlings occur from early June to late July, and dependent fledglings have been observed from late June to mid-August (Tozer 2012).

There does not appear to be any information on how long it takes to build a nest or how soon nest construction is initiated after the females arrive. At 1 nest, the first egg was laid 2 days after the nest was completed. One egg is laid per day. One 5-egg clutch took 6 days to lay, with a gap between the second and third eggs. Incubation begins with the laying of the penultimate or last egg. The incubation period is typically 10-12 days but 1 nest containing 8 cowbird eggs was incubated for 20 days. The nestling period is 8-12 days (Byers 1950; Harrison 1984; Kricher 2020; Smith 1934; Tyler in Bent 1953).

A single brood is raised annually. Peck and James (1987) indicated that Ontario egg dates suggested the possibility of second broods, but none have been documented. It is likely that renesting occurs if a clutch is lost, but this has not been confirmed. In Vermont, a male sang frequently following the loss of a brood suggesting a second nest, but no evidence of it was found. In Ontario, clutches of 3-6 eggs have been reported (average 4.18 eggs). Most clutches contained 4 or 5 eggs and only one 6-egg clutch was reported. Throughout its range, the Black-and-white Warbler typically lays 4 or 5 eggs; 6-egg clutches are rare (Chapman 1907; Harrison 1984; Kricher 2020; Mousley 1916a; Peck and James 1998a; Smith 1934; Tyler in Bent 1953).

The age at first breeding is unknown (Kricher 2020), but is probably 1 year. No information is available on the mating system of the Black-and-white Warbler, but it is likely monogamous.

The Black-and-white Warbler regularly forages on tree trunks and large limbs, unlike any other warbler species. It also gleans adeptly in foliage. In addition to trunks, it frequently forages on the inner surfaces of large limbs and on foliage in typical warbler fashion, occasionally searching the tips of vegetation. One study determined that it fed 45% of the time on dead limbs, 25% on the large inner part of limbs, 15% on trunks, 8% on the tips of vegetation, and 7% on the outer part of limbs.

In Parry Sound District, it foraged mostly in early successional hardwoods during all seasons and primarily in white birch during spring migration. Foraging height was 5-12.5 m during the breeding season. Birds rarely hovered while foraging. It occasionally pursues insects on the wing and feeds on insects attracted to Yellow-bellied Sapsucker sap wells. During spring migration at Point Pelee, 50% of foraging was on trunks, 30% on branches, and 20% on saplings. During autumn migration in Ontario, it foraged 3-13 m from the ground, but concentrated its foraging at 3-5 m and 10 m. Birds spent 38% of their foraging time on inner branches, 29% on saplings, 25% on trunks, and 8% on outer branches. Although it tends to feed at mid-heights, it may occur anywhere from the forest floor to the canopy (Kricher 2020; Mills 2007; Morse 1989; Smith 1934; Tyler in Bent 1953).

Nestlings at 1 nest were fed entirely small green caterpillars that were cut into half lengths. Nestlings have been fed white grubs and white moths. Adults feed mostly on insects, but also eat spiders, harvestmen, and their egg sacs. Lepidopterans are favoured foods, especially caterpillars, and the Black-and-white Warbler eats gypsy moth larvae. Caterpillars may constitute a significant portion of the diet during spring migration. Beetles are important prey, including click beetles, long-horned beetles, weevils, leaf beetles, and willow flea beetles. Other insects it eats include ants, moths, flies, bugs, some hymenopterans, jumping plant lice, hackberry emperor butterfly caterpillars, hackberry gall psyllids, plant lice, scale insects, tent and forest tent caterpillars, and leafhoppers. A captive bird ate 80% of its body weight daily and consumed insects only. These included moths, leafhoppers, treehoppers, stink bugs, and crickets and grasshoppers as long as 2.5 cm. Many potential food items were refused, including dog food, various types of berries, 5-cm long grasshoppers, full-grown crickets, small ants, beetles, and mites. Some birds favour ants and beetles; 3 warblers observed during autumn migration in Ontario ate an average of 2.5 beetles each (Chapman 1907; Kricher 2020; Nice and Nice 1950; Smith 1934; Tyler in Bent 1953; Whelan et al. 1989). Near Manitouwadge, density of the Black-and-white Warbler increased with increasing spruce budworm populations in young (1-21 years) and intermediate-aged (24-36 years) mixed stands of black spruce, balsam fir, and aspen (Venier et al. 2009).

The Black-and-white Warbler is commonly parasitized by the Brown-headed Cowbird and accepts its eggs. In Ontario, 9 of 55 nests (16.4%) were parasitized. In Michigan, 4 of 14 nests (28.5%) were parasitized. In New York, 1 of 4 nests (25%) was parasitized. In British Columbia, only 1 nest has been reported, and it was parasitized. In British Columbia, 1 adult fed a single cowbird fledgling. One Michigan nest contained 2 warbler eggs and 8 cowbird eggs that were apparently laid by 4 different females. The warbler eggs were destroyed or punctured and the warbler continued to incubate the cowbird eggs until the nest was depredated. One other nest contained 5 cowbird eggs (Byers 1950; Campbell et al. 2001; Hahn and Hatfield 1995; Harrison 1984; Kricher 2020; Peck and James 1998a; Villard in Gauthier and Aubry 1996).

Forest fragmentation has the potential to affect the Black-and-white Warbler, but it appears to be less vulnerable to this than some other area-sensitive species. It is affected if forest patches become smaller than the size that it requires, if woodlots become increasingly isolated, or if the amount of regional forest cover declines. It exhibits a high frequency of occurrence in Quebec agricultural landscapes, but urban development and intensification of agriculture have caused it to decline near Montreal. Forest fragmentation may increase the incidence of parasitism and

predation, although this has not been specifically studied. In Alberta, there was no significant difference in pairing success of males in small forest fragments and large contiguous forests. The western Boreal Forest Region has a history of natural fragmentation due to fire and insect outbreaks. It may have adapted to cope with some level of habitat disturbance. In an annual roadside survey conducted in Maryland, its density declined by 88% after the road was daylighted. In New Jersey, it was more abundant near unpaved road corridors that were 8 m wide than it was adjacent to paved roads (16-m corridors) and 23-m-wide power-line corridors (Bushman and Therres 1988; Kricher 2020; Morse 1989; Rich et al. 1994; Sodhi and Paszkowski 1997; Villard in Gauthier and Aubry 1996). It is possible that birds do not perceive narrow corridors to represent a gap in the forest, especially along roads where the canopy from either side is very close to being continuous over the road.

Activities that decrease the amount of woody growth in the understorey can be detrimental. Clearing shrubs and saplings from the understorey on cottage lots in central Ontario is likely to cause declines (Bushman and Therres 1988; Clark et al. 1983). In North Carolina, abundance of the Black-and-white Warbler was negatively correlated with the number of houses and buildings within 200 m of the centre of the habitat patch (Lumpkin and Pearson 2013).

The Black-and-white Warbler responds positively to forest harvesting, although large clear-cuts and intensive site preparation temporarily decrease populations. In the Boreal Forest Region of Ontario, clear-cuts tend to be recolonized 5-6 years after cutting. Habitat modelling in this area revealed that existing forest conditions, if they persisted, would result in a decline in the Black-and-white Warbler. Optimum habitat would consist of younger forests, a more fragmented mature forest matrix, and a higher percentage of deciduous forests than current conditions. It was predicted that it would increase if natural disturbances were allowed to occur or if silvicultural guidelines for replanting, tending, or harvest volume objectives were met. If all guides for target species were met, a decline was predicted. In New York, where the harvest system consisted of removing different percentages of the allowable cut, it increased with logging intensity, but a significant response did not occur until the heaviest logging (100% of allowable cut) was implemented. Densities were highest in Pennsylvania where 75% of the forest was clear-cut. In central Massachusetts, it increased as a result of fuelwood harvesting. Forest management activities that retain some canopy but create openings for shrub and sapling growth are tolerated and may be beneficial (Bushman and Therres 1988; Kricher 2020; Rempel et al. 2007; Webb et al. 1977; Welsh 1993; Yahner 1993). Vanderwel et al. (2007, 2009) reviewed several studies that investigated the effects of partial harvest of forests. No change in its abundance was observed when 30%, 50%, or 70% of tree cover was removed. In the Canadian Shield of Ontario, it was significantly less abundant in early successional clear-cuts than in early successional burns and significantly more abundant in mid-successional clear-cuts than in mid-successional burns. It was significantly more abundant in early successional and mid-successional stands than in mature stands (Zimmerling et al. 2017).

In New Jersey and Pennsylvania over a 15-year period, hemlock declined from representing 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The Black-and-white Warbler increased in response to hemlock decline, probably due to the increased deciduous understorey (Toenies et al. 2018).

Chemicals used in forest management may affect the Black-and-white Warbler. During 1974-75, it exhibited a 58% decline on Breeding Bird Survey (BBS) routes sprayed with pesticides such as fenithrothion and phosphamidan. It increased 39% on unsprayed routes during the same period (Kricher 2020). Hunter and Witham (1985) studied the effects of carbaryl spraying on spruce–balsam fir forests in Maine. This chemical is used to control the spruce budworm and it depresses arthropod abundance. In the first year of the study, spraying was incomplete and patches of forest were left intact. On the day of spraying, the number of Black-and-white Warblers foraging in the sprayed area declined to 0. Numbers remained low until 7 days after spraying, when a gradual recovery began. Numbers of foraging warblers returned to normal 14-19 days after spraying. The use of spruce for foraging decreased by all warbler species postspray and they foraged lower during this period. The change in foraging height was probably because the pesticide would have the greatest impact on arthropod abundance at the top of the trees. Shifting to foraging areas off the territory would increase travel time and energy requirements, but searches for prey would be more profitable. The following year, spraying was more complete and no unsprayed patches remained. There was no decrease in the number of warblers feeding in the sprayed area or any changes in foraging heights. Birds did not have the option of shifting their foraging areas because the distance to an unsprayed area was too great. It is likely that foraging success was less in sprayed areas.

Klaus et al. (2010) examined the effects of fire in woodlands on the Black-and-white Warbler in Georgia. Numbers were depressed 1-2 years after low-intensity fires but recovered after 3-6 years; medium- and high-intensity fires had lesser effects. One to 2 years after fire, its abundance was negatively associated with shrub height. Habitat during this period was characterized by reduced canopy cover and BA.

In Michigan, abundance of the Black-and-white Warbler was not correlated with precipitation or moisture anomalies. It did not appear to be affected by drought (Blake et al. 1992).

In Alberta, Bayne et al. (2008) found similar occupancy rates of the Black-and-white Warbler at noisy compressor stations and quiet well pads. In the western boreal forest, it was 52% more abundant on average along seismic lines and 65% more abundant along pipelines than in adjacent forest interior. There was no difference in its abundance at well pads and in adjacent forest interior (Bayne et al. 2016). Farwell et al. (2019) studied its response to shale gas infrastructure (well pads, access roads, and pipelines) in contiguous forest in West Virginia and did not detect any effects on it.

Price (2004) predicted that the range of the Black-and-white Warbler might contract in southern Ontario if the average summer temperature increased by 2°C.

Status

McIlwraith (1894) stated that only a few Black-and-white Warblers nested in southern Ontario, but provided no information on the remainder of the province. Fleming (1907) noted that it was a rare breeder in Toronto. In Elgin County, it was a common breeder in 1891 but by 2000 it was a very rare and local breeder (Lancaster et al. 2004). Baillie and Harrington (1937) considered it a common breeder from the southern border of the province north to Lake of the Woods and the southern end of James Bay. It was also recorded along the Manitoba-Ontario border between latitudes 53-54°N in 1930. It was found in 2 squares in Niagara Region during the second atlas and was not detected

during the first atlas. Black and Roy (2010) knew of only 3 historical breeding records. James (1984b) reported that it bred throughout Ontario north to Fort Albany, but that it was becoming increasingly scarce near Lake Erie. The first atlas confirmed that its breeding range was similar to that reported by James (1984b), with gaps in its distribution in southwestern Ontario, Niagara Region, and Toronto. James (1991) considered it a common summer resident across the province, north to Big Trout Lake and Attawapiskat, but local to absent in the Carolinian Forest Region. Wilson and McRae (1993) observed that it reached its northern limit in the southern Hudson Bay Lowland. They reported it from Long Ridge and Moosonee, but not from the Hudson Bay coast.

The second atlas revealed that the range of the Black-and-white Warbler covered almost the entire province, except for the extreme northeast and Essex County, and it continued to have a patchy distribution in agricultural areas west and southwest of London and in Niagara Region. Its probability of observation increased significantly province-wide since the first atlas, with significant increases south of the Canadian Shield and in the Boreal Forest Region. There was probably an increase in habitat south of the Shield due to retirement of agricultural land and natural succession to forest. It was most abundant in the eastern Shield portion of the Great Lakes–St. Lawrence Forest Region. It was also common from the eastern shore of Lake Superior to Lake Abitibi and north to Moosonee. Densities were lower in the northwest but moderate densities occurred in the Rainy River area and west of Lake Nipigon (McLaren in Cadman et al. 2007).

BBS data indicate that the Black-and-white Warbler increased at an annual rate of 0.043% in Canada and decreased at an annual rate of 0.763% in Ontario 1970-2021. The trends 2011-21 were an annual increase of 0.00294% in Canada and an annual decrease of 2.51% in Ontario. All results were of medium reliability except that the short-term trend for Canada was highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young cannot fly well when they leave the nest. Initially they scurry and hide near the ground and later occupy low to mid-level branches (3-7.6 m from the ground) near the nest. Fledglings remain within 100 m of the nest and may stay within the territory for 2-3 weeks after learning to fly. The fact that fledglings may remain in the territory may explain why the Black-and-white Warbler defends its territory later into the season than many other warblers. Family groups that nested on a Mississippi clear-cut and a Pennsylvania hydro right-of-way remained in these habitats. In Pennsylvania, family groups remained together into August (Chandler et al. 1994b; Kricher 2020; Smith 1934; Yahner et al. 2002).

Although fledglings may remain within the territory, some move to early successional habitats or to forested areas with dense shrub cover. In Michigan, Akresh et al. (2009) netted birds during the postfledging period in upland and riparian forests. Upland forests were 100-year-old stands of trembling and large-toothed aspen. Riparian forests were similarly aged trembling aspen with an understorey of alder and honeysuckles. Eighty-eight percent of juveniles were caught in riparian habitat.

Streby et al. (2011b) studied postfledging bird assemblages in 2-10-year-old clear-cuts in Minnesota. During the breeding season, 6 adult Black-and-white Warblers were caught in clear-cuts compared with 61 adults and 57 juveniles during the postfledging period. It was the most abundant

forest-breeding species captured, representing 6.8% of all birds caught and 8.9% of forest-breeding birds. Birds actively moved to clear-cuts after fledging occurred. In 4-10-year-old clear-cuts in West Virginia and Virginia, Marshall et al. (2003) captured 26 adults, 16 juveniles, and 4 family groups. It was one of the 6 most common forest-breeding species captured in clear-cuts. In Ohio, Vitz and Rodewald (2006, 2007) captured 23 adults and 34 fledglings in 12 regenerating clear-cuts. Although the clear-cuts were dominated by dense shrub and sapling growth, considerable heterogeneity occurred within them, especially in the lower shrub layer which ranged from fairly open to very dense. More birds were captured in the more open areas of the layer that was less than 1.5 m tall. In more open areas of this layer, 1.5 times more adults and 2.5 times more juveniles were captured than in denser lower vegetation. In Missouri, Porneluzi et al. (2014) netted during the postfledging season 2-15 years after an oak-pine-hickory forest was clear-cut. Including early successional breeders, the Black-and-white Warbler was fourth in abundance of birds captured. Its numbers exhibited a significant curvilinear trend that increased gradually to a peak 6-9 years after harvesting followed by a decline.

MIGRATION

The Black-and-white Warbler is a nocturnal migrant. During the day, it often occurs in mixed foraging flocks (Kricher 2020). It is one of the first warblers to arrive. Due to its habit of foraging on tree trunks and limbs, it does not need to wait until leaves emerge before it can migrate (Tozer 2012; Villard in Gauthier and Aubry 1996). Males migrate northward significantly earlier than females. In Massachusetts, males arrived an average of 5.8 days before females, and females arrived 5-7 days later than males in Alberta (Bauböck et al. 2012; Kricher 2020; Tyler in Bent 1953). At Prince Edward Point, the mean date of spring arrival was 13.1 May for males and 19.0 May for females, a significant difference of 5.9 days. Males occurred from 6 to 31 May and females from 4 May to 6 June. The Black-and-white Warbler had the longest interval between arrival of the sexes of all birds studied. Few were recaptured, indicating that most did not stay more than 1 or 2 days (Francis and Cooke 1986). At Long Point, the mean capture date for yearling males was 8.8 May compared with 5.7 May for older males, a significant difference of 3.1 days. The mean arrival date for males of unknown age was 9.8 May; there were insufficient data for females (Stewart et al. 2002). In Maine, the mean stopover time of spring migrants was 5.7 days (range 1-11 days). In spring, 7.9% of females were recaptured but no males were recaptured, suggesting that they may not stay over as long (Morris et al. 1994). In Louisiana, the quality of winter habitat affected spring migration timing. Males arriving from dry habitats arrived later, but were not in worse condition than those that wintered in mesic habitat (Paxton and Moore 2015).

The Black-and-white Warbler arrives in southern Ontario in late April or early May and is usually present until late May. Birds may arrive as early as the last week of March and some remain into early June. The peak flight is around mid-May coincident with the arrival of the females (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Keast 1980; Mills 1981; Tozer 2012; Weir 2008).

Autumn migration in Ontario may start in late July, but most migrants pass through in August. The Black-and-white Warbler is one of the earliest warblers to leave Algonquin Park. It may be seen there in mixed-species flocks from late July through August. In the south, migration is underway by mid-August and the largest numbers move through between late August and late September, with

some lingering into early October or rarely as late as early December (Curry 2006; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). At a banding station in Maine, 15.25% of birds were recaptured. The average stopover period was 4.1 days (range 1-17 days; Morris et al. 1994).

During migration, the Black-and-white Warbler occurs mostly in forested habitat, but may occur in lower numbers in other habitats such as pasture fields, treed lawns, and orchards. In Niagara Region, it highly favoured old apple orchards during spring migration where the rough bark of the trees provided a good foraging substrate. During spring and autumn migration in Illinois, highest densities occurred in bottomland forests and at forest edges, but it also occurred in upland forests, pine stands, and pastures (Campbell et al. 2001; Chapman 1907; Graber et al. 1983; Kricher 2020; Sheppard et al. 1936). During spring migration in Pennsylvania, it was significantly more abundant in shrub habitat than forest. There was no significant difference in invertebrate biomass in forests and shrubs except early in the migration period when biomass was higher in shrubs (Smith and Hatch 2008). During spring migration in Ohio, it was significantly more abundant in upland forests than riparian forests. Upland forests were mature, closed-canopy stands of oaks, hickory, and sugar maple with a patchy distribution of shrubs and saplings. Riparian stands were dominated by Manitoba maple, silver maple, cottonwood, and sycamore (Rodewald and Matthews 2004). During spring migration in Wisconsin and Minnesota, it was equally abundant in floodplain and upland forests (Kirsch et al. 2013). Parnell (1969) examined its habitat use during spring migration in North Carolina. It was not observed in dry thickets and occurred mostly in forested habitat, particularly deciduous forests, although it also used wet thickets. Its adaptation to foraging on boles and large limbs that are present in all forest types makes it less restricted by forest type. Of all observations of this warbler, 54.3% were in the canopy, 45.7% were in low trees, and 0% were in shrubs or on the ground. In the canopy, 6.2% of observations were at the top, 6.2% in the inner crown, 2.5% in the lower crown, and 39.4% on the bole. In low trees, 2.5% of observations were at the top of the crown, 7.4% in the inner crown, 6.2% in the lower crown, and 29.6% on the bole. It was highly selective, being recorded 69% of the time on the bole or larger limbs. It was observed at heights of 3 m to more than 15 m. Mean height of observations was 8.5 m for birds that were singing and 6-7 m for birds undertaking other activities. During autumn migration in Pennsylvania, it occurred in equal numbers in forest-agricultural edges, suburban forests, forest interior, shrub-sapling-stage forests, and pole-stage forests (Rodewald and Brittingham 2002, 2004).

During autumn migration, the Black-and-white Warbler may remain aggressive toward conspecifics and other warbler species (Morse 1989). There is no evidence that it maintains regular feeding territories.

In central Ontario, foraging height was 5.5-15 m during autumn migration (Mills 2007). Near Kingston during autumn migration, the Black-and-white Warbler fed at heights of 3-13 m, with peaks at 5 m and 10 m. Thirty-eight percent of foraging occurred on inner branches, 29% on sapling branches, 25% on tree-trunks, and 8% on outer branches. At Point Pelee, it fed largely on the inner branches and trunks of trees and saplings, with 50% of foraging observations on tree trunks, 30% on branches, and 20% on sapling trunks in spring (Keast 1980). During autumn migration in New York,

Lebbin et al. (2007) observed Black-and-white Warblers foraging by creeping along large tree branches. This occurred at night in trees illuminated by lights from a football stadium.

The stomachs of 3 Black-and-white Warblers killed during autumn at a tower near Prince Edward Point had eaten an average of 3 beetles each (Keast 1980).

During migration, the Black-and-white Warbler frequently collides with windows and tall structures such as buildings, communication towers, and lighthouses. From 1972 to 1982, 335 were killed at the Lennox generating station chimneys near Kingston (Chapman 1907; Graber et al. 1983, Kricher 2020; Weir 2008). Loss et al. (2014) examined bird-building collisions in the United States and determined that it was more vulnerable to collisions than average. At all types of buildings, it was 11.1 times more likely to strike a building than the average for all species. It was 68.7 times more likely than average to strike 1-3-storey residences, 22.7 times more likely to strike low-rises, and 18.3 times more likely to strike high-rises than average.

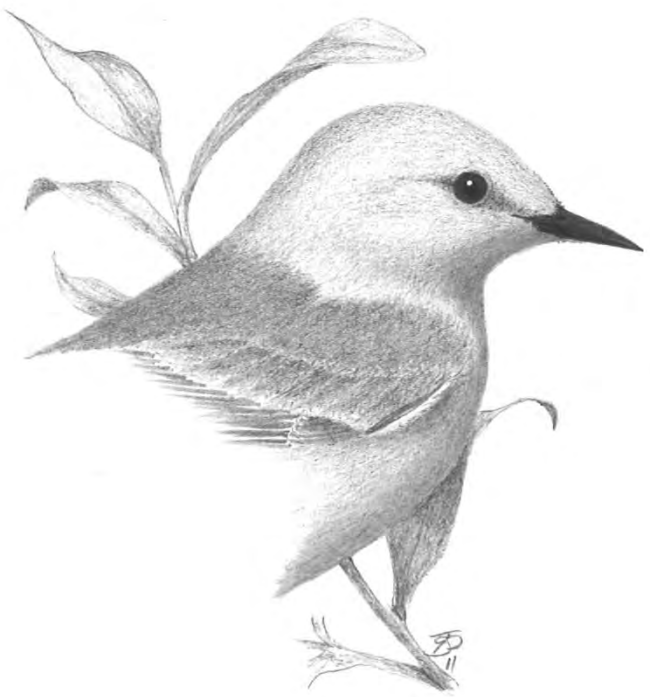
Strode (2003) studied the impact of climate change on spring migration of the Black-and-white Warbler in Illinois and North Dakota. Over 100 years, no change in spring temperatures occurred in Illinois but spring advanced by 8.6 days over 40 years in North Dakota. There was no change in spring arrival dates over time in either Illinois or North Dakota. In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and the length of the breeding season during 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming occurred during the second period. There were no significant differences in spring arrival dates and length of the breeding season for the Black-and-white Warbler, but autumn departure dates were significantly later in the second period.

Hanowski et al. (1996) studied the effects of extremely low electromagnetic fields on spring migrants in Michigan. The abundance of the Black-and-white Warbler was similar over time in reference and treatment areas. They concluded that no pattern was present to suggest a negative effect of electromagnetic exposure.

James (1991) considered the Black-and-white Warbler a common migrant in Ontario. Hussell et al. (1992) summarized trends in numbers of Black-and-white Warblers banded at Long Point Bird Observatory. The overall trend was –0.9% per year 1961-88. Trends by period were –6.2% 1961-70; +0.4% 1970-79; and +1.3% 1978-88. None of the trends were significant.

Prothonotary Warbler

Protonotaria citrea

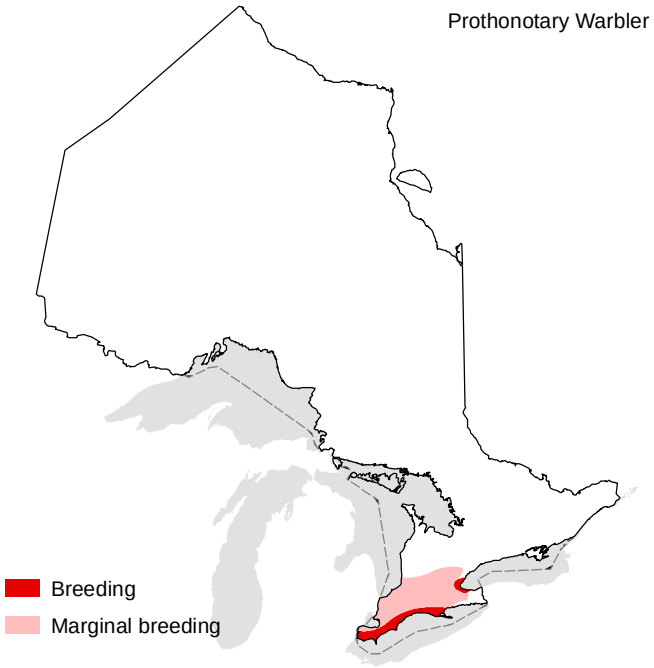


BREEDING SEASON

Habitat Requirements

In Ontario, the Prothonotary Warbler breeds in deciduous swamps. Most of these are treed but a few are dominated by shrubs and small trees. At Rondeau, it has bred in mature maple-beech-ash-oak forests (44 nests), in silver maple woods (5 nests), and in growths of buttonbush and dogwoods (4 nests). Many nests were in areas with open forest canopies (Peck and James 1987).

In Ontario, the Prothonotary Warbler nests most frequently in flooded mature deciduous treed swamps. It may also nest along margins of slow-moving warmwater creeks and rivers lined with willows. The swamps it uses most consistently and that support highest concentrations are associated with sand spits, such as at Rondeau and Long Point. The most common tree species in the canopy of its habitat include silver maple, red maple, ash, yellow birch, and black willow. The swamps it uses may be riparian, typically on the shoreline of Lake Erie or Lake Ontario, but it may inhabit mosaics of slough swamp forests within upland forest. Tree canopy cover at nesting areas



ranges from 20% to 90%, but averages slightly above 50% and is usually extensive enough to limit development of permanent growth of a herbaceous or shrubby understorey. It usually avoids open swamps with extensive emergent herbaceous vegetation. Sites may support scattered stands of cattails, common reed, grasses, and sedges, but these are usually not dominant, particularly early in the breeding season before mid-June. Swamps that it uses are intermediate in age or mature because several shallow nesting cavities a short distance above water or ground are essential within the territory. Dead or dying trees are necessary. Presence of standing or slow-flowing water is also essential. Open water is usually a dominant feature around nest sites and emergent vegetation is sparse. At Ontario territories, water is typically 0.5-1.5 m deep and surface water represents 70-100% of the territory. Pools in territories may be 1 ha or larger, although sites containing smaller pools are readily occupied. The most productive territories contain permanent pools of water but it also nests in seasonal sloughs that dry up entirely by mid- or late breeding season. Pools that contain water from May through until at least mid-June are important. A final habitat component is presence of plentiful green mosses, which are used as a base for the nest. Moss is most abundant in swamps with a long history of flooding, especially those where canopy cover provides shade (Austen et al. 1994; Bird Studies Canada 2001; Black and Roy 2010; McCracken 1984, 2007; McCracken et al. 2010).

McCracken (1984) summarized habitat characteristics of Prothonotary Warbler territories in Hahn Woods, at the base of Long Point. Silver maple was the dominant living tree (48.2% of trees), and 47.1% of the tree cover was dead. Other water-tolerant tree species present included red maple, ashes, and alder, but they were rather sporadic in occurrence. Tree density was high (860 per ha), largely due to adventitious growth of small trees clustered around larger trees. The canopy cover was sparse and averaged 34% (range 20-75%). This reflected the openness of the habitat combined with the presence of large numbers of dead and partly drowned trees. Shrub coverage was sparse and never exceeded 25% at any site. The most prominent understorey woody species were grey alder, dogwoods, buttonbush, and silver maple saplings. The ground cover was dominated by arrowheads, bur-reeds, rice cutgrass, and beggarticks. Open water covered an average of 50% of territories (range 30-90%), but usually became densely overgrown with emergent plants and duckweed by late summer. Water depth averaged 27 cm (range 9-48 cm).

Throughout its range, the Prothonotary Warbler nests in riparian floodplain forests and lacustrine treed swamps. In Virginia, it nests in tidal swamps where water levels fluctuate by as much as a metre. It may nest around shallow ponds surrounded by willows. In Mississippi, it nested in

planted cottonwood stands that were harvested on a 10-15-year rotation period. Nesting occurred in this habitat only when nest boxes were provided. Rarely, it nests in anthropogenic habitat such as backyards and bridges over rivers. Tree composition in swamps used for nesting is often similar to Ontario habitats. In many areas, willow is the dominant species. Other swamps that it uses may be dominated by red maple, silver maple, ashes, elms, black gum, sycamore, tulip tree, river birch, oaks, hackberry, Manitoba maple, and cottonwood. Buttonbush is frequently a dominant shrub in these wetlands and alder may be present. It selects intermediate-aged and mature forest stands and avoids early successional stands are avoided. Its abundance was significantly correlated with basal area (BA) and abundance of trees larger than 38 cm diameter at breast height (DBH) in the mid-Atlantic states. Canopy height in Tennessee ranged from 12 to 40 m but was mostly 16-20 m. In the mid-Atlantic states, it was negatively correlated with canopy height confirming that it selects areas of tree cover with medium height. In Tennessee, canopy cover was 50-75% but in Michigan it preferred heavily shaded areas for nesting. The shrub and ground layers of vegetation are usually sparse and less than 0.5 m tall. A Maryland study concluded that it required dense underbrush along stream banks, contrary to the findings of other studies (Blem and Blem 1991, 1992; Brush 1994; Buffington et al. 1997; Bushman and Therres 1988; Chapman 1907; Flaspohler 1996; Graber et al. 1983; Hodges and Krementz 1996; Mossman 1988; Petit 1989, 1991a, 2020; Petit and Petit 1996; Robbins et al. 1989; Twedt and Henne-Kerr 2001; Walkinshaw 1938, 1941, 1953).

Preferred habitat contains standing or slowly flowing water. The Prothonotary Warbler occasionally nests in areas without water, but these sites are almost always close to flooded habitat or in low-lying areas subject to occasional inundation. In some areas, it may delay nesting until flood waters recede and expose suitable nesting cavities. Nesting may occur in areas that dry out so that nests are over dry land by the end of the breeding season. When it nests over dry land, it is usually within 100 m of water. In Michigan, dry-land nests were 0.61-137.8 m from the river bank, usually in spots that were readily flooded. In Michigan, it was observed exclusively in riparian forests and avoided the portion of swamps that were distant from the river and the outer band of upland forest. In New Jersey, it was rarely detected in oak-pine forests and was significantly more abundant in hardwood swamps. In Illinois, a population nested where the water depth was 7-61 cm deep. Of 84 natural nests in Michigan, 34.5% were over standing water, 38.1% were over or at the edge of running water, and 27.4% were over dry land (Chapas-Vargas and Robinson 2013; Graber et al. 1983; Inman et al. 2002; Petit 1991a, 2020; Petit and Petit 1996; Rich et al. 1994; Twedt and Henne-Kerr 2001; Walkinshaw 1953). Flooded areas are preferred and superior habitat to dry areas. In North Carolina and Tennessee, breeding density was more than 3 times higher in flooded swamps than in dry habitats (Lyons 2005; Petit and Petit 1996). In Tennessee, densities varied more among plots and years in dry and mesic habitats than in flooded areas. Birds clearly preferred flooded habitat. Both males and females settled first in flooded areas before dry habitat was occupied, and dry areas were settled only once all flooded habitat was defended. Territories of males nesting in flooded habitat were less than half the size of those in dry habitat. Between years, no males moved from flooded to dry habitat, but several moved from dry to flooded habitat, reducing their territory size by about half. Within a season, 1 male moved from flooded to dry habitat and his territory size almost doubled. All males in flooded habitat were mated but some males in dry habitat were unable to attract a mate. Females in flooded habitat were more likely to attempt a second brood (34.8%) than those in

dry habitat (10.0%). Arthropod abundance was significantly higher in flooded areas than in dry habitat, with peaks in abundance in flooded areas due to large emergences of flies early in the season and mayflies in June and July. Over dry land, emergences of flies were smaller and mayflies were found only once over dry land. This study was done using nest boxes so that nest sites were not a limiting factor. Nonetheless, the relative abundance of natural cavities decreased with distance from water. The number of potential nest holes per 0.16 ha was 1.5 at the shoreline, 0.8 35 m inland, 0.3 70 m inland, and 0.1 105 m inland (Petit 1991a; Petit and Petit 1996). Beck (2013) established a breeding population of Prothonotary Warblers in Louisiana by erecting nest boxes. Boxes above water were preferred and significantly fewer nests over water were depredated compared with those over dry land. Males with brighter yellow colouration and older females that were brighter yellow occupied nest boxes over water indicating that these birds had a competitive advantage over duller-coloured males and younger females. Even when only males 2 or more years old were considered, brightness of plumage provided a competitive advantage whereas age did not.

In Illinois, preferred tree species in order of preference were red maple, sugar hackberry, silver maple, Manitoba maple, blue beech, swamp chestnut oak, black gum, and white elm. Avoided species, from most to least avoided, were sweetgum, pumpkin ash, overcup oak, shellbark hickory, Shumard oak, pin oak, baldcypress, green ash, sycamore, and bitternut hickory. Red maple was strongly preferred over other species. Silver maple was a preferred species but was only 18th in tree abundance. Sweetgum and pumpkin ash were avoided, yet they were the third- and second-most abundant trees, respectively (Gabbe et al. 2002).

In New Jersey, the Prothonotary Warbler was consistently more abundant on forest-interior than edge plots (Rich et al. 1994). It is unlikely that it is a forest-interior species. In most areas, it is more likely to occur along edges adjacent to lakes and water bodies, and it occasionally nests in non-forest habitat such as isolated snags in lakes and in backyards. In an Iowa forest, no breeding sites were more than 200 m from edge and most were less than 40 m from edge (Brush 1994).

Most authors consider the Prothonotary Warbler an area-sensitive species, but some studies determined that it is not. In Ontario, nearly all known breeding sites occur within forest tracts that are at least 25 ha, and over 95% of breeding sites are in forest patches that are at least 100 ha (McCracken 2007; McCracken et al. 2010). Petit (2020) concluded that it avoided forests smaller than 100 ha and Robbins (1979) concurred. In Maryland, it was found only in forests larger than 70 ha (Bushman and Therres 1988). In the mid-Atlantic states, Robbins et al. (1989) found no relationship between its abundance and forest size, although abundance was significantly correlated with the amount of forest cover within 2 km. In Iowa, it nested regularly in a highly fragmented forest that was 42 ha (Brush 1994). In Michigan and West Virginia, it nested in 32-36-ha swamps (Shields and Shields 1948; Walkinshaw 1953). In Wisconsin, it nested in riparian strips 0.1-1.5 km wide (Flaspohler 1996). In Maryland and Delaware, its overall probability of occurrence was 21% in riparian forests. Its probability of occurrence increased significantly with forest width: 5% in 50-m wide corridors, 9% in 100-m wide corridors, 23% in 200-m wide corridors, 49% in 300-m wide corridors, and 100% in 800-m wide corridors (Keller et al. 1993). Hodges and Krementz (1996) conducted a similar study in Georgia and found that its probability of occurrence increased with corridor width, but not significantly. Its probability of detection was 55% in 50-m wide corridors, 82% in 100-m wide

corridors, 95% in 200-m wide corridors, 99% in 500-m wide corridors, and 100% in 1,000-m wide corridors. They concluded that it was not area sensitive and that forest corridors 100 m should be sufficient to support it. Graber et al. (1983) observed that it did not ascend into upland stream branches and concluded that stream and floodplain size were important factors. Petit (2020) concluded that it avoided waterways with wooded borders that were 30 m or less in width and, to be suitable, this would have to be floodplain forest. It is probable that area sensitivity of the Prothonotary Warbler varies considerably geographically depending upon whether a site is in the core or periphery of its range. The local abundance of its spottily distributed habitat may also affect area sensitivity.

The Ontario habitat requirements of the Prothonotary Warbler may be summarized as extensive deciduous swamps that are intermediate or mature in age, permanent standing or slowly flowing water, numerous shallow cavities in trees (or nest boxes) a short distance above water, moderate tree canopy closure, sparse coverage by shrubs and herbaceous emergent vegetation, and an ample supply of moss.

At night, females roost in the nest cavity. Males roost on a perch in low vegetation or in an unoccupied cavity if one is available (Petit 2020).

All Ontario nests were above or at the edge of water; 82.8% were in natural cavities and the remainder were in old woodpecker holes. Nest cavities were in standing tree stumps (75.9% of nests), standing dead trees (19.0%), and fallen branches (5.2%). Occasionally nest cavities were in living or partially living trees. Nests were in maples, ash, basswood, birch, and buttonbush. An unusual nest site was in a cavity in a detached branch suspended vertically from a branch on a dead tree. Tree diameters at nest cavities ranged from 10 to 45.5 cm. Height of nests above water were 0.3-3 m with most 0.9-1.7 m up. Prothonotary Warblers used both large and small cavities, with 1 opening measuring 7.5 by 10 cm. Most cavities were shallow and ranged in depth from 2.5 to 30.5 cm. Two atypical cavities were horizontal from the opening and had no depth below the entrance (Peck and James 1987). In 1949, a Prothonotary Warbler nested in a drain pipe of an old building at Turkey Point. At Hahn Woods, nest trees were smaller than average. Two nests were in living trees and the remainder were in rotting dead trees or stubs. Most nests were not shaded by foliage. Of 20 nests, 11 were in natural cavities and 9 had been excavated by Downy Woodpeckers or Black-capped Chickadees. Nest height averaged 1.7 m (range 0.65-3.2 m). The Prothonotary Warbler readily uses nest boxes in Ontario and elsewhere and appears to prefer them to natural cavities. Several different nest-box designs were provided at Cootes Paradise and the most successful was a natural cavity made from a hollowed-out elm log with a natural slab top. The entrance opening was 3.18 cm. In 1997, 8 of 14 nests (57%) were in nest boxes, 17 of 21 (81%) were in nest boxes in 1998, 16 of 18 (89%) were in nest boxes in 1999, and 15 of 25 (60%) were in nest boxes in 2000 (McCracken 1984, 1999b, 2000, 2001; McCracken and Dobbyn 1997; McCracken et al. 2010; Peck and James 1998a; Wills and Barrett 2006).

Throughout its range, the Prothonotary Warbler nests in shallow cavities over, beside, or near water. Nest cavities are typically a short distance above water or ground in dead or partially dead trees, snags, or stumps. Less frequently, it nests in living trees. Typical habitat is flooded deciduous treed swamps, riparian swamps, and lacustrine swamps. In much of its range, it appears to prefer

willows for nesting, although it nests in a wide variety of deciduous tree species. In Illinois, 64 of 168 nests (38.1%) were in willows, 3 of which were alive, and an additional 46 (27.4%) were in dead trees or stumps of unknown species. Other nest tree species were elm (4.8% of nests), oak (3.0%), red or silver maple (2.4%), cottonwood (2.4%), river birch (1.2%), sycamore (1.2%), and 0.6% each in 2 species that do not occur in Ontario. Mean diameter of trees or stumps at nest height were 29.9 cm in Wisconsin and 13.6 cm in Tennessee. Nests are either in natural cavities or those previously excavated by a chickadee or Downy Woodpecker, with woodpecker holes often preferred. Of 84 natural nests in Michigan, 43 were in natural cavities and 41 were in woodpecker holes. In very rotten stumps, it may partially excavate or enlarge an existing cavity. Some nesting cavities, including old chickadee and woodpecker holes, may be rotted out and quite large. Excessively large cavities take much more moss and time to fill and are less desirable. Some cavities are so shallow that the female can be seen from some distance as she sits on the nest. In Michigan, nearly all nests were shaded most of the day. All young died 1 hot afternoon in a nest that was exposed to the midday sun. Significantly more nests in natural cavities in Tennessee were oriented toward the river than in other directions. In Michigan, 6 of 44 nests (13.6%) were in stubs over water (2 over running water), 1 (2.3%) was in a bridge support in a slight depression, 9 (20.5%) were in natural cavities over standing water, and 7 (15.9%) were in old woodpecker holes 0.6-48.8 m from the river bank. Nests have been reported from a few centimetres above water to 10.4 m up, but most average about 2 m above water or ground. In Michigan, nests were 0.3-3.7 m high over water (average 1.71 m). Nests over land were 1.2-4.6 m up (average 2.06 m). Of 84 natural nests, 41 (48.8%) were 0.61-1.52 m above the substrate, 21 (25.0%) were 1.52-3.04 m up, 20 (23.8%) were 3.04-4.50 m up, and 2 (2.4%) were even higher. In Illinois, the height of 99 nests averaged 1.85 m (range 0.08-8.0 m). Mean height of nests above ground in Wisconsin was 43 cm. Nests above water were not included in the analysis because of fluctuating levels. There is 1 record of it nesting in an abandoned Red-winged Blackbird nest. The Prothonotary Warbler has nested in a variety of unusual sites including under an overturned motorboat, in a bridge support, in gourds, in a paper sack near a window within a building, in a mailbox, in a coffee can, in a coffee pot hanging in a gazebo, in an old hornet's nest, in a glass jar laying on its side, in the pocket of a pair of pants hanging on a clothesline, in a metal pail hanging on a porch, in a guard over a pulley wheel on a ferry that was continuously in operation moving from 1 side to the other of a river, in a metal toolbox on a log-loader in use along the Mississippi River, in a gas inlet pipe in an unused houseboat, in an orchard over plowed ground, on a bulldozer, on or in a pump, on a freight-car coupler, in a rubber tire, over artificial pools near buildings, in a cigar box, on a pier, in a metal ventilator cap 10 cm in diameter at a pier, in a cleft in a pile in a river, in lanterns, in a tea cup, and in the pocket of a coat hung in a garage, which was used in 3 consecutive seasons (Bent 1953; Brush 1994; Chapman 1907; Flaspohler 1996; Graber et al. 1983; Harrison 1984; Petit 2020; Petit and Petit 1988a; Shields and Shields 1948; Walkinshaw 1938, 1941, 1953).

The Prothonotary Warbler readily uses artificial nest boxes. In many places, nest boxes are preferred to natural cavities; the opposite is true in some locations. Usage of nest boxes may be dependent upon their design, with those with smaller volumes preferred. Nest boxes may increase local populations where natural cavities are limited, reduce territory size, and increase nesting density in areas even where there are sufficient cavities present. Properly installed and designed nest

boxes may also reduce the incidence of nest predation and brood parasitism. A negative factor associated with nest boxes is that they increase local populations of competitors for cavities, especially the Northern House Wren. This species may depress warbler populations by puncturing eggs and filling potential nest cavities with sticks. The Prothonotary Warbler has used many designs of artificial nesting structures including wooden boxes, cardboard milk cartons, metal cans, polyvinyl chloride pipes (30 cm long, 10.2 cm in diameter and with plastic caps on the top and bottom), 0.7 L Metamucil jars, plastic gallon milk jugs, and gourds. Two studies tested its preference for artificial nest structures. In Tennessee, warblers were offered standard wooden bluebird boxes, cardboard milk cartons (1.9 L volume with a 3.75-cm diameter hole centered 5 cm from the top), and polyvinyl chloride tubes. The milk cartons were preferred (67.5% of those available were used), the tubes were used in proportion to their availability (27.4%), and bluebird boxes were avoided (5.1%). In Mississippi, large wooden boxes with a volume of 16.5 L, small wooden boxes with a volume of 3.5 L, and the 1.9 L milk cartons were erected. It nested in 0 of the large wooden boxes, 1 of the small wooden boxes, and 28 of the milk cartons, showing a clear preference for the milk cartons. In Virginia, it readily used wooden boxes 28 cm tall, 9 cm wide, and 6 cm deep with a 3.8-cm diameter hole. This is equivalent to a 1.5-L box. Smaller boxes are likely preferred because less moss is required to fill the base of the cavity. In Virginia, equal numbers of boxes were placed facing each 30° angle of the compass. The direction that nest boxes faced did not affect usage, but it preferred boxes on trees near water surrounded by large trees. Nest boxes were erected at heights of 20-280 cm above the high water level or ground and it showed no preference for box height. Increases in the distance of the nest box from water, in the percentage of ground cover under the nest, and percentage of the day that the box received direct sunlight all increased probability that boxes would be used by wasps instead of warblers. Its use of boxes could be increased by placing them on trees near or in the water on trees with a large DBH at sites that are not frequently exposed to full sunlight. Facing boxes north reduced the probability of their being used by wasps. In Virginia, temperatures in nest boxes were measured and boxes were divided into low-temperature (30-34° C) and high temperature (35-39° C) boxes. Warblers selected high-temperature boxes for their first clutch and avoided them for later clutches (Blem and Blem 1991, 1992, 1994; Brush 1994; Fleming and Petit 1986; Guillory 1987; Petit 1989; Petit and Petit 1987; Petit et al. 1987; Twedt and Henne-Kerr 2001).

In Arkansas, Slevin et al. (2018) monitored 84 nests in natural cavities and 60 in nest boxes. In natural cavities, nests were significantly higher (average 2.11 m, range 1.18-3.47 m) than random natural cavities (average 1.83 m, range 0.93-2.61 m). Cavity orientation was not a significant predictor of use. The Prothonotary Warbler preferred dead trees, with about 95% of nests in dead trees although they represented only 50% of trees with cavities. Water depth was not correlated with cavity use. Nest boxes that it selected had larger cavity openings and were under less canopy cover than unused boxes. Canopy cover was negatively related to daily nest survival in natural cavities. Pole-mounted nest boxes had greater survival than those in trees. There was no difference in overall nest survival between natural cavities and nest boxes. It may select higher nest cavities to minimize the risk of flooding.

The Prothonotary Warbler is strongly territorial, expelling all other males from its territory. It routinely attacks Northern House Wrens, chickadees, and Yellow Warblers. The first 2 species are nest-site competitors while the latter has similarly coloured plumage. In Wisconsin, a Prothonotary

Warbler pair took over a Black-capped Chickadee nest and laid eggs on top of it, only to have a Northern House Wren pair ultimately claim the nest. Most territories contain several potentially suitable nest cavities, and the male adds mosses to each of these. The mean number of cavities within 25 m of Ontario nests was 2.3 (range 1-10). These extra cavities and dummy nests are important as they confuse predators and competitors and can be used for replacement nests, second broods, for a second female's nest in the case of polygynous birds, and also as a nocturnal roost by the male. Birds may also be able to detect temperature and humidity differences in cavities with moss, and this may help in the nest-selection process. In Tennessee, nest-site availability was one of the most important attributes used by females in selecting a mate. In Ontario, the Prothonotary Warbler nests both singly and in groups, with groups most typical. This is most likely a function of its specialized habitat requirement as it is not colonial. Territories are initiated by the male as soon as he arrives. At that time, territories are large and encompass large areas of river or swamp. As new males arrive, battles ensue for portions of the territory and they may last 2-3 days before boundaries are settled. Occasionally a nest site is selected first and the territory is established around it. Birds nest and usually forage within the territory, although females sometimes forage outside the territory when they are feeding nestlings. In Georgia, it frequently flew over a river more than 100 m wide. Most Ontario territories are 1-2 ha, usually with about 1 ha of water present. In Illinois, the average size of 13 territories was 0.49 ha but 0.69 ha when a tape recorder was used to locate territorial boundaries (range 0.12-1.2 ha). In Tennessee, territory sizes were 0.19 ha for polygynous males and 0.24 ha for monogamous males. Overall territory sizes averaged 0.48 ha (range 0.1-1.2 ha). Territories in Tennessee were larger in dry (average of 0.30 and 0.37 ha over 2 years) than in flooded (0.13 and 0.16 ha) habitat. Individuals that moved between flooded and dry habitats adjusted their territory sizes accordingly. All nesting in the Tennessee population occurred in nest boxes, so territories were smaller than where natural cavities were used. Populations nesting in natural cavities in Tennessee had an average territory size of 0.64 ha. In another nest-box population in Virginia, territory size averaged 0.26 ha (range 0.02-0.71 ha). In Michigan where birds were nesting in natural cavities, 13 territories averaged 1.48 ha (range 0.77-2.58 ha). Some territories were much larger (5.03 ha), but only a portion of these were used at one time. Over 5 years, this territory averaged 3.82 ha (range 2.57-5.03 ha. One male that occupied the same area in 4 successive years had an average territory size of 1.28 ha (maximum 2.4 ha). In Alabama, the foraging area of females feeding young averaged 5.4 ha compared with 3.7 ha for males (Bird Studies Canada 2001; Blem and Blem 1994; Clarkson 2007; Graber et al. 1983; Hodges and Krementz 1996; McCracken 1984, 2007; McCracken et al. 2010; Petit 1989, 1991a, 2020; Petit and Petit 1996; Walkinshaw 1941, 1953).

Natal philopatry rates are low. In Michigan, 2 of 138 nestlings (1.4%) returned, one of each sex. Both nested 0.8 km from their natal nest. The male occupied the same territory in the next 4 years and the greatest distance between his nests in those years was 148.3 m. In Virginia, 50 of 2,968 nestlings (1.7%) returned. Of 33 nestlings banded there in 1998 that were recaptured in 2000, 20 (60.6%) were not found in 1999. In Tennessee, the mean distance between the natal site and first breeding site averaged 3.9 km for females (range 50 m to 12 km) compared with 875 m for adults (range 200 m to 1.5 km; Blem and Blem 1992; Blem et al. 1999; Petit 2020; Podlesak and Blem 2001; Walkinshaw 1941, 1953).

Adult site fidelity rates are much higher than natal philopatry rates. In Illinois, 9 of 10 males (90%) returned the next year but only 2 returned the following year. Three of 5 females (60%) returned the following year and 1 returned the subsequent year. Return rates are higher for males than for females. In Michigan, return rates for adult males were 50% the first year, 22.2% the second year, 11.1% the third year, 11.1% the fourth year, and 0% the fifth year. Female return rates were 20.3% the first year, 10.2% the second year, 1.7% the third year, 1.7% the fourth year, and 0% the fifth year. The overall return rate of adults was 27.3% the first year, 13.0% the second year, and 3.9% the third and fourth years. Most males occupied the same or adjoining territories each year, but one moved 296-510 m after 4 years. If a female's old mate returned and was already mated when she returned, she was forced to mate with another male. Consequently, females often nested considerable distances from their previous year's nest. In Virginia, 47.9% of females banded as adults were recaptured at least once in subsequent years. Of these, 5.7% were not found the year after they were banded. In Indiana, 4 of 7 males (57%) returned to breed the following year and 39% of adults returned in another study. Two used the same territory and the other 2 moved 0.8 and 1.2 km away. At another Indiana site, 31 of 101 males (31%) nesting in natural cavities returned. Twenty-one (68%) returned to the territory they held the previous year. Thirteen returned to different territories and moved an average of 1,095 m along the stream (range 214-3,262 m). Eleven males, 9 of which failed to attract a mate, switched territories within a breeding season. Mean distance they moved along the creek was 1,738 m (range 185-9,000 m). Five of the 11 males that relocated within a season returned. Three returned to the relocated territory, one returned to his original territory, and one settled equidistant between his original and relocated territories (Kowalski 2024). In Illinois, 13 of 14 returning males (93%) used the same territory. In Tennessee, site fidelity was higher in flooded than dry habitat. Between years, males moved an average of 43 m and 71% returned to within 50 m of their previous nest. Females moved an average of 203 m and 29% returned to within 50 m of their previous nest. By moving, 46% of returning birds changed the habitat in which they were nesting (Blem et al. 1999; Graber et al. 1983; Petit 2020; Petit and Petit 1996; Podlesak and Blem 2001; Schlossberg 2001; Walkinshaw 1941, 1953). Colour-banding of adults in Ontario 1998-2005 demonstrated that there was some interchange of individuals among different populations. An adult female banded north of Long Point was relocated nesting at Rondeau 3 years later, a dispersal distance of approximately 120 km (McConnell et al. 2011; McCracken 2007).

Limiting Factors

Eggs have been reported in Ontario nests from late May until the third week of July, with most present in the first half of June (McCracken 2007; Peck and James 1998a). Upon arrival, the male adds green moss to cavities within his territory. When the female arrives, she inspects the cavities, selects one, and completes the nest. Occasionally, she selects a cavity that the male has not added moss to and builds a nest in it. In Virginia, nests were under construction 1-2 days after the birds arrived. In Illinois and Tennessee, 6-7 days elapsed between the arrival of males and the initiation of nest construction. In Michigan, first nests took an average of 5.3 days to build (range 2-13 days). Second nests were completed in an average of 1.8 days (range 1-6 days). In Illinois, birds took 7-10 days to complete nests. The average amount of time required to build a nest in Tennessee was 8.8 days (range 6-12 days). In Michigan, the average amount of time between nest completion and egg laying was 3.2, 1.7, 1.4, and 1.1 days over 4 years (overall average 2.1 days, range 1-12 days). In

Tennessee, the elapsed time averaged 8.8 days (range 6-12 days). For second and later nests, the first egg is laid the day after the nest is completed. Usually 4-7 days pass between nest loss to laying of the first egg in a replacement clutch. In Tennessee, egg laying began about 5 days earlier in flooded habitat than in dry areas. One egg is laid per day and incubation begins with the laying of the penultimate egg. In Ontario, incubation took at least 10 days at 3 nests, 11 days at 1 nest, and no more than 12 days at another nest. Incubation took an average of 12 days 10 hours in Tennessee (range 12-13.5 days) and an average of 12 days 17 hours in Michigan (range 12-14 days). The incubation period was not influenced by air temperature. In Virginia, the incubation period ranged between 10 and 16 days for 1,036 clutches over 22 years. Low temperatures, young females, and small clutch sizes contributed to longer incubation periods. There were no differences in incubation period lengths for early and late clutches (Peterson et al. 2025). The entire clutch typically hatches within a 12-hour period but occasionally 1 egg hatches as much as 24 hours later than the rest. The average nestling period was 11 days in Michigan and 10.75 days in Tennessee, with about 50% of young fledging when they were 10 days old. Overall, the nestling period ranges from 10 to 12 days. Excluding nest building, a nesting cycle takes about 25 days. After the young fledge from the first nest, the average period to laying of the first egg in the second clutch was 17 days in Tennessee and 5.3 days in Michigan (Bent 1953; Bird Studies Canada 2001; Blem and Blem 1991, 1992; Graber et al. 1983; McCracken et al. 2010; Peck and James 1998a; Petit 1989, 2020; Petit and Petit 1996; Walkinshaw 1938, 1941, 1953).

Double broods are common in the southern portion of the Prothonotary Warbler's range, but rare in the north. Usually there is time for only a single brood in Ontario, but there is 1 report of a second brood. The young from the first nest must fledge before mid-June if a second brood is to be attempted. Second broods were common in Tennessee and Virginia, but rare in Michigan. Second broods may be raised in either the same or a different nest cavity. Three Michigan pairs attempting second broods nested directly across a river 46-152 m from their first nest. In Tennessee, 5 of 20 pairs (25%) nesting in natural cavities attempted a second brood. Two second nests were in the same cavity, 2 were in a nest box, and 1 was in a different natural cavity. In Tennessee nest boxes, 45-77% of females attempted a second brood and 50% (20-30% of the entire population) were successful. Females nesting in flooded habitat were more likely to attempt a second brood than those nesting in dry habitat (34.8% compared with 10.0%). In Virginia, some females attempt a third brood after successfully rearing 2 broods, but there are no known cases of successful third broods. If the first nest is lost, renesting is common. Replacement nests may occur in the same or a different cavity. Clutches of 3-6 eggs have been reported in Ontario (average 4.68 eggs, mostly 4 or 5 eggs). Throughout its range, clutches of 2-10 eggs have been documented, with the typical range 3-8 eggs and 4- and 5-egg clutches most common. Clutch size increases northward and adult females have larger clutches than yearlings. Clutch size declines with the season, so first clutches are significantly larger than clutches in second broods or replacement nests. Average clutch sizes reported elsewhere are 4.73, 4.6, and 4.53 in Tennessee; 4.96 for first clutches and 3.94 for second clutches in Virginia; 4.98 in Michigan; and 4.31 in Wisconsin. Five eggs is the most frequent clutch size for first nests; 4 eggs is most common for second nests. In Virginia, yearlings laid an average of 0.4 egg less than adult females in first clutches and 0.24 egg less in second clutches. The clutch size of 1 Virginia female was observed over 8 years and there was no decline in its clutch size with age (Beck 2013;

Bent 1953; Bird Studies Canada 2001; Blem and Blem 1992; Blem et al. 1999; Chapman 1907; Flaspohler 1996; Fleming and Petit 1986; Graber et al. 1983; McCracken 1984, 2007; Peck and James 1998a; Petit 1989, 1991a, 2020; Petit and Petit 1996; Walkinshaw 1938, 1941, 1953).

The Prothonotary Warbler is capable of breeding when it is 1 year old, but some do not breed until they are 2 years old. Yearlings may be relegated to inferior habitat by older males and the lower-quality territories may not be attractive to females. In Tennessee, 2 of 5 males first bred at age 2 years. Females are more likely to breed in their first year than males. Once a bird has bred, it typically breeds every year. In Virginia, 5.7% of adult females were not detected in 1 year, but bred the previous and subsequent years. It was surmised that these females did not breed because habitat conditions were inferior the 1 year. In Ontario, approximately 37% of territorial males fail to attract a mate. The sex ratio is male biased so that there are insufficient females present so that all males can be paired. The mating system is typically monogamous, but polygyny occasionally occurs. At least 3 cases of polygyny are known from Ontario, all involving adult males. In Tennessee, abundant nest boxes were provided and this created an artificial opportunity for polygyny. In order for polygyny to occur, there must be more than 1 suitable nesting cavity within the territory. In the Tennessee population, polygyny occurred only by older males holding territories in flooded habitats where food was much more abundant. In flooded habitat, 9 of 188 matings (4.8%) were polygynous compared with 0 of 58 in dry habitat. Under normal circumstances, usually less than 1% of matings are polygynous. Most polygyny in Tennessee occurred during the second nesting period. Females chose to be polygynous in higher-quality flooded habitat rather than nesting monogamously with a male defending a territory in dry habitat. Secondary females in polygynous relationships had lower reproductive success rates than primary females but their success rate was similar to those nesting monogamously in inferior dry habitat. Of 23 polygynous matings, 22 were bigamous and 1 was trigamous, and 2 males each had 2 different consecutive polygynous matings within a season. Three cases of polygyny were documented in Indiana and 2 were polyterritorial. In most cases, pair bonds last throughout the season. In Tennessee, some females switched habitats and mates for different nesting attempts within a season. In Michigan, only 1 pair remated in a second season and nested in the same box. Three other pairs had the opportunity to remate but did not. Of 10 observed copulations in Tennessee, 3 were extra-pair (Graber et al. 1983; Kowalski 2024; McCracken 2007; Petit 1991a, 2020; Petit and Petit 1996; Podlesak and Blem 2001; Walkinshaw 1941, 1953).

Intraspecific parasitism is another breeding strategy of the Prothonotary Warbler. Tucker et al. (2016) examined a population breeding in nest boxes in Virginia. Of 233 broods, 60 (25.8%) contained one or more parasitic nestling. Most parasitized broods contained 1 or 2 parasitic nestlings (range 1-4). Of 805 nestlings, 12.7% were parasitic. It often had multiple broods in a single season, but no female was parasitized more than once in a year. Clutch size of parasitized nests was larger than unparasitized nests. Host females fledged more young than non-host females but fledged significantly fewer biological offspring. Host females were less likely to raise a second brood than non-host females. Parasitic females were not older or younger than nonparasitic females and were not significantly older than host females. Parasitism appeared to occur opportunistically without deliberate targeting of hosts based on host or nest-box characteristics.

The Prothonotary Warbler usually forages lower than 7 m, but occasionally as high as 15 m. It takes prey from the water's edge, fallen logs, trunks and branches of trees, foliage of trees and shrubs, and the subcanopy of trees. At least 75% of foraging is by gleaning, 10-20% by hovering, and less than 5% by flycatching. It often probes into curled leaves to capture spiders and caterpillars. While foraging on bark, it occasionally forages upward on tree trunks in a manner similar to that of the Black-and-white Warbler. It may perch on tall grasses and aquatic plants in search of minute snails, which it consumes. One fed almost continuously on live insects as they became entangled in a spider's web. It may also take spiders from their webs. Juvenile foraging behaviour is similar to that of adults: usually below 5 m, 90% by gleaning, 7% by hovering, and 3% by aerial flycatching. It takes 66% of prey items from live leaves, 23% from twigs or branches, 6% from trunks, 2% from dead leaves, and 3% from the air (Bent 1953; Chapman 1907; Flaspohler 1996; Graber et al. 1983; Petit 2020; Petit and Petit 1988b). In North Carolina, the Prothonotary Warbler foraged in both flooded and dry habitats. Search speeds for prey were similar in both habitats, but attack rates were significantly higher in swamps, indicating greater food availability and therefore greater reproductive success. Foraging techniques consisted of 82% gleaning and 18% aerial attacks. These proportions did not vary by sex, with 80% gleaning by females and 84% gleaning by males. The sexes combined used 70% hops, 20% short flights, and 10% long flights to secure prey and this did not differ between habitats or stages of the nest cycle (Lyons 2005). At another North Carolina area, it foraged only in floodplain swamps and avoided upland forests and dry thickets. During the breeding season, 19.1% of observations of it were in the canopy, 47.6% in low trees, 28.5% in shrubs, and 4.8% on the ground. In the canopy, 4.8% of observations were at the top of the crown, 4.8% in the inner crown, 9.5% in the lower crown, and 0% on the bole. In low trees, 9.5% of observations were at the top of the crown, 23.8% in the inner crown, 4.8% in the lower crown, and 9.5% on the bole. In shrubs, 9.5% of observations were in the inner crown, 9.5% in the lower crown, 9.5% in brush piles, and 0% at the top of the crown or in dense thickets or grass. On the ground, 4.8% of observations were in dense thickets and no observations were made of it in grasses, at water's edge, or in open areas. Singing birds occurred at heights of 0-15 m (mean 4.6 m). Birds engaged in other activities were observed at heights of 0-7.6 m (mean 3.3 m; Parnell 1969). Petit et al. (1990a, 1990b) studied the foraging ecology of the Prothonotary Warbler in Tennessee. They compared the foraging strategies of males and females during the prenestling (territory establishment, pair formation, nest building, and incubation) and nestling periods. During spring before leaf-out, males foraged significantly higher (3.0 m) than females (1.5 m). Females spent two thirds of their time foraging below 1 m. Males spent only half of their time foraging at this height. Females foraged in shorter trees and shrubs than males, often using trees less than 3 m tall. Males frequently foraged in trees taller than 7 m. During the prenestling period, both sexes foraged primarily by gleaning (90% of the time), less than 1% by hawking for both sexes, and 5% for females and 9% for males hovering. It used small (1 cm or less) and intermediate-sized (1-2.6 cm) branches as foraging substrates 50% of the time. Both sexes used a variety of plant species for foraging, but concentrated on willows, buttonbush, maples, and dead fallen branches. Both sexes foraged more often in the inner and outer third of trees than in the middle third. Use of the outer third was related to foraging on emerging leaves and small twigs. Usage of the inner third was related to gleaning from trunks early in the season. During the nestling period, foraging of the sexes varied significantly for foraging height, substrate type, substrate height, and prey location. Almost two-thirds of foraging by females was at

3 m or lower (average 2.7 m). Males spent only 40% of their time foraging at this height (average 4.8 m). Males used willows and maples more frequently than females. Females foraged more on buttonbush and fallen dead branches than males. Females searched for prey in trees and shrubs that were smaller than those used by males. During the nestling period, both sexes foraged most often on leaves, but males used more leaves and fewer branches than females. The sexes had similar foraging techniques during summer with gleaning accounting for 75% of foraging tactics. Both most frequently used perches that were 1 cm or less in diameter and used the middle and outer parts of trees and shrubs. Throughout the breeding cycle, males significantly altered their foraging techniques for all 7 variables studied. During the prenestling period, less than 28% of the time was spent by males above 3 m compared with 60% during the nestling period, when the average foraging height was 2 m higher. During the nestling period, males reduced usage of branches, trunks, and the ground and increased usage of leaves and aerial foraging. After full leaf-out, males spent more than 40% of their foraging bouts in willows and maples and reduced used of buttonbush, vines, and fallen branches. During the nestling period, males still gleaned predominantly, but hawked and hovered more. During this period, males perched on smaller substrates than earlier in the season, reflecting a preference for perching on small twigs and an almost complete elimination of trunks as perch sites. Late in the season, males spent less time foraging in the inner third of trees and more time in the outer two-thirds. As the season progressed, females significantly changed their foraging behaviour for 4 of the 7 variables. They foraged at greater heights while feeding nestlings, averaging 1.2 m higher than during the prenestling period, yet still rarely searched higher than 5 m. During the nestling period, females increased their foraging on leaves and while in flight and decreased the amount of time spent on the ground, branches, and tree trunks. Females perched on smaller branches and twigs during the nestling period and spent more time hovering and hawking. During the nestling period, females increased their foraging on sweetgum, maples, and other trees and reduced their usage of vines, buttonbush, shrubs, and fallen branches. The sexes partitioned habitat vertically with the male maintaining the territory from higher perches and the female involved in activities associated with the nest. During the nestling period, both sexes hovered more frequently to capture caterpillars from the undersides of leaves. The emergence of mayflies and mosquitoes required more diversified foraging techniques than early in the spring when prey items were less abundant. After leaf-out, both sexes switched to foraging on smaller branches and twigs in the outer portions of trees where prey was more abundant. Changes in foraging strategies during the breeding season were a reflection of prey availability and location, but the sexes still maintained distinct height preferences in relation to their reproductive duties. Annual habitat changes due to flooding and delays in leaf-out resulted in a shift in foraging strategies that reflected the abundance and distribution of prey. These factors suppressed insect emergence, and females foraged below 1 m significantly more and took prey from leaves significantly less during this year than during the average for the previous 3 years.

Nestlings are fed primarily smaller caterpillars, spiders, mayflies, grasshoppers, and beetle larvae. For the first 4 days, young are brought food items less than 15 mm in length, including geometrid moth larvae, flies, and ants. By day 5, the prey fed to young includes larger (25-35 mm) caterpillars, mayflies, and spiders (Petit 2020). Rogers et al. (2023) used DNA barcoding to analyze the nestling diet at 9 locations in the eastern United States. The frequency of aquatic prey in the diet was 61-

100%. The early season diet contained more aquatic prey and the late-season diet contained more molluscs and terrestrial insects. Important prey items included spiders (nursery web spiders, long-jawed orbweavers, and jumping spiders), flies (mostly midges and crane flies), burrowing mayflies, bugs, molluscs (freshwater snails, pond snails, land snails, and Venus clams), hymenopterans, pill woodlice, orthopterans, moths (crambid snout, underwing, tiger, tussock, and geometer moths), whirligig beetles, and crayfish.

During the breeding season, adults are largely insectivorous. Caterpillars, flies, midges, mayflies, and spiders comprise the bulk of the diet. The Prothonotary Warbler also eats beetles, ants, leafhoppers, aquatic insects, snails, isopods, and grasshoppers. In Tennessee, the diet shifts from midges, spiders, and small insects early in the season to predominantly caterpillars and spiders later on. Prey taxa that were most important during the nestling period were significantly more abundant in flooded than dry habitat. In Alabama, the breeding season diet consisted of 75-88% terrestrial insects (caterpillars, true bugs, ants, flies, and grasshoppers), 11% spiders, and 1-10% aquatic organisms including dragonflies, mayflies, and snails. In the nonbreeding season, it is less selective in its diet and feeds on seeds, fruit, and nectar in addition to invertebrates. During autumn migration in Louisiana, 1 bird ate a 3-cm-long lizard (Bent 1953; Bird Studies Canada 2001; Bulluck et al. 2017; Davis and Komar 2003; Graber et al. 1983; Petit 2020; Petit and Petit 1996; Walkinshaw 1938, 1953).

The Prothonotary Warbler is the most heavily parasitized cavity-nesting species in North America. This is probably due to 2 main factors: it is a secondary cavity nester and older or natural cavities may have larger entrance holes that facilitate cowbird access and it fills most of the cavity with moss which also increases the likelihood of cowbirds gaining access. Even populations breeding in nest boxes may experience high parasitism rates. Cowbirds appear to remove a warbler egg in about two thirds of parasitism attempts. In Tennessee, cowbird eggs were accepted in 29 of 36 nests (80.6%). Warblers made no attempt to eject cowbird eggs, but 19.4% of parasitized nests were abandoned, significantly more than for unparasitized nests. The tendency to abandon a nest varied with the availability of other nest sites. Nests were abandoned more frequently where males defended 3 or more cavities. Where cavities are limited, nest abandonment and renesting may not be an alternative. In 1 instance a nest was parasitized where there were no other nesting cavities. The first clutch was completely buried with a new nest that was also immediately parasitized. Parasitism occurred significantly more frequently in early (30.2%) than late (13.2%) nests. Both early and late parasitized nests had significantly smaller warbler clutches than unparasitized nests (4.0 compared with 4.6 eggs for early clutches and 3.9 compared with 4.6 eggs for late clutches). Most parasitized nests fledge both warblers and cowbirds. Some warblers in parasitized nests starved or were trampled. The overall cost of parasitism was approximately 1 young in both early and late nests, or about 22-26% of the potential young. In Ontario, 13 of 48 nests (27.1%) reported to the Ontario Nest Records Scheme were parasitized. Over a third of nests are parasitized in some Ontario populations (36% at Long Point), and parasitism by the Brown-headed Cowbird is the second-most important cause of nest losses. Parasitism rates vary considerably geographically and tend to be higher in the Midwest where cowbirds are more abundant. The parasitism rates recorded in Ontario are among the highest documented for this species. Parasitism rates may vary considerably in a single location from year to year. In Tennessee, parasitism rates were similar in natural cavities (19.1%) and in nest boxes (21.2%). The overall parasitism rate was 22% in 1984 and 1985 but only

1.8% 1987- 89. Parasitism rates reported from other areas were 26.9% in Wisconsin, 25.7% and 46.3% in Iowa, 10.7% in Michigan, 12.3% in Louisiana, 15.6% and 38% (in nest boxes) in Illinois, 44.8% in Mississippi, and 0.013% in Virginia, where all nests were in boxes. A nest in Toronto in 1933 contained 7 cowbird and 0 warbler eggs. In an agricultural landscape in Illinois, parasitism rates were not influenced by patch size or the amount of natural habitat in the landscape. It was surmised that the landscape was so fragmented that it was saturated by nest predators and brood parasites (Bent 1953; Bird Studies Canada 2001; Blem and Blem 1991; Blem et al. 1999; Chapas-Vargas and Robinson 2013; Flaspohler 1996; Graber et al. 1983; Hoover et al. 2020; Lowther 1985, 1997; McConnell et al. 2011; McCracken 1984, 2000, 2001, 2007; McCracken and Dobbyn 1997; Peck and James 1998a; Petit 1989, 1991b, 2020; Petit et al. 1987; Twedt and Henne-Kerr 2001).

In Iowa, a Prothonotary Warbler laid an egg in a Northern House Wren nest in a nest box. The nest contained 3 wren eggs and 1 warbler egg. One wren egg disappeared and the other 2 did not hatch. The warbler egg hatched and the wren provisioned the warbler nestling with insect larvae, spiders, and winged insects. The warbler successfully fledged from the nest (Dodson et al. 2024).

Throughout its summer and winter range, habitat loss is the biggest threat to the Prothonotary Warbler, although direct habitat loss is less of a concern in Ontario. In the core of its breeding range in the southeastern United States, less than 25% of the original bottomland forest remains in moderate to high-quality condition. Coastal mangrove swamps that are critical wintering habitat in Central and South America are declining at an alarming rate. The decline in mangrove swamps corresponds to declines in breeding populations, but no direct link between these factors has been established. The Ontario population relies upon recruitment of birds from the United States breeding population. Small numbers occur in New York, Ohio, Pennsylvania, and Michigan, providing a small pool of potential immigrants. Many of these populations are declining and they also rely on recruitment from the core area in the southeast, where it is also declining. The continued existence of the Prothonotary Warbler in Ontario is increasingly dependent upon what happens in the United States and Latin America. In Ontario, 700-800 ha are occupied by the Prothonotary Warbler and 85% of this is protected government-owned land. The most significant threat to privately owned habitat is development. One occupied site was developed into a marina and trailer park. There were extensive losses of wetland habitat in southern Ontario until 1982, but losses have slowed considerably due to government policies. Nonetheless, there are now few large, unfragmented patches of swamp forests left that provide suitable habitat, and it is possible that all suitable habitat is occupied. The extensive system of municipal drains and tile drainage is still drying out many swamp forests (Austen et al. 1994; Bird Studies Canada 2001; Blem and Blem 1992; Flaspohler 1996; McCracken 1984, 2007, 2010; McCracken et al. 2010; Petit 2020).

In most areas, availability of suitable nesting cavities is a significant limiting factor, but this does not appear to be a problem in Ontario. Competition for nest cavities by other species is a significant factor throughout the Prothonotary Warbler's range. In Ontario, the 2 most significant competitors are the Northern House Wren and Tree Swallow. The Northern House Wren is responsible for a high percentage of nest losses in Ontario. It is particularly a problem because it fills all available cavities with dummy stick nests and these sticks may persist for several seasons making the cavity unavailable. In addition, the wren may remove or puncture warbler eggs and kill nestlings. The wren

is double-brooded with a long breeding season that spans the entire warbler breeding season. The Tree Swallow is a less serious nest-site competitor because it only uses 1 cavity, does not disturb warbler nests, and usually raises a single brood so it is present only during the early portion of the breeding season. In Iowa, 38.4% of Prothonotary Warbler nests were usurped by wrens and 1.5% by Tree Swallows. The deaths of 2 adult warblers were attributed to Tree Swallows. In Ontario and other areas where these 2 species are common, nest-box programs designed to increase Prothonotary Warbler populations instead increased wren and swallow populations to the detriment of warbler populations. At Rondeau, several cottagers erected nest boxes and these increased the local wren population. In other areas, it has been determined that nest boxes should not be used where the Northern House Wren is common unless the warbler habitat is in large, unfragmented, and flooded habitat. In Ontario, there are few such sites remaining. Although large, the forest cover at Rondeau is naturally fragmented by wetland sloughs that provide habitat for the Northern House Wren. Other species are a problem in different areas. These include House Sparrow, Carolina Wren, Eastern Bluebird, European Starling, chickadees, white-footed mice, southern flying squirrels, paper wasps, and mud-dauber wasps. In Tennessee, competing species represented 95.2% of nests in dry habitat compared with 4.8% in flooded habitat. Fortunately, the core areas of distribution of the Prothonotary Warbler and Northern House Wren do not overlap, so this wren is not a problem in the southeastern United States. The Northern House Wren is a major limiting factor in its core range, which includes Ontario, where it greatly outnumbers the Prothonotary Warbler and is increasing its population while the warbler is declining (Austen et al. 1994; Bird Studies Canada 2001; Blem and Blem 1991, 1992; Brush 1994; Flaspohler 1996; Graber et al. 1983; Guillory 1987; Knutson and Klaas 1997; McCracken 1984, 2000, 2001, 2007, 2010; McCracken and Dobbyn 1997; McCracken et al. 2010; Morse 1989; Petit 2020; Petit and Petit 1996; Scerbicke et al. 2024; Twedt and Henne-Kerr 2001; Walkinshaw 1938, 1941).

Regular water-level fluctuations within Prothonotary Warbler habitat are beneficial because they retard succession of shrub species and certain aquatic species. Extreme water-level fluctuations or long-term changes in water levels or the water table are detrimental. Although it has not been identified as a factor in Ontario, flooding in riparian swamps is an issue in many areas. This is a common cause of nest loss in much of its range. In Minnesota and Iowa forest cover along the Mississippi River, periodic flooding had a beneficial effect. Flooding of riparian forests allowed it to nest in areas that were typically occupied by the Northern House Wren. In Ontario, habitat is influenced most by water levels in the Great Lakes. Sustained high-water levels can kill trees and open up the canopy. Over the long term, high-water levels can result in a swamp forest being converted to a marsh or thicket swamp, thereby rendering the habitat unsuitable. If water levels remain low for an extended period of time, swamps dry up. This makes the habitat essentially unsuitable, although birds that have previously bred in such an area may continue to do so because of site fidelity. Dry swamps are unlikely to attract any new recruits. The dryness of such areas improves habitat for Northern House Wrens, promotes the growth of herbaceous and woody undergrowth, allows invasion by nonnative plant species, and provides access for terrestrial predators such as raccoons, squirrels, chipmunks, and mice. Under optimal conditions, there is a natural cycle of high and low water levels in the Great Lakes that provides a turnover of living and dead trees while some standing water remains. Much of the natural cycling of water levels in the

Great Lakes has been curtailed by current water management programs. Water levels in swamps may be adversely affected by direct wetland drainage or indirectly through lowering of the water table by irrigation or systems of tile drainage and municipal drains. Drought is another factor that can significantly lower the water table and surface water levels and adversely affect Prothonotary Warbler habitat (Bird Studies Canada 2001; Flaspohler 1996; Graber et al. 1983; Knutson and Klaas 1997; McConnell et al. 2011; McCracken 1984, 1999b, 2000; McCracken et al. 2010; Walkinshaw 1938).

Forest management has the potential to have significant effects on the Prothonotary Warbler and its habitat. Forest fragmentation creates edge that may improve habitat for the Northern House Wren and other nest-site competitors. Opening of the canopy due to logging may reduce water levels due to increased evaporation, may promote encroachment of invasive plant species, and may result in the loss of nest trees. Fuelwood cuts may remove dead and dying trees and stumps that are important sources of nest cavities. The population at Rondeau was drastically reduced in the mid-1930s following a cleanup program that involved removal of most of the dead stumps. This population has never recovered to its former levels (Baillie 1967; Bird Studies Canada 2001; Bushman and Therres 1988; McConnell et al. 2011; McCracken 1987, 2007; McCracken et al. 2010; Petit 2020).

Invasive plant species are a significant issue at some of the best areas for the Prothonotary Warbler in Ontario. Both common reed and black alder can significantly degrade habitat, particularly where water levels are low or canopy cover is reduced. Common reed has expanded dramatically at Rondeau where it has filled in open pools of water, rendering the habitat unsuitable. Black alder is highly invasive and can significantly degrade Prothonotary Warbler habitat in open swamp forests. It is already abundant in Hahn Woods and is a major problem at several restoration sites in Norfolk County. Reed manna grass has become dominant in a large portion of the Dundas Marsh, another Prothonotary Warbler breeding site. It is highly invasive and has the ability to out-compete native emergent wetland plant species (McCracken et al. 2010).

The emerald ash borer is another significant concern, as it eventually kills all affected ash trees. Ash is a frequent component of swamp forests that are inhabited by the Prothonotary Warbler in Ontario and it represents 47% of the tree cover in the Rondeau sloughs (McCracken 2007; McCracken et al. 2010).

Catastrophic weather events are potential significant factors. Populations within Ontario are clumped in isolated geographic areas, particularly along the northern shore of Lake Erie. An intense windstorm struck Rondeau in July 1998 that dropped thousands of trees and created hundreds of gaps that provided suitable habitat for Northern House Wrens. A similar storm at Point Pelee in the late 1970s resulted in significant windfall and may have reduced habitat availability. The intensity and frequency of storms is anticipated to increase as a result of climate change (McCracken 1999b, 2007, 2010; McCracken et al. 2010).

Drought is another potential limiting factor. A drought in Ontario in 1998 completely dried up most nesting areas and adversely affected Prothonotary Warbler habitat. As late as 2000, effects of this drought were still being manifested. Dry summers are likely to become more prevalent with climate change (McCracken 2001, 2007).

Predation can result in significant nest losses, with nest predation rates of approximately 40% occurring in Ontario. The raccoon is the most significant predator. Its population has increased dramatically in the province and is still increasing. Raccoons are the predominant predators of nests in natural cavities and of those in boxes without predator guards. The southern flying squirrel is the predominant predator in nest boxes with predator guards (Bird Studies Canada 2001; McCracken 2010; McCracken et al. 2010).

Toxic chemicals and other pollutants are an additional threat. Insect control programs in Ontario for mosquitoes and gypsy moths may reduce arthropod food supplies. Of greater concern are insecticides in Latin America, where DDT is still widely used for malaria control (McCracken et al. 2010).

Small populations at Turkey Point and near London were extirpated in the 1970s following development of the woodlands in which the Prothonotary Warbler was nesting. Direct development of habitat could not occur now due to the current wetland policies and the fact that it is protected under the *Endangered Species Act*. Nonetheless, development adjacent to occupied habitat is likely to increase the local raccoon population and possibly Northern House Wren numbers (McCracken 1984; McCracken et al. 2010).

Most nests in natural cavities are in dead and decayed trees. These are vulnerable to blowing down or simply collapsing during the nesting period. These types of losses have been confirmed in Ontario and many other locations. Nest trees along creeks may slump or fall down due to shore-bank erosion (Blem and Blem 1991; McCracken 2001; Petit 2020).

In Ontario and the northern portion of its range, the Prothonotary Warbler is likely to decline in response to climate change. Climate change models for the Great Lakes area suggest an increase in temperature, a reduction in precipitation, and lower lake water levels. This is likely to reduce the amount of standing water in swamps (McCracken 2007, 2010).

Status

Although it is possible that the Prothonotary Warbler was present in Ontario prior to European settlement and extirpated as a result of wide-scale forest clearing, this is unlikely. Historically, it was restricted to the swamps of the southeastern United States and later extended its breeding range northward, especially in the Mississippi River valley, to Wisconsin and Minnesota. The first record for Ontario was a spring migrant overshoot collected in Hamilton on 23 May 1888. The first nest for the province was found at Rondeau in 1929, although it was likely nesting there previously. In 1930 and 1933, it was estimated that more than 100 pairs bred at Rondeau, although it is now thought that this may have been an overestimate. Nonetheless, it was locally common at Rondeau at that time and this was the only known breeding site in the province. After stumps were removed from Rondeau in the mid-1930s, hardly any remained but it soon began to appear at Long Point. Birds observed there probably dispersed from Rondeau. It first nested at Point Pelee in 1955 and occurred there regularly until 1989. The bulk of the breeding population is almost entirely restricted to a few areas on or adjacent to the Lake Erie shoreline: Holiday Beach, Pelee Island, Wheatley, Rondeau, Long Point, and Point Abino, although it probably no longer breeds at the latter site. The Prothonotary Warbler began breeding intermittently in the Dundas Marsh in Hamilton in 1953. From the mid-1990s to mid-2000s, 0-1 pair nested annually, and 0-6 young fledged each year (average 3.1 per

year). In 1981, it nested in Pinery Provincial Park, but this appears to have been an isolated event. Territorial but unmated males occasionally defend territories in suitable habitat in inland locations in Brant, Middlesex, and Huron counties and Halton and Peel regions. These occurrences are not enduring and inland nesting has rarely been documented. Most of the population nests at Rondeau and Long Point, with lesser numbers at Holiday Beach. It formerly nested at Point Pelee and Turkey Point and near London and Aylmer. Habitat for this species has been destroyed at Turkey Point and near London. The Rondeau population recovered somewhat after stumps were removed, but the population never approached former numbers. In the mid-1980s, the entire Ontario population was estimated at a maximum of 50 breeding pairs. By 1996, there were only about 10 pairs remaining in the province. Restoration work began in 1997 and by 2000 there were an estimated 22 mated pairs and 8 unmated males present. This was the highest number recorded since intensive surveys began in 1996. By 2010, however, the population had declined again to no more than 10 pairs. Despite the population decline, there has been no significant change in the breeding distribution of the Prothonotary Warbler since about the 1940s (Austen et al. 1994; Baillie 1967; Baillie and Harrington 1937; Bird Studies Canada 2001; Curry 2006; Harrison 1984; McCracken 1984, 1999b, 2000, 2001, 2007, 2010; McCracken and Dobbyn 1997; McCracken et al. 2010; McIlwraith 1894; Peck and James 1998a; Wills and Barrett 2006).

In 1984, the Prothonotary Warbler was designated vulnerable in Canada and its status was upgraded to endangered in 2007. It is also designated endangered in Ontario and protected under the *Endangered Species Act*. The objective of the recovery strategy is to recover its historical population to 40 pairs spread among at least 6 geographically distinct nesting areas by 2015. These nesting areas are to be separated by at least 20 km (McConnell et al. 2011; McCracken 1984, 2007; McCracken et al. 2010).

There have been no recent historical changes in the breeding range of the Prothonotary Warbler. Breeding Bird Survey data from 1966 to 2007 indicate that the continental population declined at a significant rate of 1.1% per year (McCracken et al. 2010; Petit 2020).

POSTFLEDGING PERIOD

When young leave the nest, they fly to a nearby low-hanging branch. Any that fall into the water are capable of swimming to shore. One or more shrubs or saplings within a short distance of the nest provide immediate refuge for newly fledged young. Fledglings work their way up trees until they are in the canopy, and remain there for approximately a month. Within this time, they may range as far as 300 m from the nest and occur in any type of forested habitat, including dry upland areas. Juveniles that fledge from first broods may wander considerable distances prior to migration. One young that fledged in early June was found in early July 7 km from the natal territory. Four other juveniles 35-40 days old were found within 200 m of the nest. During this period, juveniles prefer trees that are at least 15 m tall. The adults divide the brood immediately upon fledging but if a female attempts a second brood, the male cares for all the fledglings from the first brood. The adults feed the young for at least 2 weeks after they leave the nest but young may still be fed as late as 35 days after fledging. Fledglings often occur in flocks of 3-5 in late June and July and flock members include those from different broods (Bird Studies Canada 2001; McCracken et al. 2010; Petit 2020; Walkinshaw 1938).

MIGRATION

The Prothonotary Warbler is a nocturnal migrant, with diurnal observations of migrants occurring mostly over water close to landfall. There is some evidence to suggest that it may follow watercourses during migration. In spring, it occasionally travels in small, single-species flocks when crossing the Gulf of Mexico. It is believed to travel singly in Ontario (Graber et al. 1983; McCracken 2007; Moore 1990; Petit 2020).

Males arrive on the breeding grounds prior to the females, and the interval between their arrivals may vary geographically or due to weather conditions. In Michigan, males arrived 2-3 days prior to females; the interval was 3-7 days in Tennessee. In Arkansas, females arrived 1-2 weeks after males. In Ontario, males typically precede females by about 2 weeks and older birds of both age groups arrive before younger birds (Bird Studies Canada 2001; Blem and Blem 1992; McCracken et al. 2010; Petit 1989; Petit and Petit 1996; Slevin et al. 2018; Walkinshaw 1938). The Prothonotary Warbler returns to southern Ontario in the first week of May or in very late April. Most are back on the breeding grounds by the first week of June, but some younger females may not arrive until the end of June (Bird Studies Canada 2001; McConnell et al. 2011). In the Gulf Coast states, average spring stopover times were 2.0, 4.2, and 8.4 days. Areas with the highest food availability had the shortest stopover times (Moore and Kerlinger 1987; Moore and Simons 1992).

The timing of autumn migration is difficult to ascertain because males stop singing and the adults and fledglings move to the tree canopy prior to migrating. In Michigan, family groups can be seen until mid-August some years, but most leave by the second or third week of July. In Ontario, almost all birds are beginning to migrate in mid-August. In the Hamilton area, average departure is 26 August and the latest record is 3 October. The sole Niagara record of an autumn migrant was on 27 August. On the Gulf Coast, hatching-year females tend to be the latest autumn migrants (Bird Studies Canada 2001; Black and Roy 2010; Curry 2006; McCracken et al. 2010; Petit 2020; Walkinshaw 1938).

There are no known differences in the habitat preferences of the sexes during migration. Although the Prothonotary Warbler has broader habitat preferences during migration than the breeding season, it is still found mostly near water along coastal areas and near inland lakes, watercourses, swamps, and marshes. It may occur away from water in young second growth. In Illinois, few were recorded outside their lowland breeding habitat during spring migration. During migration in Wisconsin and Minnesota, it was recorded only in floodplain forests and not in upland forests. During spring migration in North Carolina, the average number seen per hour was 0.70 in floodplain forests and 0.08 in wet thickets. It was not observed in pine-hardwood forests, pine forests, beech forests, oak-hickory forests, or dry thickets. During spring migration in Winnipeg, one spent most of a day at a pond in an urban park (Graber et al. 1983; Kirsch et al. 2013; Parnell 1969; Petit 2020; R.M. Underwood and T.J. Underwood 2001).

During spring migration in North Carolina, 18.6% of observations of the Prothonotary Warbler were in the canopy, 53.5% were in low trees, 16.2% were in shrubs, and 11.6% were on the ground. In the canopy, 2.3% of observations were in the top of the crown, 11.6% in the inner crown, 4.7% in the lower crown, and 0% on the bole. In low trees, 9.3% of observations were in the top of the crown, 14.0% in the inner crown, 30.2% in the lower crown, and 0% on the bole. In shrubs, 2.3% of

observations were in the inner crown, 2.3% in the lower crown, 11.6% in dense thicket and 0% at the top of the crown, in brush piles, or in grasses. On the ground, 2.3% of observations were in dense thickets, 9.3% were at water's edge, and 0% in grasses and open areas (Parnell 1969).

During spring migration at a pond in Winnipeg, one foraged among dead cattails most of the day. Occasionally it flew up and perched at the top of cattails before dropping down into them again (R.M. Underwood and T.J. Underwood 2001).

The Prothonotary Warbler is occasionally killed during migration at communication towers and tall buildings, but not in high numbers (Graber et al. 1983; Petit 2020). Because of its low population, it is possible that these losses are significant.

As would be expected based on its small breeding population, the Prothonotary Warbler is a rare migrant in Ontario (James 1991). There are no major concentration areas in the province during migration apart from Point Pelee, Long Point, and Rondeau (McCracken 1984).

Tennessee Warbler

Leiothlypis peregrina

BREEDING SEASON

Habitat Requirements

Most Ontario Tennessee Warbler nests were in wet habitats, including sphagnum bogs, with black spruce characteristically present or, less frequently, alder, tamarack, and poplar. One nest was in an area of willow shrubs with scattered taller poplars. Four nests were in dry locations: 2 in black spruce woods, 1 in a jack pine–spruce stand on a rocky outcrop, and 1 in an area of jack pine reforestation (Peck and James 1987). James (1984b) concluded that it was associated mostly with coniferous forests, but also mixed forests and less frequently deciduous forests. It requires coniferous trees of medium to tall height. It also needs open forests or edges and openings where deciduous shrubs are common. It may occur in riparian areas or swamps, but also inhabits drier forests.

In the northern portion of the Boreal Forest Region and Hudson Bay Lowland, the Tennessee Warbler nests in deciduous shrubs and saplings. Along the Hudson and James bay coasts, it is frequent along forest edges where it uses habitat similar to that selected by the Yellow Warbler. It occurs in willow thickets, patches of tall willow shrubs at edges of barrens, and deciduous shrubs in

swamps between the spruce forests and barren coastal areas (Manning 1952). Near Attawapisak and Winisk, it was common in open willow and willow-alder thickets and in spruce-willow bogs (Schueler et al. 1974). In northwestern Ontario, it was the most abundant species in deciduous shrubs and saplings 0.5-5 m tall. Other habitats it occurred in, in order of abundance, were coniferous forests with an understorey, mixed forests, deciduous forests, mixed scrub, heaths, coniferous scrub, and coniferous forests without an understorey. It was absent in tundra (McLaren and McLaren 1981). On the southwestern coast of James Bay, it occurs in all wooded habitats, including willow and alder swales, stands of balsam poplar on former beach ridges, and in lowland spruce–balsam fir forests. It is strongly associated with shrubs, particularly grey alder (Rimmer and McFarland 2020). Near Manitouwadge, it occurred in mixed stands dominated by black spruce, balsam fir, balsam poplar, and trembling aspen. It preferred mature (60-223 years) stands. Habitat choice became more generalized with increasing abundance of spruce budworms, settling in intermediate (24-36 years) and young (1-21 years) stands as budworms became abundant. Numerical responses of the Tennessee Warbler to budworm infestations were lower in younger than mature stands (Venier et al. 2009). Near Longlac, it used mixed boreal forests of balsam fir, white spruce, black spruce, trembling aspen, and white birch for nesting. It selected dry open sites for nesting. Of 14 nests, 5 were along road edges and 5 were in or at edges of small clearings. The other 4 were under a closed canopy, but in sparsely wooded areas. Average coverage by trees within 1 m of nests was 16.5%, and these were balsam fir, spruce, willow, and grey alder in order of abundance. Most nests were in dense ground cover including 20.2% coverage by feather mosses and 50.1% coverage by other species. In order of abundance, these were bunchberry, grasses, large-leaved aster, Labrador tea, strawberry, prickly rose, raspberries, naked bishop's cap, wild sarsaparilla, sweet coltsfoot, low sweet blueberry, Canada mayflower, horsetails, pearly everlasting, twinflower, goldenrods, and sphagnum moss. Most nest records from other locations refer to boggy wet areas with black spruce, tamarack, or white cedar. At Longlac, it frequently foraged in boggy or wet habitats, particularly in grey alder, but no nests were found in this habitat (Holmes and Nixon 2000). Near Lake Nipigon, it nested in forests dominated by balsam fir, black spruce, and white spruce that contained some white birch, jack pine, Labrador tea, and trembling aspen. Nesting occurred in clear-cuts and forest cover of all ages, including virgin mature forest. Trees appeared to be essential; a male attempting to establish a territory in a young treeless clear-cut eventually abandoned the site. The Tennessee Warbler nested there in wet alder thickets containing scattered trees. Spruce, white birch, and balsam fir trees were the most frequent singing perches, where it sang from an average height of 3.7 m from the tops of trees. Singing also occurred

as close as 30 cm from the ground and from alder shrubs (Kendeigh 1947). Near Pickle Lake, it occurred irregularly in small numbers in disturbed mixed woodlands (James 1980). Near Hearst during a spruce budworm outbreak, habitats it used included mixed forests of black spruce, white spruce, balsam fir, white birch, and trembling aspen; lowland forests of black spruce and tamarack; and well-drained sites dominated by jack pine. It was absent in 3-year-old clear-cuts, but was present in clear-cuts 5-24 years old and in mature undisturbed forests. It occurred in all types of stands but was most common in mixed and coniferous stands, and was most abundant in lowland coniferous stands followed by lower-slope mixed stands (Welsh and Fillman 1980). In the Clay Belt, it occurred in all forest types and along the full range of moisture regimes in woodlands with moderate to rich amounts of nutrients. It was most abundant in black spruce, jack pine, trembling aspen, tamarack–white cedar, and balsam poplar forests, and least abundant in balsam fir–white spruce stands (Welsh and Lougheed 1996).

In jack pine stands near Gogama in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Tennessee Warbler preferred very open edges of spruce forests. The managed jack pine forests were too dense to support it, but a few occurred where there were openings in the pines and when spruce budworm populations were high. It was attracted to forests older than 20 years when budworms were abundant (James and Peck 1995a).

Throughout its range, the Tennessee Warbler is most frequently associated with coniferous and mixed boreal forests where it requires deciduous undergrowth. It is characteristic of spruce and balsam fir stands, frequent in jack pine stands, and rare to absent in hemlock stands. It is typical of tamarack swamps and treed bogs where it is associated with alder in the understorey. It may nest in bogs or fens dominated by black spruce, tamarack, or white cedar. Due to its requirement for a deciduous understorey, it is typically associated with forest openings or edges. Nesting also occurs in regenerating clear-cuts, which it first invades about 5 years after cutting, but peak numbers occur 13-25 years after cutting. Nests are frequently in natural and artificial openings other than clear-cuts, including roadsides, ponds, bogs, farmsteads, burns, logging roads, trails, power-line cuts, overgrown pastures, and grassy openings on abandoned farmland. In taiga areas, it is often associated with large spruce trees, but also nests in second-growth forests that are often dominated by balsam poplar. These stands typically have a dense growth of deciduous understorey shrubs and saplings such as alder, rose, red-osier dogwood, or trembling aspen. Although it is most frequent in forests dominated by spruce and balsam fir, it also nests in trembling aspen, balsam poplar, poplar-birch, white birch–red oak, and spruce-poplar forests and thickets dominated by alders or willows. It is associated primarily with conifers, but coniferous stands must have a deciduous understorey to be suitable, and it frequently nests in alder and willow thickets and regenerating clear-cuts where conifers are scarce or absent. In Wisconsin, it is a rare breeder in pine and oak barrens (Back 1979; Beals 1960; Bent 1953; Bowdish and Philipp 1916; Campbell et al. 2001; Chapman 1907; Crawford and Titterington 1979; Dawson 1979; Erskine 1977; Harrison 1984; Jehl and Smith 1970; Kirk et al. 1996; Limoges and Gauthier in Gauthier and Aubry 1996; Manning and MacPherson 1952; Mossman et al. 1991; Rimmer and McFarland 2020; Sinclair et al. 2003; Welsh and Fillman 1980).

Differing preferences for forest stand ages have been reported for the Tennessee Warbler. Near Manitouwadge, it showed a clear preference for mature stands and inhabited younger stands only

when budworms were abundant (Venier et al. 2009). Near Hearst, it was more abundant in 17-24-year-old clear-cuts than in mature stands (Welsh and Fillman 1980). In Quebec, it was absent in previously cut or burned black spruce forests where trees were less than 5 m tall. It occurred in low densities in cuts and burns where saplings were 5-11 m tall and in 120-year-old forests, but was absent in 200-year-old forests (Imbeau et al. 1999). In Alberta aspen-dominated forests, there were no significant differences in its abundance in young, intermediate-aged, and old stands, although it was most abundant in young stands. It was associated with low aspen density, low shrub density, few snags, few trees larger than 20 cm diameter at breast height, low shrub richness, low canopy height, lower amounts of downed woody material larger than 20 cm in diameter, low tree species richness, and low conifer density (Schieck et al. 1995). In Saskatchewan, it occurred significantly more often in white spruce–trembling aspen forests that were more than 140 years old. The probability of detecting it at a point count was 50-79% in forests 50-60 years old, 80-90% in forests 100-110 years old, and 100% in stands older than 140 years. In old forests, the percent coniferous cover increased, the amount of shrub and moss coverage was significantly higher, and the amount of litter was significantly less than in young forests (Cumming and Diamond 2002). In boreal stands in Saskatchewan, Kirk et al. (1996) considered it an early successional species. Its probability of occurrence was 100% in very young stands (0-9 years), 67% in young stands (15-20 years), 100% in mature stands (40 years), and 67% in old stands (80 years). The percent coverage by coniferous trees and deciduous shrubs and saplings may be a more important habitat determinant for the Tennessee Warbler than forest age.

The Tennessee Warbler is tolerant of a wide range of moisture regimes. Early studies concluded that it was restricted to wet habitats such as bogs, coniferous and mixed swamps and lowland forests, and willow and alder thickets. More recent work demonstrated that it also nests in dry habitat including very dry sites on hillsides. Near Longlac, it selected drier sites and in the Clay Belt it occurred in very wet to dry habitats. Near Hearst, it showed no particular preference for moisture. In Saskatchewan, it occurred on average in mesic stands, slightly drier than average. In Alberta, it typically nests in poplar and poplar-spruce stands, but also in dry muskeg. In British Columbia, it is generally associated with moisture (Bent 1953; Bowdish and Philipp 1916; Campbell et al. 2001; Holmes and Nixon 2000; Kirk et al. 1996; Rimmer and MacFarland 2012; Welsh and Fillman 1980; Welsh and Lougheed 1996).

At the landscape level, the Tennessee Warbler does not appear to be adversely affected by forest fragmentation. In Saskatchewan, Hobson and Bayne (2000) found that it was randomly distributed within fragmented landscapes.

Nests reported to the Ontario Nest Records Scheme were predominantly in hollows in hummocks of sphagnum moss. One was at the base of a grass tuft, 2 were under Labrador tea, 1 was at the base of an alder, and 1 was under an alder branch (Peck and James 1987). Holmes and Nixon (2000) described additional nests from Longlac. Five were in depressions sunk into hummocks of moss or lichen. Additional cover was provided to these nests by conifer seedlings, dead conifer branches, shrubby plants such as Labrador tea, and a mixture of shorter plants including bunchberry, large-leaved aster, grasses, and sweet coltsfoot. Plant coverage at 2 nests was less dense, but they were still inconspicuous due to cover from overhanging mosses and dead leaves.

Two other nests were in holes in the sides of decaying, moss-covered stumps. One was at the bottom of the stump beneath an overhanging root, concealed by spruce seedlings, wild sarsaparilla, naked bishop's cap, and feather moss. The second nest was midway up the stump, hidden behind a dense growth of horsetails, prickly rose, and grasses. Two additional nests were in long grass and willows at the edge of a laneway. They were completely obscured by grass that had settled into thick mats among the sparse willow stems. Entrance to these nests was possible only through a small hole at the edge of the nest. Of the remaining 5 nests, 3 were in depressions at the base of conifer seedlings surrounded by grasses, large-leaved aster, common strawberry, and other plants; one was in a hole beneath the stem of a black spruce seedling encircled by feather moss, bunchberry, and blueberry; and the other was in a depression in the middle of a mat of feather moss, surrounded by willow stalks, Canada mayflower, bunchberry, and other small plants. Bent (1953) described 4 nests near Sudbury that were all in a clump or mound of sphagnum on margins of black spruce bogs.

Nests of the Tennessee Warbler are very inconspicuous and few have been described despite the fact that it is the most abundant species in many habitats. Almost all nests are on the ground, buried deep in moss, and concealed by seedlings, grasses, herbaceous species, or overhanging moss or limbs. Of 79 nests reported elsewhere, 62% were in moss hummocks, 9% were in grass or sedge tussocks, and 13% were at the base of a small tree or stump. A few nests were in moss on top of decaying logs. Others were under tangles of dead fallen branches or in mats of dead herbaceous vegetation. One New Brunswick nest was above the ground on a low-hanging spruce bough touching, but not buried in, sphagnum. A British Columbia nest was 3 m from the ground on the trunk of a trembling aspen tree and another was in a recess in a mossy stump. Other atypical nest locations include a depression in a mat of lichens, under a clump of clubmosses, and in a hollow in leaf mould (Bent 1953; Bowdish and Philipp 1916; Campbell et al. 2001; Rimmer and McFarland 2020; Sinclair et al. 2003).

Males establish a territory on the day of their arrival on the breeding grounds. In a New Brunswick study, the Tennessee Warbler appeared to be somewhat gregarious, with high densities occurring in clearings in forest cover. It was not considered truly colonial because it defended a territory, but other publications have interpreted these same results differently and concluded that it sometimes nests in small, loose colonies in ideal habitat. This conclusion is incorrect. It sometimes attains extremely high densities and territories may be tightly packed, but territories are vigorously defended and there is no evidence of colonial nesting. The only information on territory size is from near Lake Nipigon. The average size of 52 territories was 0.36 ha (range 0.16-0.69 ha). Only 3-7 records were made of each bird, so territories could have been larger. There were often spaces between territories, although others were contiguous. It was present at a supersaturated population level due to a spruce budworm outbreak. Territory sizes would probably increase with decreasing densities and this was observed at this site. On a plot where only 9 pairs were present, the average territory size was 0.36 ha. On same-sized plots supporting 16 or 17 pairs, the average territory size was 0.25 ha. Not all activities are confined to the territory, so the home range may be larger than the territory. Birds may wander considerable distances from the territory. One female gathered nest material and flew into the forest across a river for a distance of at least 120 m (Bowdish and Philipp 1916; Harrison 1984; Holmes and Nixon 2000; Kendeigh 1947).

No information on natal philopatry is available, but it is probably very low. There is no direct evidence of adult site fidelity, but few studies have been completed. On the southern coast of James Bay in Ontario, 0 of 290 adults were resighted in subsequent years. Reoccupation of nesting territories in subsequent years suggests site fidelity, but there are no data to confirm this (Rimmer and McFarland 2020). In the Gaspé Peninsula of Québec, 0 of 32 adults returned (Moison Perrier et al. 2021). Because the Tennessee Warbler responds strongly to spruce budworm populations, it is possible that it is nomadic. It may not nest in large geographic areas for long periods of time until a spruce budworm outbreak occurs, and deserts the area once the outbreak has run its course (Morse 1989).

Limiting Factors

Eggs have been found in Ontario nests from the first week of June to the third week of July, with most reported in the last half of June (Peck and James 1998a). Near Longlac, territories were established by 28 May, the first evidence of nest building occurred on 8 June, egg laying occurred 8-22 June, incubation occurred 20-30 June, and hatching occurred 27 June-1 July, with a median date of 29 June (Holmes 1998; Holmes and Nixon 2000). In Algonquin Park, dependent fledglings have been observed from late June to late July (Tozer 2012). Of 91 nests reported in the eastern portion of the Tennessee Warbler's range, 26% were found before 15 June, 64% between 15 and 30 June, and 10% after 30 June (Rimmer and McFarland 2020). Harrison (1984) reported some late nest dates including a 4-day-old nestling on 2 August and nestlings on 13 and 14 August.

The interval between arrival and initiation of nest building is unknown. Near Longlac, a partially built nest was found 11 days after males settled on territories. No information is available on how long it takes to build a nest. Information from 1 nest suggested that egg laying commenced immediately after the nest was complete. One egg is laid per day. It is uncertain when incubation is initiated. The incubation period is 11-12 days. At Longlac the period from laying of the last egg to first hatching was 7 and 8 days in 2 nests. This very short incubation period may be an adaptation that synchronizes the nestling period with the presence of late-instar budworm larvae and pupae. Alternatively, incubation may have started prior to the laying of the last egg, in which case the incubation period would have been longer. Near Longlac, hatching occurred within 24 hours at 4 nests and within 48 hours in 6 nests with 81% of nestlings hatching in the first 24 hours and 19% over a 24-48 hour period. It is possible that the onset of incubation is variable, with initiation of incubation of most clutches occurring with the laying of the last egg, but with some clutches being incubated prior to that. If young are disturbed, they may leave the nest when they are only 6-7 days old, but many remain in the nest until they are 7-12 days old (Bent 1953; Bowdish and Philipp 1916; Campbell et al. 2001; Holmes 1998; Holmes and Nixon 2000; Rimmer and McFarland 2020).

The Tennessee Warbler raises a single brood. Renesting may occur and late nesting records are probably from replacement nests. Large-scale departures from the breeding range often occur in early summer suggesting that many do not renest. Nests reported to the Ontario Nest Records Scheme had clutches of 4-7 eggs, but mostly 5 or 6 eggs (average 5.45 eggs). Near Longlac, clutch size was 5-7 eggs (median 6, average 6.09 eggs). Hatching success was correlated with clutch size, with a hatch rate of 87% for 5-egg clutches, 93% for 6-egg clutches, and 100% for 7 eggs. Clutch sizes may increase by 50% during spruce budworm outbreaks, when clutches of 6-8 eggs are

common. Near Longlac, average brood size was 6.2 nestlings in unsprayed areas during budworm outbreaks, and 5.5 and 5.2 in plots treated with insecticides. Broods larger than 6 nestlings may exceed the provisioning capacity of adults. Nestlings in broods of 7 had low growth rates. In British Columbia where the spruce budworm is absent, clutch size is 2-6 eggs (Bent 1953; Bowdish and Philipp 1916; Campbell et al. 2001; Harrison 1984; Holmes 1998; Holmes and Nixon 2000; Morse 1989; Peck and James 1998a; Rimmer and McFarland 2020).

No information is available on the age at first breeding, but it is likely that yearlings are capable of breeding. The Tennessee Warbler is assumed to be monogamous, but this has yet to be confirmed (Rimmer and McFarland 2020). In Maine, territorial birds that were removed from spruce–balsam fir forest were replaced suggesting the presence of a nonbreeding, floating population (Hensley and Cope 1951).

The Tennessee Warbler is one of the smaller warblers, which enables it to forage on the outer twigs and leaves of trees. Most of the time spent foraging during the breeding season is in the upper third of trees. In northern Ontario, it foraged mostly on aspen, followed by white birch, white spruce, alder, balsam fir, and black spruce. Near Lake Nipigon during a spruce budworm outbreak, budworm density was highest on balsam fir, intermediate on white spruce, and low on black spruce. Budworm density may affect the preference of trees for foraging. In the Northwest Territories, it foraged mainly on white spruce, followed by aspen, willow, birch, and black spruce. In Saskatchewan, it used white birch more than expected by chance for foraging. It used balsam fir less than expected and other tree species in proportion to their availability. The Tennessee Warbler appeared to have trouble foraging in the thin outer twigs of balsam fir and avoided it. In conifers, it used the bottom of trees significantly less than expected, the outer part of branches with small twigs more than expected, and avoided the inner portion of the top of trees. In deciduous trees, it used small twigs on the outer portion of trees significantly more than expected. Average foraging height was 8.6 m in conifers and 9.5 m in deciduous trees. In Ontario, mean tree height was 13.7 m and mean foraging height was 9.6 m (70.0% of tree height). In the Northwest Territories, mean tree height was 10.3 m and mean foraging height was 7.9 m (76.7% of tree height). It typically forages at heights of 12 m or less during the breeding season. In Ontario, 75% of foraging time was spent in the top third of trees, 22% in the middle third, and 3% in the bottom third. The percent coverage by conifers within a 50-m radius around foraging individuals was 44% in Ontario and 53% in the Northwest Territories. In Saskatchewan, 66% of observations were in canopy trees and 34% were in the subcanopy. In Ontario, the primary foraging substrate was leaves followed by twigs and curled leaves. In the Northwest Territories, it foraged primarily on conifer needles followed by leaves, curled leaves, and twigs. In Ontario and the Northwest Territories, foraging was predominantly by gleaning and reaching. It infrequently hovers, hangs upside down, or flushes and pursues prey (Cumming 2004; Greenberg et al. 1999; Kendeigh 1947; Limoges and Gauthier in Gauthier and Aubry 1996; Morse 1989; Rimmer and McFarland 2020).

Food items brought to nestlings by males averaged 1.5 cm compared with 1.38 cm by females; the overall average was 1.45 cm. Near Longlac, lepidopteran larvae and pupae, particularly those of the spruce budworm, comprised 93.6% of food items brought by males and 87.9% by females. During a spruce budworm outbreak, caterpillars constituted 91.1% of the nestlings' diet in an

unsprayed area compared with 93.2% in an area sprayed to control budworms. Gizzards of adults were collected during a spruce budworm outbreak near Longlac. Early in the season (7-11 June) the diet consisted of 41.5% beetle adults, 47.7% caterpillars, 4.6% flies, 1.5% spiders, and 4.6% other items (soft-winged bugs, hymenopteran larvae and adults, beetle larvae, snails, odonates, caddisflies, and lacewings). The diet changed significantly in mid-season (18-24 June) and consisted of 5.8% beetle adults, 80.2% caterpillars, 2.3% flies, 3.5% spiders, and 8.1% other items. In the early season, budworm larvae were too small and rarely consumed. The caterpillars eaten during this period were predominantly those of leafroller moths taken by probing in alder foliage. The diet of the Tennessee, Cape May, and Bay-breasted warblers overlapped little early in the season, with the Tennessee Warbler consuming more caterpillars than the other 2 species. Later in the season, only use of beetles differed among the species, with the Bay-breasted Warbler maintaining its preference for beetles. Four stomachs of Tennessee Warbler adults were collected during a budworm outbreak near Lake Nipigon. A male in mixed forest had eaten 3 aphids, 3 unidentified beetles, 1 spruce budworm larva, and 50 unidentified caterpillars. A female collected in a clearing had consumed 5 spiders, 15 aphids, 1 soft-winged bug, 14 beetles, 30 spruce budworm larvae, 15 caterpillars, and 20 flies. A female in spruce–balsam fir forest had eaten 1 aphid, 31 beetles, 1 lepidopteran, 1 fly, and 66 sawflies. A male in a black spruce swamp had eaten 1 soldier beetle and 99 caterpillars. Later in the season when budworms were larger, many Tennessee Warblers were observed with them in their bills. Its diet was dominated by caterpillars (59%) compared with 22.3% for birds on average. It consumed the highest percentage of lepidopterans of all bird species near Lake Nipigon. In New Brunswick when budworms were absent, 3 stomachs were collected. The diet of 1 male consisted of 35% leafroller moth caterpillars, 23% flies, 2% small spiders, and 40% vegetation fragments. One female's diet consisted of 16% carpenter ants, 75% leafroller moth caterpillars, 4% snails, and 5% vegetation. One male had eaten 8% fireflies, 3% small beetle larvae, 25% leafroller moth caterpillars, 50% caddisflies, 14% spiders, and a trace of vegetation. Over 2 years in Maine, spruce budworm larvae and pupae constituted 100% and 66% of the invertebrates consumed. It is a spruce budworm specialist and its population is closely tied to that of the budworm. During spruce budworm outbreaks, it may feed almost exclusively on budworms once the larvae become large enough. It is very efficient at foraging on budworms and is capable of exploiting very low populations of this resource. During outbreaks, budworms are extremely abundant and it has been estimated that bird populations are capable of consuming only about 4% of the larvae. Consequently, there is no competition for food among insectivorous birds during budworm outbreaks (Bowdish and Philipp 1916; Holmes 1998; Holmes and Nixon 2000; Kendeigh 1947; McMartin et al. 2002; Mitchell (1952); Rimmer and McFarland 2020).

There is little overlap in the breeding ranges of the Tennessee Warbler and the Brown-headed Cowbird. The Tennessee Warbler is a rare host of the cowbird. No parasitized nests have been reported in Ontario. Three parasitized nests have been reported in Alberta and one each in British Columbia (9.1% of nests), Saskatchewan, New Brunswick, and Nova Scotia. In Michigan, there is 1 record of warbler adults feeding a cowbird fledgling (Campbell et al. 2001; Harrison 1984; Peck and James 1998a; Rimmer and McFarland 2020).

The Tennessee Warbler specializes in foraging on spruce budworms and its breeding population, breeding distribution, and reproductive success are highly dependent upon budworm

numbers. It is considered one of the best biological indicators of the spruce budworm. Near Manitouwadge, its population increased 9.1 times over a 4-year period during a budworm outbreak and declined by 30% the following year as the outbreak diminished. Prior to the outbreak, it was the 11th-most abundant species, but became the most abundant species during the outbreak. More young are produced from nests during outbreak years. During an Ontario outbreak in 1945, its populations increased steadily throughout June, suggesting that adults settled first and that younger birds exploited vacancies as the season progressed. In New Brunswick, it showed a strong and direct response to budworm numbers. It was initially absent and responded very late in the budworm outbreak suggesting that it might not respond to outbreaks of short duration. In the 1960s, there were no budworm outbreaks of any consequence in Ontario. A massive outbreak began to build in the 1970s, reaching a peak in 1980 when approximately 18,850,000 ha of forest were defoliated. Since 1992, budworm infestations have fallen dramatically, with only 280,000 ha of forest affected in 2004. As a result, significant declines in Tennessee Warbler populations have occurred and they are currently slightly below the 1960s levels prior to significant budworm outbreaks (Erskine 1977; Kendeigh 1947; McCracken 2004; Morris et al. 1958; Venier et al. 2009).

Spraying for the spruce budworm has been an annual event in eastern Canada since the early 1950s. A number of studies determined the impacts of spraying various chemicals and biological-control agents on birds, and some were specific to the Tennessee Warbler. Typically only in the order of 50-60% of budworms are killed by spraying because the material concentrates in the upper foliage. Foliage lower in trees is less exposed to the chemicals. Most studies concluded that spruce budworm control programs pose little threat to songbirds, including the Tennessee Warbler. Chemicals in use early on may have killed birds, but this was not well documented. Less potent chemicals are used now, but their effects are not well known. The bacterium known as Bt is highly specific for lepidopteran larvae and is now widely used and appears to be much less hazardous to birds. In the Gaspé region of Quebec, insecticides have reduced the seriousness of budworms without completely eliminating them. This has helped to maintain Tennessee Warbler populations there at stable levels (Holmes 1998; Kendeigh 1947; Limoges and Gauthier in Gauthier and Aubry 1996).

In Algonquin Park and near Lake Nipigon, Kendeigh (1947) studied the effects of spraying DDT for budworm control on birds, including the Tennessee Warbler. There was no significant decline in numbers on plots that were sprayed late in June once all birds had become established. Plots where it settled first and in largest initial numbers eventually had the largest stabilized breeding populations. There was a significant decline in numbers on a plot sprayed on 2 June before many territories were established. Early spraying and the decrease in abundance of insects did not prevent it from using the area in an apparently normal manner. Numbers of pairs on late-sprayed plots were 9, 16, 17, and 17; there were 9 pairs on the early sprayed plot compared with 16 on the control. The author concluded that DDT had no effects on birds and that any differences in densities on plots were due to differences in habitat and food abundance.

Hunter and Witham (1985) studied the effects of carbaryl spraying on the Tennessee Warbler in Maine over a 2-year period. In the first year, spraying was incomplete and only about 30% of the area was sprayed. Spraying was complete the following year. In the first year, the number of all warblers

foraging in the sprayed area dropped and remained low for 7 days, when a gradual recovery began. The proportion of Tennessee Warblers of all warblers prior to spraying was 22.3% in the experimental area and 12.4% in the control area. After spraying, Tennessee Warblers comprised 5.0% of all warblers in the sprayed area and 4.1% in the control area. During the recovery period, it represented 0% of warblers in the sprayed area and 6.7% in the control. The use of spruce for foraging by all warblers was significantly lower postspray and there was an increase in the use of other species such as alder, yellow birch, beech, ash, white pine, cherry, white cedar, and hemlock. In the experimental area, warblers of all species foraged on conifers 53% of the time prior to spraying and 24% postspray, compared with 62% and 63% in the control area. The number of Tennessee Warblers decreased following spraying, but this decline continued through the study period and also occurred on the control area. Pesticides may affect bird foraging behaviour by reducing food availability and this is likely to be the case only when birds have the opportunity to forage on nearby unsprayed areas. No effects are likely when an entire area is sprayed and birds cannot forage in unsprayed areas.

In New Brunswick, experimental applications of fenithrothion at conventional doses had potentially lethal effects on the Tennessee Warbler. Thirty-eight percent exhibited 50% or more brain cholinesterase inhibition, and 62% showed 20% or more inhibition. The impacts of spraying fenithrothion were highly variable with higher doses having less apparent effect (Rimmer and McFarland 2020).

Holmes (1998) examined the effects of Bt near Longlac and tabufenoxide near West Hill. Both these agents are highly specific in treating lepidopteran larvae. In treated areas, clutch sizes were smaller and the hatch rate was lower. There were no significant differences in nestling growth rates among treatments, although growth rates were highest in the tabufenoxide treatment area, followed by the Bt treatment area and the control area. There was no significant difference in the number of feedings or the size of prey brought to nests among treatments. Because brood sizes were smallest in the tabufenoxide treatment area and the same amount of food was delivered to each nest, nestlings in this treatment area grew faster. The tabufenoxide treatment had high efficacy and reduced spruce budworm populations by more than 90% on spruce and 77% on aspen. There were no reductions of budworms on spruce in Bt treated areas and only 15% in aspen. Even where spraying was effective, it is likely that Tennessee Warblers and other species were finding budworms in refugia that did not receive spray deposits. The author concluded that pest control programs using lepidopteran-specific insecticides pose little threat to the Tennessee Warbler and songbirds in general.

There are contrasting opinions on whether forest management is detrimental or beneficial to the Tennessee Warbler. Vanderwel et al. (2009) completed a literature review on the effects of partial harvest in the Boreal Forest Region, with particular reference to Ontario. It decreased in response to partial harvesting that retained 70%, 50%, and 30% of forest cover. The most important habitat feature was considered understorey cover. Rimmer and McFarland (2020) concluded that it may benefit from forest management in Ontario, where highest densities occur in regenerating clear-cuts. Forestry has the potential to change the composition of forest stands which could alter their suitability for this warbler (Venier et al. 2009). In Ontario in the Canadian Shield, there was no difference in its abundance in mid-successional clear-cuts and stands of the same age created by

fire, but it was significantly more abundant in early successional clear-cuts than burns. It was equally abundant in mid-successional and mature stands, but significantly less abundant in early successional than mature stands (Zimmerling et al. 2017). In Alberta, it is most abundant in stands older than 140 years, but the rotation age is 80-90 years. Cumming and Diamond (2002) concluded that it was likely to decline if stands older than rotation age were lost from the landscape. Also in Alberta, it was more abundant in control areas than in clear-cuts. Leaving unharvested trees in clear-cuts had no effect on abundance (Tittler et al. 2001). Another Alberta study examined the effects of partial timber harvesting on birds. The Tennessee Warbler usually disappeared when areas were clear-cut. In deciduous and mixed stands, it increased when 25-90% of forest cover was removed. Increases were not noted until 2 years postharvest, by which time shrub and sapling regrowth had occurred (Harrison et al. 2005).

Ferris (1979) examined the effects of an interstate highway on the Tennessee Warbler in Maine. Its abundance was negatively correlated with increasing distance from the highway. It was probably responding positively to the opening along the edge between the forest and highway right-of-way.

In Alberta, Bayne et al. (2008) compared the Tennessee Warbler's density and occupancy rates near noise-generating compressor stations and noiseless well pads. There were no significant differences in its density or occupancy rate as a result of differing noise intensities. Bayne et al. (2016) examined the effects of energy sector disturbances on it in Alberta. It responded positively and was significantly more abundant at seismic lines, pipelines, and well pads than in forest interior adjacent to these habitats.

Miscellaneous factors that may affect the Tennessee Warbler include forest fire suppression, wetland drainage, and peat mining (Rimmer and McFarland 2020; Venier et al. 2009).

Price (2004) concluded that the Tennessee Warbler could possibly be extirpated as a breeding species in southern Ontario if the average summer temperature increased by 2°C. DesGranges and Morneau (2010) and DesGranges and LeBlanc (2012) examined its sensitivity to climate change in Quebec. In the southern portion of the province, its presence was correlated with cooler and wetter summers. It was considered highly sensitive to climate change there. The other study area was near the northern extent of its range in Quebec. There it was closely associated with stands having a high summer temperature and high summer precipitation. In this area, it was not particularly sensitive to climate change and may benefit from warmer summers. These studies demonstrate that it may not be valid to project findings on climate effects from 1 area to broad geographic areas.

Status

McIlwraith (1894) had only 2 records of the Tennessee Warbler, one each during spring and autumn migration. He noted that it bred in the vicinity of Hudson Bay, but provided no additional information. Baillie and Harrington (1937) stated that it bred throughout the province north of latitude 47°N, where it was fairly common. Manning (1952) found that it was one of the most common warblers along forest edges near the Hudson and James bay coasts. In the Boreal Forest Region, it is very common and may be the most abundant species during spruce budworm outbreaks. Near Hearst during the peak of budworm populations in Ontario, it occurred in the highest densities that have been reported for this species. Of 22 plots surveyed, it was the most abundant species on 9 plots (Welsh and Fillman 1980). During the first atlas, it nested from

Algonquin Park northward, with the exception of West Pen Island and the Cape Henrietta Maria area. Scattered records further south may have represented nonbreeding birds. It frequently sings during migration, so these records may have been of late spring or early autumn migrants, or of unpaired males (Welsh in Cadman et al. 1987). James (1991) considered the Tennessee Warbler a common to locally abundant summer resident across the north that became uncommon in the south to the Algonquin Park area. It is occasional but rare on the Bruce Peninsula and on the Frontenac Axis south to Kingston.

The second atlas demonstrated that there had been no significant change in the distribution of the Tennessee Warbler since the first atlas. It occurred regularly from Lake Nipissing north to the Hudson Bay coast, with lesser numbers in the Shield south of Lake Nipissing. It continued to be absent in the West Pen Island area, but was recorded near Cape Henrietta Maria. There was no significant change in its probability of observation province-wide between atlases. There was a significant decline in its probability of observation in the eastern portion of the Great Lakes–St. Lawrence Forest Region. In the Shield, the decline may have been due to reductions in the spruce budworm population, which had been decreasing since 1985. During the first atlas, breeding evidence was reported in 20 squares south of the Shield compared with 12 during the second atlas. It was most abundant in the Hudson Bay Lowland and the northern Boreal Forest Region. Abundance declined in the western portion of the Great Lakes–St. Lawrence Forest Region and the southern portion of the Boreal Forest Region, and was very low in the eastern portion of the Great Lakes–St. Lawrence Forest Region (Crins in Cadman et al. 2007).

It appears as though the Tennessee Warbler was uncommon around the turn of the 20th century, although some authors attributed this to its being overlooked because of its drab appearance. It became noticeably more common during migration in Massachusetts and several other New England and eastern states during 1909-16. This was presumed to be an indication that northern breeding populations had increased, although it could represent a change in migration routes. The apparent increase near the beginning of the 20th century has been attributed to logging and clearing of coniferous forests with subsequent growth of deciduous species, and spruce budworm outbreaks. Breeding Bird Survey (BBS) data 1966-95 showed a nonsignificant increase in the Tennessee Warbler in Canada and the United States. From 1966 to 1979, populations increased significantly in response to spruce budworm epidemics but declined significantly 1980-95 as budworm populations diminished. BBS data may not provide the full picture, given that much of the core of the Tennessee Warbler's range is north of the region that is sampled by the BBS (Kendeigh 1947; Limoges and Gauthier in Gauthier and Aubry 1996; Rimmer and McFarland 2020). BBS data indicate that it experienced an annual increase of 0.0338% in Canada and an annual decrease of 1.37% in Ontario 1970-2021. The trends 2011-21 were an annual decrease of 2.65% in Canada and an annual increase of 0.243% in Ontario. The long-term trends were of medium reliability; the short-term trends were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

In Quebec, Major and Desrochers (2012) netted birds during the postfledging period in 5-12-year-old clear-cuts. Within some of their plots, they removed all elderberry fruits. They did not consider the Tennessee Warbler to be a frugivore or a mature-forest species. In their first year of study, they

captured 6 Tennessee Warblers: 2 in control plots and 4 in plots where fruit had been removed. None were captured the following year. It was unknown if it nested within the clear-cut the initial year of study. Over a 4-year period in 2-10-year-old clear-cuts in Minnesota, Streby et al. (2011b) caught 58 Tennessee Warblers (36 adults and 22 juveniles) during the postfledging period. They did not catch any during the breeding season.

MIGRATION

The Tennessee Warbler is a nocturnal migrant. Although it may cross the Gulf of Mexico in small homogenous flocks during spring migration, in other locations it migrates in mixed-species foraging flocks, particularly in autumn. It is one of few neararctic migratory birds that may undertake its prebasic moult during autumn migration. Some adults remain on the breeding grounds later and complete the moult there (Brewer et al. 2018; Graber et al. 1983; Leighton et al. 2002; Morris et al. 2013; Rimmer and McFarland 2020; Stewart 1986; Vogt et al. 2012; Winker et al. 1991).

Males arrive a few days earlier than females in spring. From 1984 to 1998 at Long Point, the mean capture dates for males were 14.5 May for after-second-year birds, 17.7 May for second-year birds, and 17.6 May for males of unknown age. Yearling males arrived significantly later than older males. Mean capture dates for females were 18.1 May for after-second-year birds, 20.6 May for second-year birds, and 22.0 May for birds of unknown age. Younger females did not arrive significantly later than older females (Stewart et al 2002). At Prince Edward Point, males arrived significantly earlier than females, with mean arrival time of males 21.0 May compared with 23.2 May for females. Differences in mean arrival dates were greatest in years when males arrived the earliest (Francis and Cooke 1986). In southern Ontario, most pass through between mid- and late May, with some arriving in the last week of April. Most leave by the end of May, but some remain into early or even late June (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). Migrants pass through the southern Shield from mid- to late May. Some are occasionally seen into June (Mills 1981; Tozer 2012). Near Lake Nipigon, Kendeigh (1947) first observed the Tennessee Warbler on 25 May. On the southwestern coast of James Bay, the first bird was observed on 25 May in 1982 with the main influx occurring during the first 2 weeks of June (Rimmer and McFarland 2020).

Autumn migration is protracted, and adults may arrive in southern Ontario a month in advance of juveniles. Of 280 adults banded on the southwest coast of James Bay from 28 June to 15 July 1982-85, only 12 (4.2%) were recaptured. This suggests that most of the breeding population left the area during that period, and that there may have been widespread reproductive failure. Nineteen of these adults (6.8%) remained on the breeding grounds through the prebasic moult, with some still present in early September (Rimmer and McFarland 2020). In the southern Shield, the peak of autumn migration occurs from mid-August to mid-September. Migrants may occur from mid-July until mid-October (Mills 1981; Tozer 2012). In southern Ontario, average arrival is in mid-August. The peak of autumn migration occurs in late August and September. Birds may arrive in early July and remain until late October or even mid-November (Black and Roy 2010; Curry 2006; Keast 1980; LaForest 1993; Lancaster et al. 2004; Weir 2008).

Lengths of stopovers at staging areas vary among sites, seasons, and years. Factors that affect the duration of stay include abundance of food, number of birds competing for the food, and whether an individual is moulting. During autumn migration at Prince Edward Point, 6% of adults

were recaptured and the mean duration of their stay was 6 days. Only 1% of juveniles were recaptured and this occurred the day after the initial capture. At 2 sites in Mississippi, the mean duration of stay in spring was 3.3 and 3.7 days. In Texas, only 6 of 222 of spring migrants (2.7%) were recaptured with only 2 staying longer than 3 days. In Louisiana, the mean length of stay was 2.7 days during high migrant density and 3.1 days at low migrant density; these differences were significant. In Minnesota, 1 male was captured in 3 successive autumns and underwent the prebasic moult each time. Stopover times for this bird were a minimum of 4, 17, and 18 days over the 3 years. During autumn migration in Michigan, recapture rates and stopover times were similar for adults and juveniles, and averaged 8.7 days for adults and 5.6 days for juveniles. Twenty-three of 51 adults (45.1%) were undergoing moult and their recapture rate was 4 times that of nonmoulting birds. Adults undergoing moult migration may leave early or move south more rapidly, explaining the very high proportion of juveniles (92% of birds) that occurred at this banding station. In Montreal, moult migrants arrived on 2 August on average compared with 12 September for post-moult migrants. Moult migrants stayed longer (46 days) than post-moult migrants (8 days). Moult migrants had average home range sizes of 14.6 ha compared with 5.8 ha for a post-moult migrant (Kuenzi et al. 1991; Morris et al. 2013; Poirier et al. 2024; Rimmer and McFarland 2020; Winker et al. 1991).

During migration, the Tennessee Warbler is found mostly in wooded areas, but also in shrub habitats and urban gardens and rural lots to a much lesser extent. Rimmer and McFarland (2020) noted that it showed no habitat preferences during migration, but it may select habitat on the basis of food availability. Conflicting reports on its preference for upland or lowland forests support the suggestion that food availability may be the most important factor. In southern Illinois, it was 3 times more abundant in bottomland forests than in upland forests, but densities were highest in upland forests in central Illinois. During spring migration in Wisconsin and Minnesota, its probability of detection was the same in floodplain and upland forests. During spring migration in Ohio, it was significantly more abundant in upland than riparian forests. During autumn migration in Pennsylvania, the Tennessee Warbler was equally abundant in all habitats surveyed: forest edge, forest interior, shrub- and sapling-stage forest, forest-agricultural edge, suburban forest, and pole-stage forest. During autumn migration in Montreal, home ranges consisted of 48.8% forest, 33.0% agriculture, 10.1% water, 7.3% wetlands, and 0.7% anthropogenic areas. Its presence was significantly correlated with the proportion of forests and forest edges within 100 m. During spring, it is attracted to blossoming apple trees, oaks, and hawthorns; large elms; willow thickets; and roadside copses of mixed deciduous second growth. In addition to forests and shrubby areas, it may be found in weedy fields and forest openings dominated by burdocks and other weedy species. In British Columbia, it has been reported from gardens during migration, but prefers open and closed forests dominated by spruce. The most important vegetation communities for it there include spruce with an understorey of buffalo-berry and feather moss, dwarf birch–shrubby cinquefoil–willow-moss, and spruce with an understorey of Labrador tea and moss. It also uses mixed riparian stands of spruce–trembling aspen–cottonwood. As it approaches the breeding grounds in spring, preferred habitat is open mixed forests of trembling aspen and white spruce, and it is also found in second-growth sapling trembling aspen stands that have developed after clear-cutting. It has not been documented using young clear-cuts or mature trembling aspen forest (Bent 1953; Campbell et al. 2001; Fitch 1958; Graber et al. 1983; Kirsch et al. 2013; Poirier et al. 2024; Rimmer and McFarland

2020; Rodewald and Brittingham 2002, 2004; Rodewald and Matthews 2005; T.J. Underwood and R.M. Underwood 2001).

There are rare records of apparent territorial behaviour during spring migration. In Illinois, Graber et al. (1983) observed that some Tennessee Warblers appeared to establish territories that they defended vigorously for an unknown number of days before moving on. In Kansas, there was a distinct tendency for an individual to remain in a small area of a tree and exclude others from this area. One foraged for about 15 minutes in the crown of a tree, staying within a space approximately 6 m across and making regular circuits within this area. It was covering the same area as one that was observed 6 days earlier and was quite possibly the same bird (Fitch 1958).

A small proportion of birds may exhibit stopover site fidelity during autumn migration. In Minnesota, 1 male was captured in 3 consecutive years at the same site. In Tennessee, 14 Tennessee Warblers (0.3% of 4,324 captures) were caught in 2 different years and one was recaptured twice. The median interval between captures was 1 year, with a maximum of 5 years for 3 individuals. All but 2 of the 14 that exhibited site fidelity were hatch-year birds when they were first recovered. At another Tennessee site, there were 0 recaptures of 5,514 captures. At a banding station in Michigan, 3 birds returned in autumn in subsequent years (0.07% of captures), and one was recaptured in 3 different years (Morris et al. 2013; Vogt et al. 2012; Winker et al. 1991).

During spring migration, the Tennessee Warbler forages predominantly in the upper half of tall trees. In autumn, it may forage in shrubs, saplings, and patches of herbaceous species, including burdocks, sunflowers, goldenrods, and ragweed. During spring migration in Illinois, it appeared to specialize in foraging on leafroller moth caterpillars. Larvae populations were similar in forest edge–shrub habitat and forest interior, and it foraged in a similar manner in both habitats. It obtained most prey on oaks and elms and, to a lesser extent, on hickories, black walnut, and honey locust. It avoided sassafras, maples, and hackberry. During autumn migration at Prince Edward Point, it fed at heights of 1.5-18 m, but mostly at 5-10 m with a peak at 7 m. It fed part of the day at heights of 17-18 m, then in the tops of saplings, and subsequently descended into shrubbery 1.0-1.5 m tall for short periods of time. Foraging substrates were 70% outer leaves, 9% twigs and inner leaves, 6% sapling foliage, 6% sapling branches, 5% air, and 3% outer branches. It was not observed foraging on inner branches, on trunks, or on the ground. During autumn migration in New York, it was suspected that the Tennessee Warbler was foraging nocturnally in an area illuminated by football-stadium lights, but this could not be confirmed (Bent 1953; Graber and Graber 1983; Keast 1980; Lebbin et al. 2007; Rimmer and McFarland 2020; T.J. Underwood and R.M. Underwood 2001).

During migration, the Tennessee Warbler is predominantly an insectivore, but opportunistically drinks nectar or eats fruit. During spring migration in Illinois, leafroller moth caterpillars constituted 19% of available prey but comprised 93% of its diet. Spring migrants in Manitoba attempted to feed on the nectar of peach-leaved willow during cold weather, but were chased away by Cape May Warblers. Three Tennessee Warblers killed at a tower near Prince Edward Point had eaten an average of 7 beetles each. The stomach of one collected in an orchard infested with cankerworms contained 80% cankerworms and 20% beetles. It has captured young locusts during autumn migration. It occasionally eats small quantities of sumac, poison ivy, tartarian honeysuckle, and other berries. It is

known to pierce the skin of grapes and drink the liquid (Bent 1953; Bowdish and Philipp 1916; Graber and Graber 1983; Keast 1980; Rimmer and McFarland 2020; Tramer and Tramer 1977).

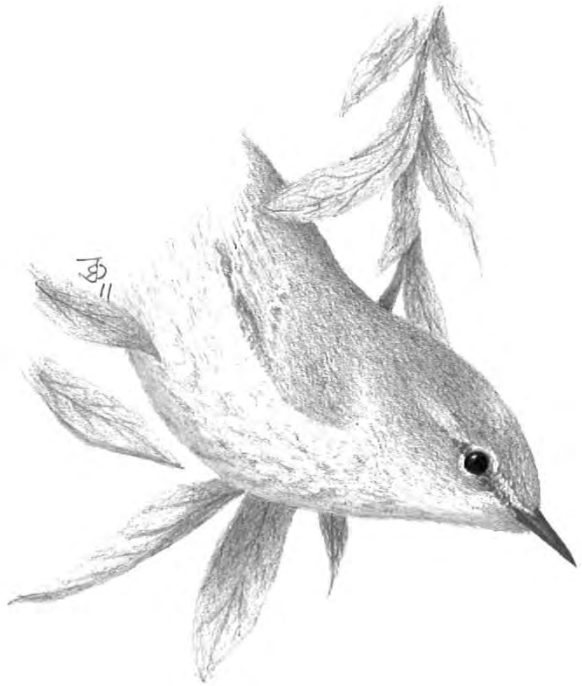
The Tennessee Warbler is a common victim at communication towers and other tall structures, particularly during autumn migration. Near Long Point, 439 were killed at 3 towers 1965-77, seventh highest of the 15 warbler species studied. At the Lennox chimneys near Kingston, 928 were killed, including 505 4-6 September 1981 (Graber et al. 1983; Rimmer and McFarland 2020; Weir 2008).

In the late 19th and very early 20th century, the Tennessee Warbler was a rare migrant in Ontario (Fleming 1907; Lancaster et al. 2004; McIlwraith 1894) but it is now common (James 1991). In Ontario, it tends to be more common during autumn than spring migration. The numbers of migrating Tennessee Warblers at a given site fluctuate considerably year to year in response to spruce budworm populations. Fluctuations are greater for this species than for any other warblers (Bent 1953; Rimmer and McFarland 2020).

Long-term monitoring data from the Long Point Bird Observatory (LPBO) indicated a nonsignificant decrease of 2.3% per year 1961-88. From 1961 to 1970, there was a decrease of 13.3% per year; from 1970 to 1979, there was an increase of 16.5% per year; and from 1979 to 1988, there was a decrease of 4.5% per year. These fluctuations coincided with spruce budworm populations (Hussell et al. 1992). More recent LPBO data indicate significant declines of 5.6% in spring between 1981-86 and 2001-06, and significant declines of 3.2% in autumn during the same periods (Venier et al. 2009). Black (2017) reported a significant increase in spring sightings of the Tennessee Warbler at the Port Weller pier 1993-2017.

Orange-crowned Warbler

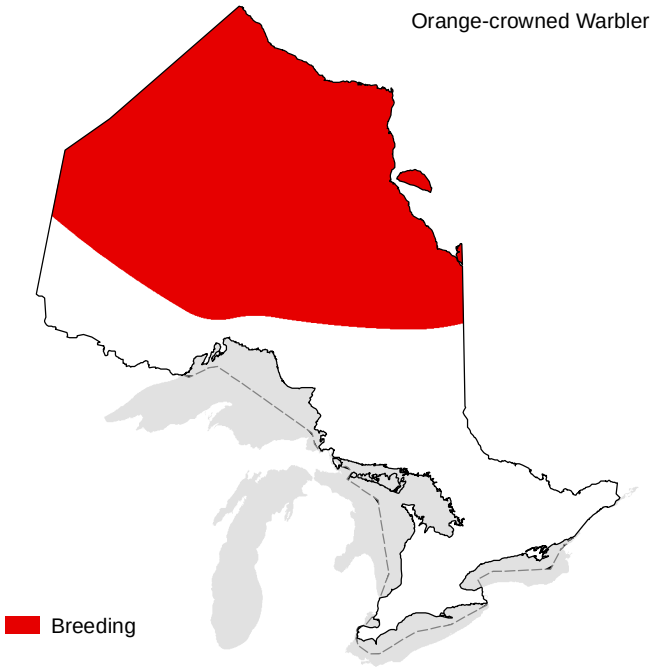
Leiothlypis celata



BREEDING SEASON

Habitat Requirements

The first Orange-crowned Warbler nest found in Ontario was in second-growth willow, poplar, and birch (Peck and James 1987). Manning (1952) collected a male during the breeding season in new growth of willow and tamarack near Moosonee. James (1980) reported it in scrub habitat near Pickle Lake. Welsh and Helleiner (in Cadman et al. 1987) stated that it preferred open woods for breeding, particularly those dominated by poplars with an understorey of shrubs such as alder, willow, beaked hazel, and mountain maple. Sutherland (in Cadman et al. 2007) reported that in the east, it breeds in open deciduous and mixed woodlands with a dense, low shrub understorey; in riparian willow, poplar, and alder thickets; in burns regenerating with willow, birch, and alder; and in other open, scrubby areas. It nests in a wide range of moisture regimes but most Ontario sites that it used were wet. In Ontario and further east, it appears to avoid pure coniferous forests. In northwestern Ontario, it was most abundant in deciduous scrub followed by coniferous scrub, coniferous forest with understorey, mixed scrub, and coniferous forest without understorey. It was absent in deciduous forest, mixed forest, heath, and tundra (McLaren and McLaren 1981).



The range of the subspecies of Orange-crowned Warbler that occurs in Ontario extends from Alaska, the Yukon, and British Columbia east of the Rocky Mountains east to southern Labrador and east-central Quebec (Gilbert et al. 2020). No detailed breeding season studies have been done on this subspecies and most available information is based on general knowledge of its habitat requirements and casual observations. Most detailed studies have been undertaken on the 3 subspecies that occur along the Pacific coast and in the western United States south to Arizona.

In Quebec, the Orange-crowned Warbler inhabits shrubby open woods, deciduous sections of mixed forests, and regenerating second growth in burns and clear-cuts. It is not associated with coniferous forests even though it is limited to the Boreal Forest Region which is dominated by conifers. It is often found in aspen stands with an understorey of shrubs such as willow and alder. It also nests in alder swamps, in alder and willow thickets along rivers, in muskeg, and in poplar–white birch stands. It also nested in a dry pine ridge, a particularly uncommon breeding habitat (Robert in Gauthier and Aubry 1996). Near Churchill, Manitoba, it was a common resident of wet brushy habitats (Jehl 2004). In Saskatchewan, it occurred mostly in mixed woods or deciduous forests but was also present in black spruce and species-poor jack pine stands. It occurred mostly in stands that were slightly wetter than average and in stands that were about mid-way between nutrient rich and nutrient poor. It was more common in younger (0-20 years) stands than 40-80-year-old stands (Kirk et al. 1996). Near Saskatoon, it nests locally on wooded hillsides (Leighton et al. 2002). In aspen forests in Alberta, Schieck et al. (1995) recorded it in young stands, but it was absent in mature and old-growth stands. In British Columbia, it nests in second-growth trembling aspen stands on south-facing slopes; on shrubby edges of aspen groves; in open balsam poplar riparian woodlands with a tall understorey of red-osier dogwood and alder; in saplings and shrubs along hydro corridors through mixed woodlands; in edges and overgrown clearings in white spruce, balsam poplar, and trembling aspen stands; in swampy areas surrounded by white spruce, willow, and alder; and subalpine areas with fir and white birch. It frequently nests on margins of coniferous forests where they meet ponds or muskeg. It is more abundant in sapling trembling aspen stands than in mature trembling aspen woodlands (Campbell et al. 2001). In the Yukon, the Orange-crowned Warbler breeds mostly in upland trembling aspen stands and in shrubby areas at the treeline and along rivers and in wetlands. It has nested in balsam poplar forests, white spruce bogs, young mixed aspen-pine forests, and mixed black spruce–white birch forests. In all these areas, it is restricted to sites with abundant shrubs. The forests it nests in are open with deciduous shrub cover (Sinclair et al. 2003). Erskine (1977) stated

that all races of this warbler frequent deciduous understorey in largely coniferous regions. Gilbert et al. (2020) summarized the habitat of the Orange-crowned Warbler in Alaska and Canada as brushy and open deciduous woodlands, shrub thickets, and edges of mixed and coniferous forests where low growth was present.

The other subspecies of the Orange-crowned Warbler also prefer shrubby areas and open forests or forest edges where there is deciduous shrub coverage. It may nest in habitats that are not available in the Boreal Forest Region such as treeless islets supporting colonies of marine birds, chaparral areas, and oak and pine forests. Some habitats are universally used by the 4 subspecies, such as alder and willow thickets, aspen stands, regenerating clear-cuts, and old burns. In Oregon, it is a common inhabitant of brushland and second-growth forest and is associated with riparian habitat to a lesser extent. In Oregon clear-cuts where the slash had been burned, it was a habitat generalist. It was equally abundant on plots where deciduous trees had been retained and where they had been removed. It showed a weak relationship with the amount of deciduous tree cover where this vegetation was available, but otherwise showed no definite pattern of habitat use. Habitat selected by singing males where deciduous trees were retained and removed were, respectively: shrub cover, 45.7% and 54.7%; coniferous cover, 8.4% and 4.8%; deciduous tree cover, 30.3% and 10.2%; and total ground cover, 84.4% and 69.7%. In many areas, it appears to select hillsides for nesting (Campbell et al. 2001; Erskine 1977; Flack 1976; Gilbert et al. 2020; Morrison 1981; Root 1967). In California, it was significantly more abundant in montane hardwoods and oak savannahs with shrubs than in oak woodlands and oak savannahs with grass (Wood et al. 2013). In Colorado, Glass and Floyd (2015) characterized the Orange-crowned Warbler as a riparian species nesting in willows, but it also nested in high-elevation aspen stands.

One Ontario nest was on the ground near fallen, moss-covered logs a short distance from a road (Peck and James 1987).

Few nests have been described for the subspecies that nests in Ontario. Three Yukon nests were on the ground, one in a willow and alder thicket swamp, one in an upland trembling aspen forest amidst soapberry and grasses, and one on a bank (Sinclair et al. 2003). In British Columbia, 81% of nests of all subspecies were on the ground sheltered by nearby vegetation; 13% were in trees and shrubs. The height of 59 nests was 0-6 m with 81% 0-0.3 m from the ground (Campbell et al. 2001). Bent (1953) described nests from Alaska that would be representative of the subspecies that occurs in Ontario. Nests were mostly on the ground but also as high as 46 cm in shrubs. Most were under a clump of willow or Labrador tea or on hillsides. One Quebec nest was located on a hillock in a peatland in a clump of Labrador tea (Robert in Gauthier and Aubry 1996).

Most other nests that have been reported are of subspecies that do not occur in Ontario. The nest is usually well concealed on or near the ground or in small crevices or depressions in the ground or rocks. Nests are often on shady hillsides, on slopes or very steep banks and sheltered by overhanging vegetation. Nests have been found in shrubs, ferns, vines, and trees, usually 0.5-1.3 m from the ground. Eighty-five percent of nests reported to the Cornell Nest Records Scheme were on the ground and 35% were on a steep bank, often along a road cut or trail. Of 28 California nests, 17 were on or adjacent to slopes greater than 60° (often nearly vertical) and the other 11 were on slopes of 30-60°. All were under a canopy of trees or shrubs, 36% were within 1 m of a hiking trail, 26 were

concealed under or within fern fronds and/or other herbaceous vegetation, and 2 were concealed in depressions in vertical banks. In California, 50 of 51 nests (98.0%) were in wooded habitat but all successful territories included open, shrubby habitat. Unusual nest sites included one in a clump of moss 2 m from the ground and 1.3 m from the trunk of a tree, one 3.2 m up in a natural tree cavity, and one in a decorative fern basket inside a bath house adjoining a California home. The ferns in the basket were watered regularly but the nest successfully fledged young. The Orange-crowned Warbler builds new nests each year and for replacement nests or second broods (Gilbert et al. 2020; Harrison 1984).

The Orange-crowned Warbler is territorial. Early arriving males may range over several potential territories before selecting one. Skirmishes with intruders may result in the resident male losing his territory prior to mating. After mating has occurred, males do not lose their entire territory, but portions of the territory may still be relinquished. Individual territory boundaries vary somewhat from year to year. Adjacent territories may share a common boundary or be separated by unoccupied habitat, but this intervening habitat is often unsuitable. Not all activities are confined to the territory. Females sometimes build the nest outside the male's territory and these males leave their territory to guard their mates and care for the young. In California, 71% of nests were within the resident male's territory and 29% were outside the territory, usually in undefended areas but 1 nest was within an adjacent male's territory. In Alaska, nests have been found as close as 6 m to each other. Birds have been seen more than 200 m from the territory. Information on territory size is limited and all data are from California. Three territories were 0.2, 0.32, and 0.7 ha in size. Two very large territories of 5.8 and 16.3 ha may have been a function of poor habitat quality (Bent 1953; Gilbert 1986; Gilbert et al. 2020).

Natal philopatry is considered low, but return rates have not been quantified. All available information is from California and these birds do not migrate far from the breeding grounds compared with northern populations which are long-distance migrants. In the subspecies restricted to an island off California, 1 fledgling was recaptured 5 years later 50 m from the original breeding site. Eight fledglings recaptured 1-5 years later were 25-200 m (average 120 m) from the banding location (Gilbert et al. 2020).

All information on adult site fidelity is from California. In the island subspecies, 3 of 5 (60%) males returned. Males are usually site faithful. Forty-seven of 59 males (79.7%) occupied the same territory as in the previous year and the other 12 occupied adjacent territories. Most adult females were not found on the same territory or even in the entire study area in the subsequent year. One female occupied the same territory in 2 consecutive years and moved to another territory 300-400 m away the following year (Gilbert et al. 2020).

Limiting Factors

Eggs are most likely to be present in Ontario nests in June (Peck and James 1987). The external portion of the nest is built in 1-2 days and another 1-2 days are required to complete the lining. The mean amount of time required to build first and replacement nests in California was 3.2 days, with a normal range of 2-5 days, but 1 nest took 6 days to complete. The first egg is usually laid 2 or 3 days after the nest is finished (range 0-4 days). Usually 1 egg is laid per day, but there was a 2-day period between successive eggs in 2 of 23 California nests. Incubation is initiated after the last egg

is laid. The incubation period is 11-14 days (mostly 11-13 days, average 12 days). A record of a 10-day incubation period is considered erroneous. All chicks hatch within 24 hours, but this is based on results from only 3 nests. The nestling period is 10-14 days (average 11-12 days). Birds that fledged from 1 nest when they were 9 days old may have been disturbed (Campbell et al. 2001; Gilbert et al. 2020; Harrison 1984).

In most of its range, the Orange-crowned Warbler raises a single brood. Birds in central coastal California may raise 2 broods per year, but a shorter nesting season probably precludes second broods further north and at higher altitudes. Renesting may occur if the first clutch is lost. Only 5-15% of birds at 1 California site initiated a replacement nest, but 10 of 27 (43.5%) did at another site. The single nest reported in Ontario contained 4 eggs. The clutch size is typically 4-5 eggs in southern populations and 4-6 eggs in more northern areas. Eighty-two percent of British Columbia nests contained 4 or 5 eggs. Clutch size declines with the season. The mean clutch size for first nests in Arizona was 4.76 eggs compared with 3.0 eggs for replacement nests (Bent 1953; Campbell et al. 2001; Gilbert et al. 2020; Peck and James 1987).

At least some birds breed in their first year. There were some unmated floating birds in California. The Orange-crowned Warbler is monogamous. At 1 nest, the female made more than 95% of the feeding deliveries to the young suggesting that she was the secondary female to a polygynous male. Polygyny has not been positively confirmed. Extra-pair copulations have not been confirmed, but intruding males have been seen within 2 m of females. Pairs that successfully fledge young remain together for the entire breeding season. In California, at least 43.5% of pairs that lost a nest remained paired for a second attempt, 21.7% of females left their mate, 4.3% of females were killed, and the fate of 30.4% of females was unknown (Gilbert et al. 2020).

In California, the Orange-crowned Warbler forages almost exclusively in overstorey twigs and foliage 2-10 m up in chaparral, thickets, and forest undergrowth. In the Great Basin of the United States, it gleans from moderate-density foliage 1.5-10 m above ground. In Oregon clear-cuts, it foraged in shrubs and deciduous trees in proportion to their availability. It was a generalist with the widest niche breadth for foraging of the 3 warbler species studied. In areas with deciduous species present and areas where deciduous species had been removed, mean foraging height was 1.7 m and 0.8 m respectively. The proportion of time spent foraging at different heights in these 2 habitats respectively was: 0-1 m, 43.8% and 86.0%; 1.1-3 m, 37.8% and 14.0%; and above 3 m, 18.5% and 0%. During the breeding season, it forages in shrubs, vines, understorey of trees, and tree canopies. It typically forages in dense green foliage but also inspects bark and outer branches. It often probes flowers and leaf clusters with its beak, and is one of the most common species seen feeding at sapsucker wells. In California, 84.9% of foraging occurred in tree foliage, 9.7% in the subcanopy, and 5.4% in the herbaceous layer. It may also search for prey among dead leaves on the ground. Foraging techniques typically involve gleaning from leaves and twigs and probing. Less frequently, it hawks for arboreal or flying insects or hovers to take non-flying insects from the undersides of leaves or the extreme periphery of the canopy (Gilbert et al. 2020; Morrison 1981; Root 1967).

All 369 food deliveries to 23 California nests consisted of insect larvae: small greenish larvae measuring 0.1 by 0.5 cm to large white larvae 0.5-1.5 cm long. Caterpillars of leafroller and geometer moths were frequently fed to nestlings. Adults feed chiefly on sedentary arthropods that are mostly

arboreal, especially insect larvae. It also consumes nectar, fruits, beetles, ants, and spiders. Most food items at 1 California site were 2.5-15 mm in length (average 10.7 mm). In another California study, prey 2.5-26.5 mm long were captured, with peaks at 4.5 mm and 14-16 mm. Sixty-five California birds consumed 91% animal material: 25% bugs, 24% caterpillars, 19% beetles, 15% hymenopterans, 7% spiders, and 1% flies. The remaining 9% consisted of seeds, fruits, leaf galls, and plant rubbish. Another California diet sample consisted of 47.8% bugs, 37.0% lepidopterans, 6.5% beetles, 4.3% hymenopterans, and 4.3% other material (Gilbert et al. 2020; Root 1967).

The breeding ranges of the Orange-crowned Warbler and Brown-headed Cowbird barely overlap in Ontario. Cowbird parasitism of this warbler is likely rare or nonexistent in the province. Overall, the Orange-crowned Warbler is a rare host of the cowbird. One Saskatchewan nest contained 2 eggs of both species and another nest contained 2 large cowbird nestlings. In British Columbia, 4% of 118 nests were parasitized. In addition, 8 fledgling cowbirds from 7 nests were observed being fed by Orange-crowned Warbler adults. In Montana, 2 of 6 nests were parasitized (Campbell et al. 2001; Gilbert et al. 2020; Leighton et al. 2002).

The Orange-crowned Warbler tends to benefit from forest fires and forest management that opens up the canopy and creates large areas of deciduous regeneration. A review of several studies on the effects of partial timber harvesting found that it increased in response to removal of 30%, 50%, and 70% of tree cover. In Alaska, it increased when spruce beetles caused tree mortality. Densities in areas of high spruce mortality were more than 6-fold higher than in areas of low mortality and significantly higher than in areas with low or moderate mortality. Stands with high mortality had significantly higher densities of alder and crowberry in the understorey (Gilbert et al. 2020; Matsuoka et al. 2001; Robert in Gauthier and Aubry 1996; Vanderwel et al. 2009).

In Alberta, the Orange-crowned Warbler was significantly more abundant at pipelines and well pads than in forest interior adjacent to these features. There was no difference in its abundance at seismic lines and adjacent forest interior (Bayne et al. 2016).

In eastern Quebec and Labrador, the Orange-crowned Warbler occurred mostly in drier forest stands. This suggests that it may not be very sensitive to climate change in this region (DesGranges and LeBlanc 2012). Yoon et al. (2017) compared female brooding and male nestling provisioning in Alaska and California to determine if climate affected these activities. In Alaska, males made the majority of food deliveries which allowed females more time for brooding. In California, the sexes contributed equally to food provisioning. The proportion of time that females spent brooding was significantly higher in Alaska than California, but there was no relationship between ambient temperature and the amount of time spent brooding.

Status

Around the turn of the 20th century, the Orange-crowned Warbler was not known to breed in Ontario. McIlwraith (1894) had only 2 records of migrants from Hamilton and reported another sighting from London. Forbush and May (1939) and Chapman (1907) reported that its range extended eastward only to Manitoba. It is uncertain if it was initially absent from Ontario eastward or if it had previously been overlooked. The Orange-crowned Warbler was first confirmed breeding in Ontario when a nest was found at Favourable Lake in 1938, and breeding was confirmed at Lake Attawapiskat and Moosonee the following year. By 1960, it was known to occur during the breeding

season from the Dryden to Lake Nipigon area northward (Baillie 1960). A nest reported near Madoc in 1906, considerably south of its known range, was likely an error. During the first atlas, it probably bred in almost every block north of latitude 50°N, but was concentrated north of latitude 52°N in the Hudson Bay Lowland and northwest portion of the Boreal Forest Region. Distribution within this area was spotty and it appeared to be most common in the northwestern portion of the province (Welsh and Helleiner in Cadman et al. 1987). James (1991) considered it an uncommon summer resident in the northern third of the province and rare and local south to Kenora and Timmins.

The second atlas demonstrated that there had been no change in the distribution of the Orange-crowned Warbler since the first atlas. It was reported from most blocks north of latitude 51°N, with scattered records south to Timmins and the south end of Lake Nipigon. Distribution at these southern locations was discontinuous and local in nature and may represent transitory breeding events or unmated singing males. Its probability of observation increased significantly from the first to second atlas due to a 100% increase within the Hudson Bay Lowland. It was uncertain if this represented an actual increase in population or was an artifact of better coverage by atlassers who were more familiar with its song than investigators that participated in the first atlas. It was most abundant in the northern portion of the Hudson Bay Lowland. Highest densities occurred along portions of the Severn, Winisk, Ekwan, and Moose rivers, corresponding with extensive areas of preferred habitat of aspen-willow riparian thickets and woodland habitat. Its abundance may be underestimated due to the similarity of its song to other more common species and because it sings infrequently (Sutherland in Cadman et al. 2007).

The Orange-crowned Warbler is most abundant in British Columbia and the west coast of the United States. The western races are common and it is often the most abundant warbler in some areas. The eastern population is relatively rare. The Breeding Bird Survey determined that it experienced annual increases of 0.231% in Canada and 1.04% in Ontario 1970-2021. The trends 2011-21 were an annual decrease of 1.05% in Canada and an annual increase of 0.0259% in Ontario. The Canadian trends were of medium reliability and the Ontario trends were of low reliability (Erskine 1977; Gilbert et al. 2020; A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Recently fledged young remain in low vegetation for an undetermined amount of time and later follow the adults in the lower canopy. Broods remain together in small groups and in some areas join other such groups to form larger flocks. These flocks forage independently of the adults. Riparian areas appear to be used as movement corridors by young after they fledge. At least some males vacate their territories shortly after the young fledge. This is followed by a period of vagrancy, with adults wandering in riparian habitat or upslope to high elevations. The period of vagrancy merges imperceptibly into migration (Gilbert et al. 2020).

MIGRATION

The Orange-crowned Warbler is presumably a nocturnal migrant judging by kills at towers. Northern populations are migratory but those breeding in California may move only short distances in autumn and winter. It migrates either singly or in small groups of 2-3 individuals. At migration stopover sites, it may join mixed flocks of chickadees and other warbler species (Bent 1953; Chapman 1907; Gilbert et al. 2020).

The Orange-crowned Warbler may migrate earlier in spring and later in autumn than many warblers because of its partly vegetarian diet and its probing foraging habit that facilitates capture of concealed prey (Gilbert et al. 2020). In southern Ontario, it usually arrives in early May, with some arriving in late April, and all leave by the end of May (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). In the southern Shield, it occurs from mid- to late May (Mills 1981; Tozer 2012). During spring migration in California, males arrived significantly earlier than females (Otahal 1994).

Autumn departure periods from the breeding grounds are not clearly defined. Dispersal or migration is initiated when arthropod abundance dwindles due to cold or drought (Gilbert et al. 2020). At Shagamu, Wilson and McRae (1993) concluded that birds seen 11-17 July may have been autumn migrants or previously undetected breeders. It is also possible that these birds had dispersed from their breeding areas during the postfledging period. Birds were observed at Shagamu into September. In the southern Shield, autumn migrants usually occur from mid-September to mid-October, but some may arrive in mid-August (Mills 1981; Tozer 2012). In southern Ontario, average arrival is in mid-September and average departure is mid- to late October. Migrants may arrive in late August and some rarely remain into November, December, or January (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). One was observed in Port Colborne from 1 December to 31 March (Black and Roy 2010). James (1991) considered the Orange-crowned Warbler a winter vagrant in Ontario, but it is unknown if any birds have successfully overwintered. During autumn migration in South Dakota, there were no differences in the median arrival dates of juveniles and adults (Dean et al. 2004).

During spring migration, the Orange-crowned Warbler prefers habitats similar to those that are selected for breeding. It prefers deciduous shrub thickets and forest edge habitats where there are tangles of vines, raspberries, and roses along with riparian alder and willow thickets. It may also occur in deciduous forests, particularly those with an open canopy and dense woody undergrowth. Young stands of trembling aspen may provide suitable habitat and those on slopes appear to be preferred. In New Jersey, it is a rare spring migrant in pine swamps. During spring migration at Point Pelee, 80% of foraging by 4 individuals was on the ground in thickets and 20% was 0.6-1.8 m above ground in low shrubs. During both spring and autumn migration, it may occur in more anthropogenic habitats such as urban parks and gardens, treed areas within urban areas, and orchards. During autumn migration, it is much less likely to occur in forested habitat. Preferred habitat at this time includes meadows dominated by goldenrods and other dense tall herbaceous species, shrubby areas, and overgrown forest-edge ecotones. In autumn in Illinois, it was detected almost exclusively in forest-edge habitats. In South Dakota, it was equally abundant in riparian woodland and an isolated woodlot. These studies did not examine goldenrod meadows, where it is most abundant in Ontario in autumn (Bairlein 1992; Bent 1953; Brush 1987; Campbell et al. 2001; Carlisle et al. 2012; Curry 2006; Dean et al. 2004; Fitch 1958; Gilbert et al. 2020; Graber et al. 1983; Keast 1980; Kelly et al. 2000; Leighton et al. 2002; Tozer 2012).

Dead leaves suspended above ground in dense undergrowth and vines were an important foraging substrate in Louisiana and they were essential to the winter presence of Orange-crowned Warblers. Of 200 records of substrates searched for prey by this warbler, 73% were dead leaves, 15%

were green leaves, 9% were branches, 2% were moss, and 3% miscellaneous. It also fed on nectar and sugar water in hummingbird feeders (Remsen et al. 1989). Although it is a winter vagrant in Ontario, suspended dead leaves may still be an important foraging substrate in late autumn.

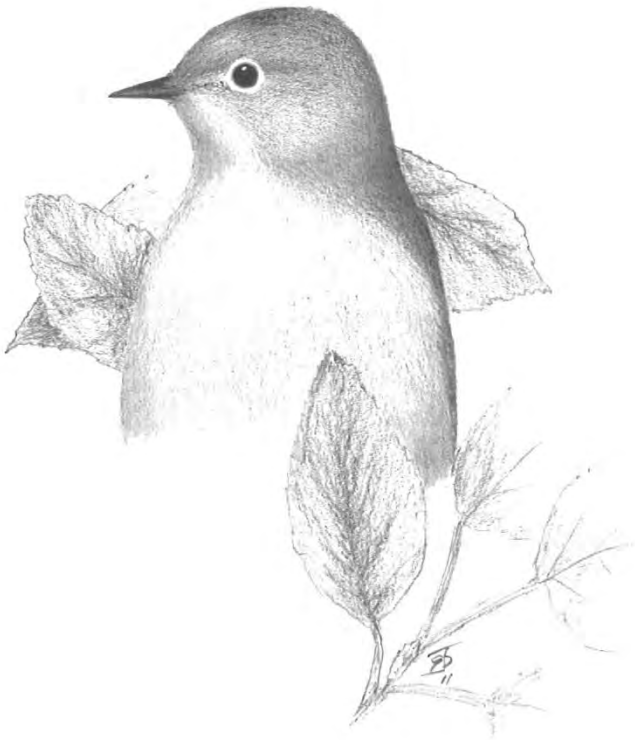
Carlisle et al. (2012) studied the diet of the Orange-crowned Warbler during autumn migration in Idaho. Prey consumed in greater proportion than its availability included spiders, bugs, stink bugs, leafhoppers, jumping plant lice, beetles, lepidopterans, and larvae. Stilt bugs, hymenopterans, ants, yellowjackets, moths, and flies were consumed proportionately less than their availability.

The Orange-crowned Warbler is occasionally killed during migration at television towers and other tall structures (Gilbert et al. 2020; Graber et al. 1983). Weir (2008) reported 1 spring and 10 autumn mortalities at the Lennox generating station chimneys.

The Orange-crowned Warbler is a rare migrant in Ontario and eastward (Chapman 1907; James 1991; Robert in Gauthier and Aubry 1996). McIlwraith (1894) considered it a straggler during migration and was aware of only 3 records for the province. It is now a regular but rare migrant that may be slightly more common in autumn than spring, possibly due to the longer duration of the migration period. Banding studies indicate that it is under-reported and many pass through without being detected. During autumn in Hamilton, a systematic search in goldenrod patches yielded a high count of 28. In other areas of the province, the Orange-crowned Warbler is either rare during both migration periods or rare in spring and uncommon in autumn (Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

Nashville Warbler

Leiothlypis ruficapilla



BREEDING SEASON

Habitat Requirements

In Ontario, the Nashville Warbler has nested in or at edges of mixed (34.3% of nests), coniferous (25.7%), and deciduous (7.1%) woods; in coniferous and open bogs (21.4%); and in open, grassy or rocky areas with scattered trees (11.4%). Wooded areas used for nesting were more often open than dense and most nest sites were in clearings or at forest edges. It selected wet and dry sites almost equally. Nesting habitat was characterized by dense ground cover. The types of cover used in order of preference were ferns (usually bracken), grasses and sedges, mosses and clubmosses, blueberries and raspberries, Labrador tea and sheep laurel, and various long-stemmed vascular plants. Thirteen nests were on slopes or hillsides (Peck and James 1987). James (1984b) reported that it was associated predominantly with mixed forests but that it also inhabited coniferous and deciduous woods. Some tree growth is necessary, but it prefers scattered trees and open forests or edges and openings where deciduous shrubs or saplings are abundant. Trees within nesting territories may be half grown to mature heights and are usually in drier and often rocky sites, but may also be at edges of bogs or fens.

In the Boreal Forest Region of Ontario from Pickle Lake northward to the Manitoba border, the Nashville Warbler was most abundant in deciduous scrub, followed by mixed scrub, coniferous forest lacking understorey, and coniferous forest with understorey. It was rare in deciduous forest and absent in coniferous scrub, heath, and tundra (McLaren and McLaren 1981). Near Pickle Lake, James (1980) observed it regularly in small numbers in open coniferous and mixed woods. North of Lake Superior, highest densities occurred in black spruce forests with slightly lower densities in black spruce–balsam fir stands (Keast 1980). In the same area, Baillie and Hope (1943) found it in a variety of habitats, but it was particularly abundant in a large spruce bog. In Quetico Park, it was common in young (1-23 years) and intermediate-aged stands (67-73 years), but absent in mature (112-176 years) and old-growth (367-370 years) stands (Apfelbaum and Haney 1985). Near White River, it was significantly associated with stands that were 23-25 years old after clear-cutting. Other age-class groups in their study area were 3-5 years, 8-10 years, 13-15 years, 18-20 years, and 40-100 years (Venier and Pearce 2005). Near Manitouwadge in black spruce, balsam fir, and aspen stands, densities were lowest in stands 24-36 years old, 2.7 times higher in stands 60-223 years old, and 6.5 times higher in stands 1-21 years old (Venier et al. 2009). Near Hearst, it inhabited uncut and clear-cut upland mixed stands and lowland coniferous stands. It occurred in clear-cuts as young as 3-5 years. Highest densities occurred in lower-slope mixed stands and lowland coniferous stands 9-24 years old. Densities in uncut upland mixed stands were 3 times those in uncut coniferous stands (Welsh and Fillman 1980). In the Clay Belt, it was associated with wetter, nutrient-poor stands. It was most common in jack pine stands followed by those dominated by black spruce, tamarack and white cedar, trembling aspen, and white spruce–white birch (Welsh and Lougheed 1987).

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Nashville Warbler occurred in both mature and old-growth white pine stands. It was more common in old-growth stands, but not significantly (Kirk et al. 2012). Near Gogama, it was one of the most abundant species in managed jack pine stands and almost as numerous in mixed forests where pine constituted at least half the mix. It began to colonize areas once trees were 5-6 m tall and reached maximum densities where trees were 10-12 m tall. Trees in territories were dense and uniformly spaced, but there was typically one and often several openings present where sunlight reached the forest floor and promoted growth of tall shrubs and saplings. Near nest sites, the ground was densely covered with sedges growing among blueberries and sheep laurel (James and Peck 1995a). The Nashville Warbler was common in jack pine stands near Parry Sound. The stands were young with open

canopies and contained a variety of deciduous tree species (James 1979a). One territory near Pimisi Bay contained both upland mixed forest and thicket habitat. The thicket was a gently sloping, dry sandy plateau overgrown with aspen, white birch, and red maple saplings with occasional tall balsam fir, white pine, and red pine. The forest had a dense undergrowth of shrubs including beaked hazel, raspberries, and willows, and numerous windfalls were present (Lawrence 1948). In Algonquin Park, it was common in tamarack and spruce swamps and in birch trees around margins of swamps (MacLulich 1938). In Algonquin Park, Knapton (1984c) summarized the habitat of the Nashville Warbler as mixed coniferous and deciduous woodlands containing open areas covered by low shrubs (primarily blueberries), ferns, and forbs. Tozer (2012) noted that it thrives in Algonquin Park in bogs with scattered small black spruce. In Algonquin Park, it was tied for third in abundance in scrub black spruce forest. It was second in abundance in a black spruce–white cedar forest. It was not detected in bogs, immature white pine stands, or hardwoods. In black spruce–white cedar, territories extended from the ground to the top of the cedars (0-12.2 m). In aspen–white birch stands, territories extended from the ground to the top of the canopy (0-8.8 m). In hemlock stands, territories ranged from the ground to about 3 m above the bottom of the canopy (0-8.8 m; Martin 1960).

South of the Shield in the Kingston area, McLeish and Robertson (1997) concluded that upland white cedar stands could provide quality breeding habitat. In the Hamilton area, the Nashville Warbler breeds in cedar swamps and in upland scrub cedars on limestone plains in Flamborough Township (Curry 2006). It breeds in white cedar–white spruce–black spruce swamps in Halton Region (personal observation). In Durham Region, it occurred in a black spruce bog (where it was most abundant), sugar maple and sugar maple–oak stands, and a coniferous forest of white cedar, balsam fir, and spruce. All forested stands where it occurred had open canopies and heavy growths of shrubs, tree seedlings, or ferns. Speirs and Orenstein (1975) considered it a mid-successional species. In southern Ontario, its abundance was positively correlated with the amount of forest cover 100 m from edge, woodlot size, the amount of forest cover within 2 km, and the amount of regional forest cover. These relationships were not significant (Austen et al. 2001).

The Nashville Warbler is represented by 2 disjunct populations that are currently considered subspecies. The western subspecies breeds in southern British Columbia and southward along the western coast. The other subspecies ranges from Saskatchewan eastward to the Quebec Atlantic coast and south from Minnesota through New England (Lowther and Williams 2020). The structure of the habitats used by the 2 subspecies is similar although they are associated with different habitat types. Most of the information presented below is associated with the subspecies that occurs in Ontario.

Erskine (1977) considered the Nashville Warbler one of the most typical bird species of the Boreal Forest Region, especially in spruce stands but also in forests dominated by balsam fir. It is frequently found in tamarack and bog forests where it is one of the dominant species. It is characteristic of edge habitats and is associated with openings supporting young deciduous growth, often in aspen–white birch forests. The first record of breeding in Saskatchewan consisted of a pair nesting in a large area of willows bordered by pine-aspen woodland (Lein and Wagner 1982). Also in Saskatchewan and the western Boreal Forest Region, it was in a guild associated with predominantly

coniferous species. It was found mostly in stands that were drier than average with below average nutrient levels. Kirk et al. (1996) recorded it only in stands 15-20 years old and not in stands 0-9, 40, or 80 years old. It nested in mixed and coniferous forests in Quebec and, to a lesser extent, in deciduous forests. It frequented clearings and young immature stands where it was associated mostly with forest edges and regenerating second growth dominated by trembling aspen, white birch, and balsam fir. In the northern part of its range in Quebec, it inhabits peatlands with a scattering of trees such as spruce and tamarack (Falardeau in Gauthier and Aubry 1996). In Quebec, it was equally abundant in riparian and nonriparian stands, although it tended to be more abundant in nonriparian areas. It nested in balsam fir–yellow birch, balsam fir–white cedar, and black spruce stands on sites ranging from dry upper slopes to wet organic depressions (LaRue et al. 1995). In black spruce stands in Quebec, it was associated with early to mid-successional stages. It occurred in recently logged areas where vegetation was less than 2 m tall but not in similarly aged burns. It was present in cuts and burns where saplings were 2-5 m tall and 5-11 m tall, but was absent in more mature stands where trees were taller than 11 m (Imbeau et al. 1999).

Habitat used by the Nashville Warbler in the central and eastern United States is similar to that reported for Saskatchewan and eastward in Canada. It nests in a variety of habitats but is associated with forest edges, forest openings and clearings dominated by deciduous shrubs and saplings, overgrown meadows and pastures, and bogs and fens with scattered trees or dense shrubs. It appears to show no preference for moisture regime. On average, it nests in nutrient-poor habitats but may nest in the entire range of nutrient levels. Presence of open areas with shrubs, saplings, or dense coverage of ferns appears to be essential in breeding territories. It is an early to mid-successional species. Habitats it uses in the north-central and northeastern United States include steep slopes overgrown with birches and other woody species, mesic climax oak-maple-hickory forests with dense undergrowth, willow and alder thickets, recent burns and clear-cuts, northern hardwoods, mixed aspen and conifer stands, trembling aspen–white birch regeneration, spruce bogs and white cedar fens, shrubby fields, tamarack swamps, bogs with sphagnum and Labrador tea, jack pine stands, thickets along streams and water bodies, open oak woodlands, fields overgrown with red cedar and dense stands of gray birch, occasionally in hemlock stands, red and white pine stands, pine barrens, occasionally in coniferous plantations, among coniferous saplings in pole-size coniferous or mixed forests, and in a variety of upland and lowland coniferous and mixed forests. It selected similar habitats in Minnesota and Maine, where it was a shrub–forest edge species. In the western portion of its range in California, it was equally abundant in savannahs with grass cover, savannahs with shrubs, montane hardwoods, and oak woodlands (Back 1979; Beals 1960; Bent 1953; Bielefeldt and Rosenfield 1994; Capen 1979; Chapman 1907; Collins 1983a; Collins et al. 1982; Crawford and Titterington 1979; Dawson 1979; Freedman and Johnson 1999; Freemark and Collins 1992; Gates and Giffen 1991; Graber et al. 1983; Harrison 1984; Hoffman 1989a; Keast 1980; Lowther and Williams 2020; Mossman et al. 1991; Noon et al. 1979; Sodhi and Paszkowski 1975; Taylor and Taylor 1979; Temple et al. 1979; Wood et al. 2013).

Several studies examined microhabitat preferences of the Nashville Warbler. In New Hampshire and Maine, its abundance was positively correlated with the number of deciduous trees 2-10 cm diameter at breast height (DBH) and the number of woody stems per ha. It was negatively correlated with canopy closure and the total foliage volume of deciduous trees 2-10 cm DBH (DeGraaf et al.

1998). In Vermont, its habitat consisted of dense vegetation less than 3 m tall with no overhead canopy and it was found in recent clear-cuts where herbaceous vegetation was less than 1 m tall. It was associated with a dense understorey and more with clear-cuts than forests. Average habitat variables included 75.0% green ground cover, 67% ground coverage by slash, 49.7% canopy closure, 7.6 m canopy height, 6.2 m canopy depth, 33.9% vegetation density at 0-0.7 m, 33.3% vegetation density at 0.8-1.4 m, 74.1% vegetation density at 1.5-3.0 m, 5.7 m^2 basal area of deciduous trees, 1.4 m^2 basal area of coniferous trees, 6.0 cm DBH for deciduous trees, 5.5 cm DBH for coniferous trees, and 5.6 snags per 0.08 ha (Thompson and Capen 1988). In Minnesota, it inhabited areas with dense coverage by mosses and grasses were usually present, providing a high percentage of ground cover. Average habitat characteristics were 81.1% ground coverage, 53.9% shrub coverage, 59.4% canopy closure, 14.8 m canopy height, 36.7% coniferous coverage, 4.2 tree species per 0.04-ha circle, 16.5 trees 7.5-15 cm DBH per circle, 10.5 trees 15.1-23 cm DBH per circle, 4.5 trees 23.1-30 cm DBH per circle, 2.1 trees 30.1-38 cm DBH per circle, 1.1 trees 38.1-53 cm DBH per circle, 0.1 tree 53.1-68 cm DBH per circle, and 0.2 tree larger than 68 cm DBH per circle (Collins et al. 1982). Vegetation around a nest in Ohio was not dense and was dominated by raspberries and grasses and, to a lesser extent, goldenrods. Other species present included hawkweeds, milkweed, cinquefoils, selfheal, common buckthorn, and a variety of mosses. Shrubs present included northern arrowwood, common hawthorn, and other hawthorns. White ash and red maple were present, saplings 2-5 m tall included red oak and white ash, and there was a nearby stand of cottonwoods. The most prominent tree species near the nest were 1-5-m tall planted blue spruce. The site was best characterized as old-field habitat progressing from field to pioneer scrub and trees (Kotesovec and Zadar 1996). Collins (1981) found no significant differences in the vegetation at nest sites and singing perches in Minnesota. At a macro scale in Michigan, its abundance was positively correlated with the amount of area covered by jack pine, the amount of lowland shrub thickets, mixed and pure red pine, and upland mixed forests (Crozier and Niemi 2003).

Some authors placed the Nashville Warbler into guilds. Based on foraging habitat preferences and techniques, Sabo (1980) placed the Nashville Warbler into a guild that included high-elevation ground foragers, deciduous tree users, lowland foragers, and those that used coniferous trees. In the northeastern United States, Niemi and Pfannmuller (1979) placed it in a guild of species that were abundant in young plantations and disturbed shrubby areas; very common in aspen regeneration and alder thickets; common in recent clear-cuts and mature coniferous lowlands; and uncommon in mature deciduous upland forests, mature coniferous upland forests, and grasslands. In Maryland, Gates and Giffen (1991) included the Nashville Warbler in the hemlock-bottomland group. In Vermont, Thompson and Capen (1988) placed the Nashville Warbler in the open-canopy association. The large number of species that the Nashville Warbler has been associated with demonstrates that it is a habitat generalist in open shrubby areas, in young forests, and in edges and openings of more mature forests.

In Ontario, the Nashville Warbler is not considered an area sensitive species (Coleman et al. 2000; James 1984b). In Wisconsin, it was not restricted to larger islands, so it did not exhibit area sensitivity (Beals 1960). Near Quebec City, territories were significantly clustered at scales of 250, 450, and 550 m. Of the species that they studied, it was most associated with forest cover, with a mean of 63.1%

forest cover near occupied areas. Bourque and Desrochers (2006) concluded that a decrease in forest size might have a negative effect on its distribution or fecundity.

Almost all Ontario nests were on the ground. One was 0.9 m from the ground in the upturned roots of a fallen hemlock, one was in a clump of sedges 0.5 m from the ground, and another was in a clump of grasses 0.3 m from the ground. Nests were in hollows in moss hummocks or in moss on the ground (66.1% of nests), in clubmosses (10.7%), in grasses (8.9%), in ferns and blueberries (8.9%), in dead leaves (3.6%), and in a small depression in a rock (1.8%). Many nests were at the base of a small tree, stump, or shrub, or were under or beside logs. Many were well concealed by overhanging bracken ferns, tree branches, grasses and forbs, shrubs, and dead leaves (Peck and James 1987). A nest near Pimisi Bay was in an open area but well hidden under a cluster of dead bracken fern fronds (Lawrence 1948).

Most publications state that the nest is always on the ground or slightly sunken into a depression, but occasionally they are on raised hummocks. The Ontario nest in upturned tree roots appears to be the only record of a truly elevated nest. Nests are frequently on hillsides, including road cuts, and they are often at the base of a tree or shrub. They are often in disturbed areas and may be adjacent to woodland trails. Nests are usually well concealed under ferns, grasses, blueberries, clubmosses, bunchberry, or wildflowers (Bent 1953; Campbell et al. 2001; Chapman 1907; Harrison 1984; Kotesovec and Zadar 1996; Lowther and Williams 2020).

The Nashville Warbler is territorial, but it has not been determined if all activities take place in the territory. Near Lake Nipigon, 7 territories averaged 1.09 ha (range 0.5-2.4 ha). Only 3-7 records per bird were obtained, so territories may have been larger (Kendeigh 1947). In Algonquin Park, the average territory size was 0.37 ha (range 0.02-2.39 ha). In most forest types, it ranged from the ground to the top of trees, but in some stands it was not observed above 9 m where it usually occupied conifers (Martin 1960). A single territory near Pimisi Bay was 0.2 ha. It stretched into a mixed forest but the nest was in the opposite corner of the territory in a more open area (Lawrence 1948). In subalpine areas of New Hampshire, the average territory size was 1.1 ha (Sabo 1980). In Maine spruce forests, territory size was 2.22 ha (Morse 1977).

No information appears to be available on natal philopatry (although it is probably low) or adult site fidelity.

Limiting Factors

Eggs have been found in Ontario nests from the last week of May until the third week of July, with most present in the first half of June (Peck and James 1987). In Algonquin Park, eggs are present from late May to mid-July, nestlings are present from early June to mid-July, and dependent fledglings have been observed from late June to late July (Tozer 2012).

Nest building begins soon after the birds arrive. The female constructs the nest over a period of 7-9 days. It is unknown if time elapses between nest completion and the initiation of egg laying. One egg is laid per day. The incubation period for 7 Ontario nests was at least 10 days at 4 nests, 11 days at 1 nest, and at least 11 days at 2 nests. Elsewhere, the incubation period has been reported as 11-12 days. Near Pimisi Bay, 2 young left the nest at age 8 days and one left when it was 7 days old. This nest contained a young cowbird; it was unknown if this affected the timing of fledging. In

other areas, young fledge at age 9-11 days (Bent 1953; Lawrence 1948; Lowther and Williams 2020; Peck and James 1987).

Only a single brood is raised. There are no records of second broods. Clutches in Ontario contained 3-7 eggs, with 88.3% of clutches containing 4 or 5 eggs (mean 4.38 eggs). Only single clutches with 6 or 7 eggs were reported. In Algonquin Park, 6 nests contained 4 young and 5 nests contained 5 young. In Illinois, the clutch size was 4-6 eggs (average 5 eggs). The mean clutch size of 14 Michigan nests was 4.71 eggs. The Nashville Warbler typically lays 4 or 5 eggs and less frequently 3 or 6 eggs. The Ontario nest containing 7 eggs is the only record of a clutch this large. Three-egg clutches may be incomplete or late clutches (Bent 1953; Graber et al. 1983; Harrison 1984; Knapton 1984c; Lowther and Williams 2020; Peck and James 1987).

No information is available on the age at first breeding, but it is probably 1 year. The Nashville Warbler is presumed to be monogamous. There are no records of polygyny (Lowther and Williams 2020).

The foraging techniques of the Nashville Warbler are very similar to those of the Tennessee, Orange-crowned, Golden-winged, and Blue-winged warblers. Consequently, only one of these species typically occupies a habitat. The Nashville Warbler is the common species of this group in young deciduous-growth forests and has minimal contact with the spruce-fir species (Morse 1989). It concentrates on foraging at the tips of branches and the western population is specialized for foraging among the needles and twigs of conifers. It often forages from unstable substrates such as leaves at the tips of twigs, in tassels of flowering trees, and on the undersides of leaves, particularly those of deciduous trees. It is in a guild with the Black-capped and Boreal chickadees for its general foraging techniques (Bock and Lynch 1970; Crawford and Jennings 1989; Lowther and Williams 2020; Morse 1989). In Quebec, LaRue et al. (1998) placed it in the shrub-foraging guild. It occasionally captures flying insects on the wing, but does not habitually flycatch. Adults capture insects on trunks, branches, and leaves of trees and shrubs, working their way up from the bottom to the top. Foraging occurs mostly in the lower storey of open woodlands and more often in low trees and shrubs around the periphery of forests (Bent 1953; Falardeau in Gauthier and Aubry 1996; Lowther and Williams 2020). In Ontario, foraging occurred 72% of the time in deciduous trees and 28% of the time in conifers on average at 72% of the tree height. Eighty-two percent of foraging occurred in foliage, and 16% of prey attacks were aerial. It captured prey in foliage by hanging upside-down 8.0% of the time and hovering 5.9% of the time. Gleaning represented the remainder of the foraging techniques (Greenberg et al. 1999). In central Ontario, it foraged mostly in white birch stands. During the breeding season, it exploited tree species more universally than during migration. Foraging heights during the breeding season were 5-15 m compared with 3-14 m during autumn migration. Unlike other species, the Nashville Warbler exhibited a greater tendency for gleaning and clinging-probing (Mills 2007). In Wisconsin, Sodhi and Paszkowski (1995) examined the habitat use and foraging strategies of the Nashville, Mourning, Chestnut-sided, and Canada warblers. The Nashville Warbler was distinctive from the other species because of its use of overstorey created by mature birch and aspen. Males foraged more frequently (54% of the time) in deciduous trees than other species. Males foraged 36% of the time in aspens, 7% in shrubs, and 4% in conifers. Females also foraged more frequently in hardwoods (57% of the time), followed by 18% in aspens, 18% in conifers,

and 6% in shrubs. Average foraging heights were 8.22 m for males (range 1.3-13.0 m) and 4.49 m for females (range 1.7-11.7 m). Both sexes foraged higher than their counterparts of other species. Substrates used by males consisted of 45% branches, 41% twigs and leaves, 4% limbs and trunks, and 7% air. Female substrate use was 67% branches, 23% twigs and leaves, 4% limbs and trunks, and 8% air. Males used twigs and leaves more than any other species. Foraging techniques used by males were 91% gleaning, 3% pouncing, 3% hovering, and 3% sallying. Females foraged by gleaning 83% of the time and pouncing 17%. Males gleaned more than males of other species. Females were more similar in their foraging habits to females of the other 3 species than they were to male Nashville Warblers. In subalpine areas of New Hampshire, foraging techniques included 57.5% leaf gleaning, 15.6% leaf hawking, 15.6% twig gleaning, 5.4% leaf hovering, 3.2% twig hawking and hovering, and 1.1% branch gleaning. Substrates used for foraging were 68.8% near the trunk and 31.2% distant from the trunk: 55% occurred on deciduous foliage and 45% on conifers. It was not observed feeding on herbaceous cover or the forest floor. Foraging heights were 43.6% at 5-8 m, 37.9% at 2-5 m, 10.0% above 8 m, and 8.5% at 0.1-2 m. The Nashville Warbler and Purple Finch used leaf gleaning the most of the species studied (Sabo 1980).

At 11 nests in Algonquin Park, the most frequent size of caterpillar delivered to nestlings was 2.5 cm long followed in decreasing frequency by larvae 2, 3, 1.5, 3.5, and 4 cm long. Prey size increased with nestling age, with 4- and 5-day olds receiving proportionately more larvae 1.5 and 2 cm long with older nestlings receiving more larvae 3-4 cm in length. Caterpillars comprised 89% of prey items delivered to nestlings. The remaining 11% of prey items consisted of adult flies, spiders, adult beetles, and unidentified insects (Knapton 1984c). Other authors observed that nestlings are fed predominantly caterpillars, especially those of geometer or owlet moths, and grubs, small beetles, flies, and other insects. Adults have been observed feeding fledglings caterpillars (Bent 1953; Harrison 1984; Lawrence 1948; Lowther and Williams 2020).

Except for spiders, adult Nashville Warblers are almost exclusively insectivorous, and caterpillars constitute a high proportion of its diet. It also consumes flies, young grasshoppers and locusts, leafhoppers, plant lice, and small wood-boring beetles (Bent 1953; Lowther and Williams 2020). The diet of 7 adults during the breeding season near Lake Nipigon consisted of 35.9% lepidopterans, 25.1% spiders, 17.2% soft-winged bugs (mostly aphids), 12.0% beetles (weevils and soldier, leaf, and click beetles), 5.9% hymenopterans, including ichneumonid wasps and sawflies, and 3.8% true bugs. It consumed more caterpillars (35.9% of the diet) than any other species. Caterpillars constituted an average of 22.3% of the overall diet for all species studied (Kendeigh 1947). Crawford and Jennings (1989) studied its response to a spruce budworm outbreak in New Hampshire spruce–balsam fir stands. They found an average of 3.5 budworms in 70 stomachs. It initially increased its budworm consumption and maximized consumption at the midpoint of availability in late June and early July and later decreased consumption of large larvae and pupae. This relationship was significant only for the Nashville Warbler and Boreal Chickadee. The Nashville Warbler exhibited no change in abundance in response to increasing budworm numbers, but it is possible that it could have increased over a period of several years. In the Manitouwadge area, Venier et al. (2009) observed no response in its numbers to spruce budworm populations. Mitchell (1952) examined the contents of 14 stomachs during a spruce budworm outbreak in Maine. In the year when budworms were

scarce, none were eaten. In the following year when budworms were abundant, 55% of the diet by volume consisted of budworm larvae and pupae.

The Nashville Warbler is an uncommon host of the Brown-headed Cowbird. Parasitized nests often fledge both warblers and cowbirds, but it is unknown what effects parasitism has on the warbler's brood size and fledging success rate. At a parasitized nest near Pimisi Bay, 1 warbler egg disappeared from the nest but the remaining warblers and cowbird all fledged. In Ontario, 10 of 93 nests (10.8%) were parasitized. In Quebec, 6 of 83 nests (7.2%) were parasitized. In British Columbia, 2 of 16 nests (12.5%) were parasitized and in 2 cases, adults were seen feeding cowbird fledglings. In New England, 1 of 14 nests (7.1%) was parasitized. Two of 8 Michigan nests (25%) were parasitized (Campbell et al. 2001; Harrison 1984; Lawrence 1948; Lowther and Williams 2020; Peck and James 1998a).

The Nashville Warbler is one of the warblers that benefitted most from European settlement, having increased significantly since pre-settlement times. Habitat loss and degradation are not significant limiting factors. It responds positively to forest fires and forest management that creates areas of deciduous second growth. Logged areas 1-30 years old in Algonquin Park have had a positive effect due to the increased shrub coverage after opening up the canopy (Tozer 2012). It colonized forest edges and regenerating second-growth forests (Falardeau in Gauthier and Aubry 1996; Lowther and Williams 2020; Morse 1989). In the Canadian Shield of Ontario, there was no difference in its abundance in early successional clear-cuts and burns, but it was significantly less abundant in mid-successional clear-cuts than in mid-successional burns. It was equally abundant in early successional, mid-successional, and mature stands (Zimmerling et al. 2017). Imbeau et al. (1999) studied black spruce stands that had been subjected to logging or fires in Quebec and concluded that the Nashville Warbler would benefit from short logging rotations. Near Quebec City, it responded positively as deciduous strips grew in areas that had been strip-cut, breeding at higher densities in old than young deciduous strips (Falardeau et al. 1999). In Idaho, Medin and Booth (1989) examined the effects of single-tree selection harvest on the Nashville Warbler. After logging, densities per km^2 increased to 21.5-40.0 compared with 12.4-30.8 in the same areas prior to logging. In Wisconsin 30-m riparian buffers adjacent to upland clear-cuts, it was more abundant in cut and partially cut buffers than in buffers that were uncut or where the upland forest and buffer were left intact. It was more common in riparian buffers adjacent to clear-cuts than in uncut forest (Hanowski et al. 2005). Its abundance did not vary significantly when full-tree or cut-to-length harvest techniques were used (Hanowski et al. 2003).

Hunter and Witham (1985) examined the effects of carbaryl spraying to reduce insect numbers in Maine. During the first year of study, only 30% of the site was sprayed. Numbers of all warblers dropped on spray day and remained low until 7 days later when a gradual recovery began. The Nashville Warbler was relatively unaffected, representing 5.9% of foraging warblers pre-spray, 10.0% post-spray, and 4.2% during the recovery period. The relative increase after spraying may have been due to many other warbler species leaving the area to forage elsewhere. In the following year, spraying covered 100% of the site and there were no differences in foraging heights, tree selection, or species composition of the warbler community. When the area was completely sprayed, birds could not fly to a nearby unsprayed area to forage.

Blake et al. (1992) studied the effects of drought on the Nashville Warbler in Wisconsin and Michigan. It exhibited significant variation in abundance among years and declined as drought progressed each year.

In Oregon, the Nashville Warbler exhibited no significant response to forest fires regardless of the severity of the burn, although it was more abundant in burned forests (Stephens et al. 2015).

In Minnesota, there were no significant differences in breeding densities under electric power transmission lines and control plots (Lowther and Williams 2020). Low-level electromagnetic fields have limited effects on the Nashville Warbler.

Price (2004) predicted that the Nashville Warbler might not breed any longer in southern Ontario if the average summer temperature increased by 2°C. In eastern Quebec and southern Labrador, it was strongly associated with stands having the warmest summer temperatures. In this area, which is near the northern extent of its breeding range, it may benefit from climate warming (DesGranges and LeBlanc 2012).

Status

The Nashville Warbler was very rare at the turn of the 19th century and was not described until 1811. In Massachusetts, it was unknown prior to 1834, irregular by 1836, very common by 1842, and less abundant by 1906. A similar pattern was observed throughout eastern North America with populations increasing starting in the 1830s and then declining around the start of the 20th century (Bent 1953; Falardeau in Gauthier and Aubry 1996; Lowther and Williams 2020).

McIlwraith (1894) reported that few Nashville Warblers remained as far south as Hamilton to breed and that most moved further north. Baillie and Harrington (1937) considered it a common summer resident north to the transcontinental railway and west to Kenora. During the first atlas, its breeding distribution included all the Boreal Forest and Great Lakes–St. Lawrence forest regions. There were scattered breeding records in the Hudson Bay Lowland and it also occurred in the Carolinian Forest Region but was absent in the intensively farmed areas of extreme southwestern Ontario. Highest densities were from the Canadian Shield north of a line from Parry Sound to Perth, through Algonquin Park to Timmins (McLaren in Cadman et al. 1987). James (1991) considered the Nashville Warbler a common summer resident across the province, north to Sandy Lake and Moosonee, and occasional and rare to Fort Severn and Winisk. It was rare south of the Shield, south to Haldimand and Norfolk counties.

The second atlas demonstrated that there had been limited change in the distribution of the Nashville Warbler since the first atlas. It was much more widespread within the Hudson Bay Lowland than previously documented. It continued to be rare in the Carolinian Forest Region, but breeding evidence was obtained from the Lake St. Clair area. Its province-wide probability of observation increased significantly since the first atlas, and also in the Great Lakes–St. Lawrence Forest Region, the Boreal Forest Region, and the Hudson Bay Lowland. A significant decrease in its probability of observation occurred in the Carolinian Forest Region. Highest density occurred in a broad band across the southern portion of the Boreal Forest Region from Sandy Lake to Moosonee. High densities also occurred in the Great Lakes–St. Lawrence Forest Region west of Lake Superior and

moderate densities occurred in the same forest region in the southern Shield (McLaren in Cadman et al. 2007).

Breeding Bird Survey data indicate that it decreased at annual rates of 0.644% in Canada and 0.32% in Ontario 1970-2021. Trends 2011-21 were annual decreases of 3.48% in Canada and 2.97% in Ontario. The short-term trend for Canada was highly reliable; the other results were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

After the parents stop feeding the young, both adult and young birds may occur singly, in pairs, or in groups of 3 in mixed-species feeding flocks while still on the breeding grounds (Lowther and Williams 2020). In Quebec, Major and Desrochers (2012) captured small numbers of Nashville Warblers in second-growth clear-cuts dominated by regenerating balsam fir, with lesser numbers of white spruce and white birch. In Minnesota, Streby et al. (2011b) considered it an early successional species during the postfledging period. During 1 breeding season, they captured 20. They captured 96 adults and 232 fledglings during the postfledging period over 4 years. In Michigan during the breeding and postfledging periods, Akresh et al. (2009) captured 16 adults and 31 juveniles. The capture rate per 100 net-hours was 0.9 in upland 100-year-old stands of trembling aspen and large-toothed aspen compared with 5.0 in riparian habitat with trembling aspen, alder, and honeysuckle. Eighty-one percent of juveniles occurred in riparian habitat.

MIGRATION

Migration occurs at night through the central United States from the Great Plains states eastward to the Appalachian Mountains and rarely through the southeastern states. Autumn migration is prompted by favourable weather conditions such as high-pressure systems, clear skies, and strong north-northwest winds (Bent 1953; Lowther and Williams 2020; Stewart 1986).

In spring, males arrive before females and older birds arrive before yearlings. At Long Point, mean capture dates were 8.5 May for after-second-year males, 11.3 May for second-year males, 10.7 May for males of unknown age, 13.3 May for after-second-year females, 14.4 May for second-year females, and 15.6 May for females of unknown age. Older males arrived significantly earlier than yearling males but there was no significant difference in arrival times of different age classes of females (Stewart et al. 2002). Also at Long Point, the spring midpoint for Nashville Warbler arrival 1975-2000 was 12 May. There was no significant change in arrival date over this period, although it did arrive slightly earlier in more recent years (Mills 2005). At Prince Edward Point, males arrived significantly earlier (13.6 May) than females (19.0 May). The difference in mean arrival dates between males and females was greatest in years when males arrived the earliest (Francis and Cooke 1986). In southern and central Ontario, migrants arrive in late April or early May and the main flight has passed through by late May, with a few persisting into the first week of June (Black and Roy 2010; Curry 2006; Keast 1980; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). Kendeigh (1947) first observed the Nashville Warbler near Lake Nipigon on 23 May.

During autumn migration, the age classes usually migrate synchronously, but at a coastal station in Virginia, yearlings initiated migration earlier than adult birds (Lowther and Williams 2020; Stewart 1986). Wilson and McRae (1993) concluded that single Nashville Warblers seen at Longridge on 5 September and Moosonee on 21 and 24 July and 3 September were migrants. It is one of the latest

warblers to leave the southern Shield. Most leave by the end of September but a few linger into October (Mills 1981; Tozer 2012). Birds first arrive in southeastern Ontario by mid-August and approximately 40% of the flight has gone through by the first week of September, with average departure in mid-October (Keast 1980; LaForest 1993; Weir 2008). In the Hamilton area, peak autumn migration is in October. There are 6 December and 1 January records from the Hamilton area, but no evidence of successful overwintering (Curry 2006). At Long Point 1975-2000, the midpoint of autumn migration was 20 September. There were no changes in autumn arrival dates over this period (Mills 2005a).

The Nashville Warbler uses a variety of habitats during migration. In Illinois during spring migration, it showed a distinct preference for forest edges, but also occurred in mature upland forests and mature bottomland forests. A preference was also demonstrated for forest edge in autumn, but it also used forests, orchards, and residential areas (Graber et al. 1983). During migration, it frequents deciduous trees or shrubs in open mixed forests at mid-canopy level; brushy edges of woodlands along streams, roads, and paths; edges of fields, meadows, ponds, swamps, or marshes; second-growth alder-willow stands; gardens and suburban parks where there are trees and shrubs; old fields and pastures with scattered trees and shrubs; orchards; gardens; and shade trees in urban and rural areas. Habitat use during migration is similar to that used during the breeding season except for the use of suburban areas and rural residential lots (Bent 1953; Campbell et al. 2001; Chapman 1907; Leighton et al. 2002; Lowther and Williams 2020).

During spring migration in Wisconsin and Minnesota, Kirsch et al. (2013) found no significant differences in numbers of Nashville Warblers in upland and floodplain forests. During spring migration in Pennsylvania, it was most abundant in suburban forests followed by, in order of decreasing abundance, forest-agricultural edges, shrub and sapling-stage forests, forest interior, and pole-stage forests. Numbers in suburban forests were significantly higher than in forest interior and in pole-stage forests. In 1 of 3 years, suburban forests were used most frequently. Forest-agricultural edges were used the most the other 2 years. Rodewald and Brittingham (2007) considered it to be in a guild of shrub-sapling breeders whose abundance during migration was correlated with the percentage of low woody cover and canopy height. Also in Pennsylvania during spring migration, detections of this warbler per 100-m transect were 0.000 in forest and 0.100 in shrubs; captures per 1,000 mist-net hours were 0.6 in forest and 6.0 in shrubs. These differences were significant and it exhibited a strong preference for shrubby areas over forest. In 2 of 3 years, there were more flying insects in the shrub habitat, but there were no differences in populations of substrate invertebrates or caterpillars in the 2 habitat types (Smith and Hatch 2008). In Ohio during spring migration, it was significantly more abundant in mature upland forests than mature riparian forests. The 2 habitats supported similar species of shrubs but differed significantly with higher shrub coverage in upland forests (39.0% compared with 18.9%). Canopy closure was 74.4% in upland forests and 83.2% in riparian forests. It selected sites with denser shrub coverage and less canopy closure (Rodewald and Matthews 2005). Rodewald and Brittingham (2002, 2004) studied habitat usage by the Nashville Warbler during autumn migration in Pennsylvania. In the first study, it occurred in all habitats surveyed with no significant differences in numbers observed. In the later study, it was not observed in forest interior. It was most abundant in forest-agricultural edges followed by suburban forests, pole-stage forests, and shrub- and sapling-stage forests. There were no significant differences in the

numbers seen within the 4 habitats it occupied. Shrubs appear to be an important habitat component of migrating Nashville Warblers. It tends to be most abundant in shrub habitats, forest edges, and forests with open canopies.

During both spring and autumn migration, the Nashville Warbler frequently joins mixed-species foraging flocks. During spring, it tends to frequent the upper half of large trees and is more common in tall trees in woodlands than in smaller groups or rows of trees. In autumn, it tends to inhabit the middle section of large trees and also taller shrubs and saplings, especially large hawthorns. During autumn, it may also forage on herbaceous species (Bent 1953; Leighton et al. 2002; Lowther and Williams 2020). Keast (1980) described the foraging habits of the Nashville Warbler during autumn migration at Prince Edward Point. Foraging height ranged from 3 to 17 m, mostly 5-13 m with a peak at 7 m. It fed at 17 m for part of the day, then in the tops of saplings, and subsequently descended to heights of 1.0-1.5 m in tall shrubbery. Foraging substrates consisted of 33% outer leaves, 33% sapling leaves, 17% outer branches, and 17% twigs and inner leaves. It was not observed foraging in the air, on inner branches, on tree trunks, or on the ground. Feeding zones included 60% low shrubs, 25% bare twigs, and 15% branches. In Algonquin Park, Peter (2008) observed a male feeding on pin cherry nectar during a damp, cool spring day when few insects were available. Two days later under more favourable weather conditions, a male gleaned and hawked insects in the same tree with no evidence of nectar feeding. It has fed on nectar of native plum in Minnesota during adverse spring weather conditions. It may feed opportunistically on tree nectar when arthropods are scarce. In New York during autumn migration, Lebbin et al. (2007) observed Nashville Warblers sallying after moths at night in an area illuminated by football-stadium lights.

Keast (1980) examined the stomach contents of 2 Nashville Warblers killed during autumn migration at a hydro tower near Prince Edward Point. Collectively, they consumed 66 4-5-mm long beetles and caterpillars 11 mm and 13 mm long. Carlisle et al. (2012) examined its diet in relation to prey availability during autumn migration in Idaho. Prey items eaten in greater proportion than their availability included true bugs, stink bugs, spittlebugs, leafhoppers, jumping plant lice, beetles, lepidopterans, and moths. Prey consumed less than their availability included spiders, hymenopterans, ants, wasps, yellowjackets, and flies.

The Nashville Warbler is a common victim of striking tall structures during autumn migration, and it also strikes windows. A total of 172 were killed at the Lennox generating station chimneys near Kingston. Of autumn lighthouse and television tower kills, it represented 1.6-7.3% of all warbler casualties in Wisconsin, Ontario, and Michigan (Graber et al. 1983; Lowther and Williams 2020; Weir 2008). Loss et al. (2014) analyzed bird collisions with buildings in the United States. The Nashville Warbler was highly vulnerable to striking residences 1-3 stories high, being 22.2 times more likely to suffer a collision than average for birds. It was not on the lists of the 20 most vulnerable species for striking low-rises or high-rises.

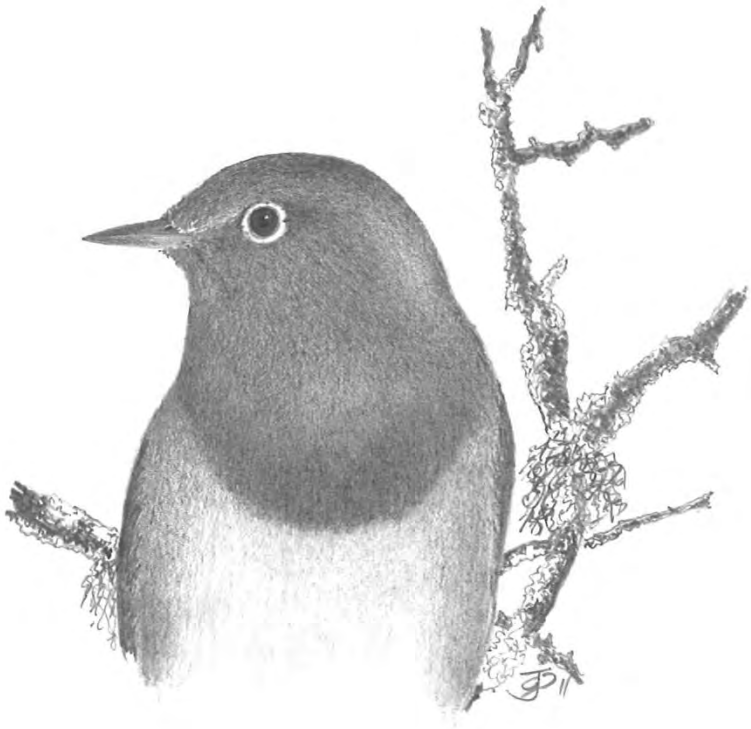
In New York, Zelt et al. (2017) compared the spring arrival dates, autumn departure dates, and length of the breeding season during 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming during the second period. The Nashville Warbler arrived significantly earlier in spring during the second period, but there were no significant differences in its autumn departure dates or length of the breeding season.

McIlwraith (1894) considered the Nashville Warbler an abundant yet irregular migrant. It was common during migration some years and scarce or even absent other years. It is now a common and regular migrant (James 1991).

At Long Point Bird Observatory (LPBO) 1961-88, the Nashville Warbler experienced a significant decline of 2.9% per year. Trends by period were: 1961-70, −5.0%; 1970-79, +2.0%; and 1979-88, −6.3% (Hussell et al. 1992). More recent data from LPBO indicate a 1.2% per year increase in spring and a 1.0% per year increase in autumn 1961-2006 (Anonymous 2008).

Connecticut Warbler

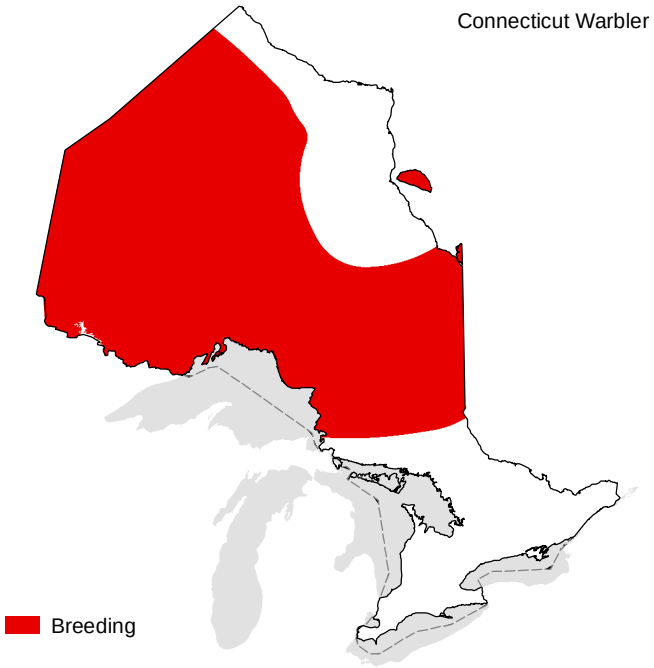
Oporornis agilis



BREEDING SEASON

Habitat Requirements

The Connecticut Warbler nests in 2 types of habitat in Ontario and Canada. In the eastern part of its range, it prefers black spruce and tamarack bogs and fens, although localized usage of immature jack pine stands occurs. In the west, it nests predominantly in open trembling aspen woods. Both habitats are used in Ontario, with the black spruce and tamarack associations used predominantly. Both types are used in Rainy River District. East of Fort Francis, the Canadian Shield is predominantly boreal in nature. Tree cover is chiefly coniferous, with jack pine in drier sites, black spruce in moist areas, trembling aspen throughout, and poorly drained areas dominated by black spruce with some tamarack. It selects these poorly drained areas for nesting. The area west of Fort Francis is flat and the landscape is mostly agricultural. Woodlands in this area are mostly trembling aspen with a few balsam fir and white and black spruce. There are some large peat bogs that may be either open or forested with mature black spruce. In this area, it avoids bogs and nests in trembling aspen forests.



The aspen woods that are occupied are fairly open with an understorey of dogwood, willow, and other shrubs. Males sing from a perch well up in aspens, often in the canopy. In the Boreal Forest Region, it demonstrates a preference for bogs with open immature or stunted stands of black spruce. The ground cover consists of sphagnum moss, Labrador tea, bog rosemary, bog laurel, and leatherleaf. In this habitat, males sing from a perch high up in a black spruce (Elder 1991). Most other information on Connecticut Warbler habitat in Ontario is from the Boreal Forest Region. An exception is the Gogama area where James and Peck (1995a) reported a single male singing in several summers in a 40-50-year-old jack pine forest where trees were 12-16 m tall. They concluded that it had not colonized this habitat type in any significant numbers anywhere within the province. From Pickle Lake north to Sachigo Lake, it occurred in coniferous forest with and without an understorey and in coniferous scrub. It was absent in deciduous or mixed forest, deciduous or mixed scrub, heath, and tundra (McLaren and McLaren 1981). Near Pickle Lake, James (1980) documented it rarely in spruce bogs. Harris (2011) provided the first documentation of an Ontario nest from north of Lake Nipigon. The habitat was an 86-ha treed fen that bordered a small lake. The fen was dominated by scattered black spruce 2-3 m tall spaced at 5-10-m intervals. The ground flora consisted of leatherleaf, bog laurel, and cottongrass within a continuous layer of sphagnum moss. Around the outer edges of the fen, the black spruces were taller and denser as they graded into coniferous swamp. The previous Ontario breeding record was from the Thunder Bay area in a cutover with dense undergrowth of raspberries (Peck and James 1987). Along the northeastern shore of Lake Superior, Baillie and Hope (1943) found the Connecticut Warbler only in spruce bogs. In the Clay Belt, Smith (1957) reported it in spruce-poplar and lowland spruce stands. In the same region, it reached its maximum abundance in black spruce stands and preferred open spruce bogs and fens. It occurred over a wide range of moisture regimes from very wet stands of black spruce to very dry stands of jack pine. It also occurred in tamarack and spruce–white birch stands (Welsh and Lougheed 1996). Welsh (1993) reported that it bred predominantly on organic soils in pure black spruce stands in the Boreal Forest Region, and that it was rare in jack pine and tamarack stands. In the Hudson Bay Lowland, it was most abundant in the Moosonee area in a tamarack fen. Wilson and McRae (1993) were of the opinion that it bred in the extensive tamarack fens inland from the Moose River and Longridge.

The Connecticut Warbler also nests in 2 main habitat types in Quebec. In the Boreal Forest Region, it nests predominantly in peatlands, in black spruce–moss forests, and in the ecotone between these 2 habitats. In more southerly areas of Quebec, a number of sightings have been

made in jack pine stands with fewer records from poplar stands, open spruce forests, and black spruce peatlands (Ibarzabal in Gauthier and Aubry 1996). At the southern extent of its range in Michigan, 1 pair nested in a mixed trembling aspen–spruce forest. The trees were widely scattered with many openings among them, creating a park-like appearance. The ground cover was extremely dense and consisted of timothy and other grasses; sedges were present in some locations (Walkinshaw and Dyer 1961). On islands in Wisconsin, it nested only in 1 aspen stand (Beals 1960). In the same state, it is a rare breeder in diverse pine and oak barrens and coniferous plantations (Mossman et al. 1991). Also in Wisconsin, it nests in oak–jack pine forests with dense underbrush and at edges of coniferous forests (Pitocchelli et al. 2023). In Minnesota, Huff (1929) reported a nest that was in an almost pure stand of black spruce, although some areas supported pure tamarack or a mix of these 2 species. Portions of the wetland were very dense, but it inhabited an area that was more open where the trees were well spaced and deep sphagnum moss covered the ground. Shrub species included Labrador tea and bog laurel and the herbaceous community was dominated by pitcher plant, sundews, bogbean, wild calla, coralroot, pink lady's slipper, and dragon's mouth. The shrubs were 38-45 cm tall and the opening was no more than 30 m from the edge of the wetland. The male sang for more than 5 hours from a tamarack 10.7-12.2 m tall standing amidst taller black spruce. Even where black spruce was the dominant tree, birds demonstrated a decided preference for singing from tamarack. Grinde et al. (2023) found nests in Minnesota in habitats dominated by tamarack or black spruce. Within 11.3-m plots around nests, the most common trees were 8-23 cm diameter at breast height (DBH) tamaracks with an average of 1,175 trees per ha, with small snags (500 per ha), small black spruce (1,075 per ha), and 23-38-cm DBH snags (125 per ha). Common understorey plants in nest plots in order of abundance were Labrador tea, leatherleaf, bog birch, and bog laurel. Other species included alder, balsam fir, blueberry, bog rosemary, gooseberry, honeysuckle, and white birch. Niemi and Hanowski (1984a) studied birds in 6 habitats (sedge fen, low shrubs, tall shrubs, open black spruce forest, closed black spruce forest, and tamarack forest) and found the Connecticut Warbler only in closed spruce forest. It was significantly more abundant in control than treatment plots. There were significant differences in tree density and heights in the 2 plots. In the preferred plots, tree height averaged 6.6 m (range 4.5-10.0 m) compared with 5.5 m (range 3.0-9.0 m) in treatment areas. Tree density was 45 per 0.01 ha (range 5-256) in control compared with 23 (range 5-100) in treatment areas. In Minnesota, breeding habitat consisted of mature lowland coniferous habitats, particularly black spruce and tamarack bogs with dense underbrush, scattered trees, and grassy openings. Of 480 observations, 90% were in black spruce, tamarack, and mixed stands of lowland conifers. Other stand types that were used included trembling aspen (4% of observations), red pine (3%), jack pine (2%), and mixed trembling aspen–balsam fir (1%). It occurred most consistently in lowland coniferous habitat within a matrix of large patches of lowland and upland coniferous habitat. Its frequency and abundance was positively correlated with the percentage of lowland black spruce and other lowland coniferous forests, positively correlated with the amount of upland coniferous cover, and negatively correlated with the percentage of upland deciduous forest, average total patch edge, and number of patches in adjacent lands. Important elements of the landscape to the Connecticut Warbler were a mosaic of coniferous forest, a combination of lowland and upland coniferous habitat, and the size of the pieces of this mosaic. Its abundance was approximately the same in buffers of 100, 500, and 1,000 m from sightings, but frequency increased with buffer size. The 1,000-m model was the best in predicting

its frequency and abundance. Important predictor variables at this scale were a high percentage of upland coniferous forest, a high percentage of lowland black spruce forest, and a low percentage of upland deciduous forest. Frequency was negatively associated with the number of patches and total patch edge. At the 500-m scale, the most important parameters were high variance of tree density, high percentage of black spruce forest, and a low density of trees. At the 100-m scale, the most important habitat variables were high density of ground cover, low percentage canopy cover, and low percentage of lowland deciduous forest (Lapin et al. 2013). Seton (1884) found the first nest for this species in Manitoba. The habitat was a large spruce forest with a tamarack bog in it. Tamarack was sparse within this area and the ground cover consisted of mosses, pitcher plants, and sundews. In Alberta and Saskatchewan, the Connecticut Warbler nests almost exclusively in trembling aspen and balsam poplar stands, usually mixed with some conifers such as jack pine, white spruce, or black spruce. Forests that it inhabits usually have a dense woody understorey that may include poplar, roses, dogwood, beaked hazel, chokecherry, juneberry, alder, and willow. In this area, it is frequently associated with clear-cuts and may be more abundant in them than in forests. Kirk et al. (1996) reported that it was associated most frequently with mixed-wood or deciduous forests in Alberta and Saskatchewan and, less frequently, with black spruce or species-poor jack pine stands. It was observed in 50% of stands 15-20 years old, but was not detected in stands 0-9 years or 40-80 years old. It occurred on average at the midpoint on the moisture and nutrient-level axes. It was associated with aspen or poplar stands rather than areas of organic soils supporting black spruce. In Alberta, it nested both in clear-cuts and forests dominated by trembling aspen and balsam poplar. It used clear-cuts by the third year after cutting when trembling aspen were 1-2 m tall. Trees were retained within these clear-cuts, and its abundance decreased with increasing basal area of trees (Tittler et al. 2001). In Alberta, it was most abundant in young aspen forests where it was a low strata species preferring deciduous forest. It was associated with high percent coverage by moss, dense small aspens, slightly above average amounts of conifers, and moderate to low canopy heterogeneity. Young aspen forests exhibited intermediate canopy heterogeneity. Mean numbers detected on point counts were 0.76 in young forests (canopy height 8-11 m, 5,000-7,000 trees per ha, 23-26 years old), 0.42 in mature stands (canopy height 15-20 m, 1,000-3,000 trees per ha, 51-63 years old), and 0.29 in old-growth (canopy height greater than 20 m, less than 1,000 trees per ha, more than 120 years old; Schieck et al. 1995)). Breeding habitat in British Columbia appears to be slightly different than what is used in the Prairie Provinces. It appears to prefer more mature stands. It breeds in old-growth and mature trembling aspen stands. There are some records from younger aspen stands, willow–trembling aspen stands, willow–balsam poplar stands, and stands of smaller trembling aspen on slightly drier ridges. Breeding habitat includes edges of old-growth and young stands of trembling aspen–spruce, mixed balsam poplar–spruce stands on islands in a river, old-growth trembling aspen with white spruce saplings in the understorey, and young to old-growth trembling aspen stands. The presence of spruce in the understorey of trembling aspen stands may be characteristic of good habitat. In all inhabited areas, there was a noticeable gap of open space between the canopy and shrub layer (Campbell et al. 2001). Another British Columbia study characterized habitat as a wide range of age of aspen stands (average 68 years), canopy containing gaps, low densities of spruce, average of less than 20% shrub coverage, less than 5% coverage by shrubs shorter than 2 m tall, more than 75% herbaceous cover, 40% coverage by grasses, and terrain with an average slope of 8.1%. Tall cover by herbaceous plants combined with low shrub coverage

was the best predictor of breeding habitat (Pitocchelli et al. 2023). In Minnesota, it was positively correlated with the amount of both productive and non-productive stands of black spruce and tamarack within 200 m, basal area, and stand age. It was negatively correlated with the amount of white cedar within 1 km, the amount of sedge meadow within 1 km, and the amount of upland forest within 200 m. It would benefit from forest management that avoids harvesting black spruce–tamarack forests with intermediate basal area, especially in landscapes surrounded by additional black spruce–tamarack forests (Zlonis et al. 2017).

The Connecticut Warbler may be area sensitive. In the United States Great Lakes region, bogs inhabited by this species are typically larger than 40 ha (Pitocchelli et al. 2023). In Minnesota, Lapin et al. (2013) concluded that it may be area sensitive, even in forested landscapes. It was often absent in areas of suitable habitat that were in small patches of lowland and upland conifers. One stand was in both a mature black spruce plantation and an area that was logged shortly after the survey was initiated. Even though the landscape still consisted of potentially suitable breeding habitat with a high proportion of black spruce forest (37.7% of the area within 1,000 m), the alteration of a portion of the stand rendered it unsuitable. The authors concluded that larger patches of lowland and upland coniferous forest within a forested mosaic were important. Lowland coniferous forests in northern Minnesota have not been extensively altered, but surrounding forests have been frequently harvested and this has the potential to have an effect on it. In Saskatchewan, its abundance was positively correlated with forest size. It was more common in large fragments or in areas with a high local percentage of forest cover within 5 km. It was randomly distributed in landscapes, occurring in both forest fragments and contiguous forest (Hobson and Bayne 2000). Also in Saskatchewan, Johns (1993) examined aspen groves ranging in size from 0.2 to 36.7 ha. Smaller groves tended to be highly isolated from their nearest neighbour; large groves were less isolated. The Connecticut Warbler exhibited a significant negative trend with increasing isolation. Despite this relationship, it was found in groves as small as 3.2 ha as well as in larger stands. In British Columbia, birds were observed in stands as small as 4 ha (Campbell et al. 2001). These studies suggest that the Connecticut Warbler may be area sensitive, particularly in coniferous wetland habitats in the east. Although it may exhibit some area sensitivity in western aspen forests, it inhabits some small patches that are only 3.2-4 ha.

The first Ontario nest of the Connecticut Warbler was found in 1971 when 3 young were observed leaving a nest in Sleeping Giant Provincial Park at Thunder Bay. The nest was on the ground in a raspberry thicket in a logged area with dense undergrowth (Peck and James 1987). Nests are notoriously difficult to find because the male typically sings 100 m or further from the nest and the female walks the last 10-15 m when approaching the nest. Harris (2011) provided the first complete account of an Ontario nest, which he found north of Lake Nipigon. The nest was in a fen sparsely treed with short black spruce. It was 50 cm from the base of a 2.5-m tall black spruce and in a hummock of sphagnum moss under a tussock of cottongrass and leatherleaf. It was sunken approximately 12 cm below the surface of the hummock. The nest was about 100 m from the edge of the surrounding poplar-dominated forest. Kells (1889) attributed several nests that he found near Listowel to the Connecticut Warbler. It appears as though this was a case of mistaken identity. The habitat described was atypical of that used by the Connecticut Warbler and the sightings were considerably south of its known range. These records were not accepted or mentioned by

McIlwraith (1894), Baillie and Harrington (1937), or Peck and James (1987). A subsequent paper by Kells (1904) on the Connecticut Warbler in Ontario did not mention nesting.

Few nests of the Connecticut Warbler have been found. Seton (1884) found the first nest in Manitoba 51 years after the species was originally described. It was sunken in moss level with the surface. A nest in Minnesota was in the open except that it was overtopped by 30-cm tall Labrador tea and bog laurel that offered it some protection (Huff 1929). A Michigan nest was on dry ground. Vegetation within 5 m consisted of bracken ferns, small basswoods, strawberries, violets, morning-glories, goldenrods, fireweed, and large-leaved aster. A Minnesota nest was among tall grasses in an abandoned field at the edge of a spruce forest. Alberta nests are frequently in open poplar woods on a ridge above a small slough. They are typically on the ground, well concealed by grasses or other vegetation. An Alberta nest was in an open growth of fire-killed aspen, small shrubs, and herbaceous species and 15 cm from the ground in a rose bush. Minnesota nests were in moss, except for one in grass. They were concealed by grass, Labrador tea, bog birch, tamarack, and moss. The dominant cover type was tamarack at 10 nests and black spruce at 1 nest. Throughout its range, the Connecticut Warbler places its nest on or near the ground in dense undergrowth of saplings, among thickets, at the base of a shrub, in a mound of moss, or in dry grasses, and it is often covered by overhanging vegetation (Bent 1953; Grinde et al. 2023; Huff 1929; Pitocchelli et al. 1997; Walkinshaw and Dyer 1961).

In many areas, populations are too sparse for territorial behaviour to be required. Where isolated pairs nest, they may occupy a large territory or home range, with males frequently singing as far as 145 m from the nest (Walkinshaw and Dyer 1961). Pitocchelli et al. (2023) reported that the Connecticut Warbler was highly territorial when conspecifics were present. In Minnesota, territory sizes averaged 0.24 ha in open spruce forest and 0.48 ha in closed spruce forest. Isolated pairs may occupy larger areas than those that have neighbours.

No information is available on natal philopatry or adult site fidelity. Lapin et al. (2013) monitored Connecticut Warbler populations at a site in Minnesota over an 18-year period. During this study, its frequency per stand ranged from 0-72%. This suggested that site fidelity was low. The authors concluded that short-term studies would unlikely be able to detect the consistency in which an individual stand was used by the Connecticut Warbler.

Limiting Factors

Peck and James (1987) concluded that eggs would likely be present in Ontario nests during the month of June. Harris (2011) reported an Ontario nest with eggs on 15 June, but young were seen leaving a nest on 24 July (Peck and James 1987) suggesting that eggs may be present at least to the first or second week of July. In Michigan at the southern limit of this warbler's breeding range, Walkinshaw and Dyer (1961) estimated that egg laying began by 5 June with nest building occurring in late May or early June. No information is available on how soon nest building begins after spring arrival, how long nest building takes, or if there is a delay between nest completion and initiation of egg laying. It is likely that 1 egg is laid daily, but this has not been confirmed. It is unknown when incubation is initiated and how long it takes. The nestling period is 7-10 days (Pitocchelli et al. 2023).

The Connecticut Warbler raises a single brood. A brood observed leaving a nest in Sleeping Giant Provincial Park consisted of 3 young, but it is possible that the clutch size was larger. The single

nest described for the province had a clutch of 5 eggs. Clutches of 3-5 eggs have been reported throughout its range, with 4-egg clutches most common (Bent 1953; Harris 2011; Huff 1929; Leighton et al. 2002; Peck and James 1987; Pitocchelli et al. 2023; Seton 1884; Walkinshaw and Dyer 1961).

No information is available on the age of first breeding, but it is probably 1 year. The mating system is monogamous (Pitocchelli et al. 2023).

During the breeding season, the Connecticut Warbler gleans invertebrates from vegetation near the ground. Two were observed hunting a spider running over water, which they captured by gliding in the same manner as a swallow does when drinking. The stomach contents of these 2 birds consisted of 50 of these spiders and nothing else. Both adults feed the young raspberries, caterpillars, moths, and small insect larvae. Adults consume mostly spiders and insect adults, larvae, and pupae. They have been reported feeding on beetles, snails, and occasionally small seeds and berries (Bent 1953; Pitocchelli et al. 2023). A male in black spruce forest near Lake Nipigon had eaten 30 spiders, 5 true bugs, 5 beetles, 30 flies, and 2 hymenopterans (Kendeigh 1947).

The Connecticut Warbler has been parasitized by the Brown-headed Cowbird, but the extent of parasitism is unknown (Pitocchelli et al. 2023). The likelihood of parasitism in Ontario is low because there is limited overlap in the breeding distributions of these 2 species. In addition, the Connecticut Warbler nests in coniferous forests, bogs, and fens in the Boreal Forest Region, habitat that is generally avoided by the cowbird. The highest potential for parasitism in the province is in Rainy River District where the Connecticut Warbler nests in aspen stands.

The effects of forest harvesting in Ontario are uncertain. In the Canadian Shield of Ontario, there were no significant differences in its abundance in early successional and mid-successional clear-cuts and burns of the same seral stage and there were no differences in its abundance in early, mid-successional, or mature stands (Zimmerling et al. 2017). In Alberta, Tittler et al. (2001) concluded that it may benefit from logging and by retention of low densities of residual trees. To retain it in this area, it was considered desirable to leave fewer rather than more residual trees in clear-cuts or to allow some natural fires to occur. Retention of high densities of residual trees may be detrimental. In other areas, higher warbler densities occurred in post-fire than post-logging stands; burned areas had fewer trees and living shrubs (Pitocchelli et al. 2023). In Minnesota, it was vulnerable to loss and fragmentation of coniferous forest. Even when the wetland coniferous stands that it inhabited were left undisturbed, harvesting adjacent upland coniferous stands made some otherwise suitable habitats unsuitable (Lapin et al. 2013). In Saskatchewan, it may demonstrate a differential response to forest fragmentation depending upon distance from contiguous forest (Hobson and Bayne 2000). In British Columbia, logging of aspen stands combined with herbicides that reduce understorey vegetation is the most important threat. Much habitat is being lost there because harvested areas tend to be converted to agricultural land or to pure white spruce or trembling aspen stands with short rotation periods (Campbell et al. 2001). Threats that have been identified in Wisconsin include loss of jack pine forest due to spruce budworm outbreaks, forest fragmentation which may cause increased predation and parasitism, fire suppression, and loss of pine barrens (Pitocchelli et al. 2023).

Niemi and Hanowski (1984b) studied the effects of a 55-m-wide hydro transmission line right-of-way through forested habitat. Breeding Connecticut Warblers were at a greater mean distance

from the transect line in treatment areas (144 m) than in control areas (108 m). The authors found little basis for suggesting any positive or negative effects of the transmission line and attributed the results to differences in habitat between the control and treatment areas.

In Alberta, Bayne et al. (2008) determined that there was no difference in abundance of the Connecticut Warbler near noisy compressor stations and quiet well pads. It did not appear to be affected by chronic noise.

In Alberta, the Connecticut Warbler was significantly more abundant at pipelines than in adjacent forest interior. There was no difference in its abundance at seismic lines and well pads than in forest interior adjacent to these features (Bayne et al. 2016).

Venier et al. (1999) used results from the first atlas to compare the distribution of the Connecticut Warbler to those derived from climate models. The only parameter used in the model for this species was the range of precipitation. The model resulted in very high rates (95.3%) of false positives. The authors concluded that this type of large-scale model is not very useful for predicting the range of rare species such as the Connecticut Warbler. It is considered highly vulnerable to climate change because bogs and lowland coniferous forests are expected to disappear in their southern range limits (Grinde et al. 2023).

Status

Based on observations of juveniles accompanied by adults during early autumn migration, McIlwraith (1894) concluded that the Connecticut Warbler nested in the province. Baillie and Harrington (1937) reported it as a rare summer resident of Cochrane, Algoma, and Thunder Bay districts. The first evidence of breeding was obtained on 17 August 1918 in Algoma District where a pair was observed feeding young. The first nest was found in Sleeping Giant Provincial Park near Thunder Bay on 24 July 1971, but details of this nesting were not documented (Peck and James 1987). The first documented nest was found north of Lake Nipigon on 15 June 2010 (Harris 2011). The first atlas extended the known breeding range of the Connecticut Warbler. It occurred sparingly from Sault Ste. Marie to Moosonee in the east, west to the Manitoba border north to the lower Sachigo River, about 300 km northeast of Sandy Lake, the previously known northern limit. There were many gaps in its distribution within this range, but it was concluded that it was potentially present throughout and that it was actually quite common in some locations (Helleiner in Cadman et al. 1987). James (1991) considered it a locally uncommon summer resident across central Ontario, north to Big Trout Lake and Fort Albany and south to Wawa and Cochrane. He considered it occasional and rare south to Sault Ste. Marie and Sudbury. At Moosonee, it was locally common in a tamarack fen (Wilson and McRae 1993).

The second atlas demonstrated that there had been little change in the overall breeding distribution of the Connecticut Warbler, and numerous gaps within that range persisted. Its probability of observation increased significantly province-wide and in the Boreal Forest Region and Hudson Bay Lowland. The most substantial increase was in the Hudson Bay Lowland where the probability of observation increased several fold. It was difficult to determine if the increase was real, a result of enhanced atlassing effort, or an artifact of a small data set. It was most abundant in the western portion of the Boreal Forest Region and in the Great Lakes–St. Lawrence Forest Region west

of Thunder Bay. Overall, it was uncommon, but high densities may occur in isolated areas (McLaren in Cadman et al. 2007).

Breeding population trends for the Connecticut Warbler are uncertain. From 1966 to 2019, Breeding Bird Survey (BBS) results indicated an annual decrease of 0.8%, or an overall decrease of 60% (Pitocchelli et al. 2023). BBS data to 2008 indicate a 1.6% annual decline in Bird Conservation Region 12, with declines in Ontario, Manitoba, Saskatchewan, Minnesota, Wisconsin, and the entire United States. Reasons for the apparent decline are uncertain, but may include nest predation, changes in landscape, loss of nesting habitat as a result of fragmentation and climate change, loss of winter habitat, and collisions with human-made structures (Lapin et al. 2013).

In Ontario, results from the BBS and atlases are contradictory. The BBS is probably not very reliable for the Connecticut Warbler in the province because much of its breeding range and habitat is inaccessible by road. Conversely, the apparent increase reported by the second atlas may have been a result of better coverage. BBS results indicate that it decreased at annual rates of 1.6% in Canada and 2.39% in Ontario 1970-2021. Trends 2011-21 were annual decreases of 3.53% in Canada and 3.32% in Ontario. All results were of medium reliability except for the Ontario short-term trend, which was of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings stay close to the ground in dense thickets and come out in the open only when being fed by the adults. They are unable to fly when they first leave the nest. Young disperse from the nest by walking on moss or through thick vegetation. In Wisconsin, a family appeared among tamaracks at the edge of a bog on 20 July. At first, the young remained near the ground in a small tamarack, other conifers, and shrubs on the bog. Later, they spent most of their time in piles of treetops and coniferous slash lying on the ground and appeared to prefer this microhabitat. On 2 August, they were found approximately 73 m away. They moved further away every day but remained in a narrow belt of conifers until 20 August. After that, they began to flock with other Connecticut Warblers and a flock of 20-25 was seen several times (Bent 1953; Grinde et al. 2023; Pitocchelli et al. 2023). In Minnesota over the entire postfledging period, the average daily distance moved from nests was 88.5 m (range 7.6-203.0 m). The average daily distance moved from nests 0-7 days postfledging was 35.5 m (range 7.6-104.0 m). Young did not move more than 100 m from the nest until 7 days postfledging. The average distance from the previous day's location was 53.5 m (range 7.6-272.4 m). Average habitat characteristics at fledgling locations were 38% canopy cover (range 0-86.3%), 16.4 m tree height (range 7.5-27.5 m), and 7.9 cm moss depth (range 2.3-24.8 cm). Habitat was similar at random plots. Tamarack was the dominant cover at all fledgling locations. Microhabitats where fledglings were located had significantly higher stem counts than random sites, but there were no differences in other vegetation characteristics. Both parents continued to feed the fledglings until 17 days after they left the nest (Grinde et al. 2023). McIlwraith (1894) reported adults accompanied by young in August in the Hamilton area. It is possible that families remain together for the first stages of autumn migration, or it is possible that the adults and juveniles were unrelated.

MIGRATION

Migration appears to be nocturnal based on kills at tall structures. In southern and central Ontario, most spring records are from mid- to late May with the earliest migrants arriving in the first week of

May. A few remain into the first or second week of June (Black and Roy 2010; Curry 2006; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Tozer 2012; Weir 2008).

One observed at Longridge by Wilson and McRae (1993) on 9 September was an autumn migrant. Further south, migration is from late August to late September with some remaining into the second week of October (Black and Roy 2010; Curry 2006; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Tozer 2012; Weir 2008).

During spring migration, the Connecticut Warbler occurs predominantly on the ground in tangles of dense undergrowth, in wet thickets, in woodlands and undergrowth in rural areas, on or near the ground in mature floodplain forests, and in moist forests and fallow fields. It is uncommon but regular in city parks and residential areas with shrubs and other low, dense vegetation. It prefers dense undergrowth during migration (Pitocchelli et al. 2023). During spring migration, Saunders (1885) reported it feeding on the ground in dry places at Point Pelee and in swamps near London. In Illinois, Graber et al. (1983) often found it during spring migration in weedy patches and gooseberries, in shrubby swamps, and occasionally in bottomland swamps. It was more numerous in forest edges and shrubs than in forests. Walkinshaw and Dyer (1961) often found it along shrubby roadsides in Michigan during spring, where it remained near the ground. In Ohio during spring migration, it occurred almost entirely in bushy tangles of remnants of swamp forests and was only seen in upland woodlands twice (Bent 1953). Within Illinois woodlands, it occurred more often in forest gaps created by treefalls with a dense understorey than in undisturbed forests (Pitocchelli et al. 2023).

During autumn migration, the Connecticut Warbler may occur in wet brushy areas, damp woodlands with dense undergrowth, weed and raspberry patches, maple swamps, shrub thickets, on the ground under or among rank vegetation, and in dense growths of willows. In British Columbia, it has been observed in autumn in tamarack-spruce bogs with dense shrub growth and in shrub willows along creeks. In autumn in Ohio, it is not confined to swamp remnants, but also inhabits shrubby, weedy, and fallow fields. It may occur in weedy growths bordering hedgerows some distance from woodlands. During autumn in Massachusetts, it was often seen in beds of jewelweed in swamps and along ditches where nightshade overhung the water. Elsewhere, it has occurred in autumn in dense undergrowths of ragweed, sunflowers, asters, greenbrier, poison ivy, and barberry (Bent 1953; Campbell et al. 2001; Chapman 1907; Pitocchelli et al. 2023).

During migration, the Connecticut Warbler may occur at all levels, but is most commonly found on or near the ground. In autumn, it may forage within mixed-species flocks. During cloudy weather in autumn, it may forage at the tops of trees 15-18 m from the ground in the company of other warbler species. It often feeds on owlet moth caterpillars during autumn migration (Chapman 1907; Pitocchelli et al. 2023).

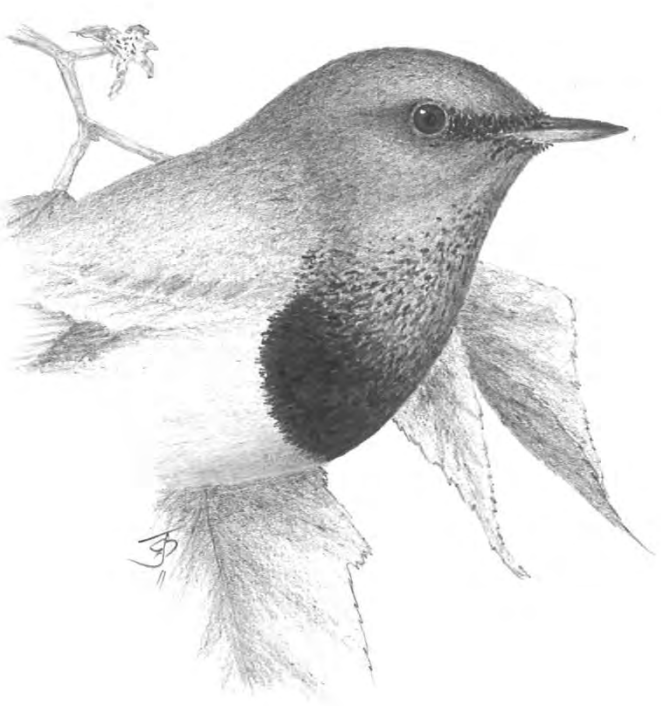
The Connecticut Warbler commonly strikes tall buildings, communication towers, and other structures during migration. During the autumn of 1981, only 2 were observed in the Kingston area but 15 were killed at the Lennox generating station chimneys: 7 each on 5 and 7 September and 1 on 4 September. A total of 19 kills occurred there 1972-82. Some tower kills were reported in Illinois, also in greater numbers than observers see. In Wisconsin, 330 were killed at towers in 1 location during autumn migration in 1 year; 140 were killed in a single night. At 2 sites, it represented 1% and

2% of all warblers killed. Both kills at structures and banding efforts reveal much larger numbers passing through than are reported by observers (Graber et al. 1983; Pitocchelli et al. 2023; Weir 2008). Loss et al. (2014) determined that it was at high risk of colliding with buildings in the United States. It was 22.9 times more likely than average to strike buildings. It was not on the list of the top 20 vulnerable species for striking residences 1-3 stories tall. At low-rises, it was 35.7 times more likely to suffer a collision than average and 52.0 times more likely at high-rises.

James (1991) considered the Connecticut Warbler a rare migrant in Ontario. All regional books on Ontario birds rank it as very uncommon, rare, or very rare, and it is also irregular in occurrence in most areas. It is rarely observed, but it is likely more common than observer records indicate. It is also likely to be more common in autumn due to the presence of juveniles in the population and the eastward migration pattern whereby birds that bred in western Canada pass through Ontario. Early accounts of migrants suggest that it may have previously been more common. The first official Canadian specimen was a bird that flew into a store in London on 15 September 1883, but McIlwraith apparently had several specimens in his possession many years prior to that. Saunders (1885) considered it tolerably common in swamps near London in May and quite common at Point Pelee for a few days in early June. In Toronto, it was considered one of the rarest warblers until 1896 when it was found to be fairly common in May. Thereafter, Fleming (1907) considered it a regular but not common migrant.

Mourning Warbler

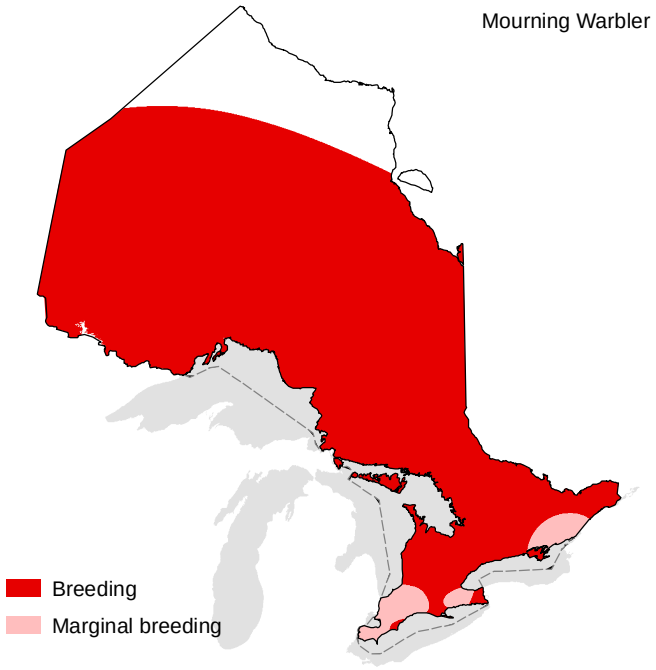
Geothlypis philadelphia



BREEDING SEASON

Habitat Requirements

In Ontario, 76.9% of Mourning Warbler nests were in forests, with 26.9% in mixed woods, 7.7% in deciduous woods, and 3.8% in coniferous woods; the other forest types were not specified. All forested areas that it used had a dense understorey and either had an open canopy or the nest was at the woodland edge, in a clearing, or near roadsides. Single nests (3.8% each) were in a brushy thicket; an alder swale; a deciduous thicket of alder, willow, and dogwood; and in a burn. Two nests (7.7%) were in residential gardens. Most nests were in upland habitat, but 7 were in damp or swampy areas (Peck and James 1987). James (1984b) reported that the Mourning Warbler nested in mixed and deciduous forests in Ontario and rarely in coniferous forests. It requires a dense deciduous layer under trees, particularly aspen, in open woods, edges, or clearings. Nesting may occur in dry or moist areas.



In the Hudson Bay Lowland, the Mourning Warbler was fairly common in aspen groves near Moosonee, especially further inland along the banks of the Moose River (Wilson and McRae 1993).

In the Boreal Forest Region near Pickle Lake, the Mourning Warbler occurred in coniferous forest with and without an understorey layer, in mixed scrub, and in deciduous forest. It was absent in mixed forest, deciduous or coniferous scrub, heath, and tundra (McLaren and McLaren 1981). In the same area, James (1980) encountered it irregularly in edge situations. North of Lake Nipigon, it nested in openings in the forest and in clear-cuts (Kendeigh 1947). Near White River in jack pine stands, it was significantly associated with the youngest forest age class, 3-5 years after clear-cutting. The Mourning Warbler had the second-highest indicator value of all species studied, indicating that it was highly specialized for inhabiting early successional habitat. Its abundance was strongly associated with the volume of coarse woody debris in decay stage 1 that had most of the bark still intact and more than 75% of the wood still hard (Venier and Pearce 2005). Near Quetico Park, it was most abundant in stands 1-23 years old where it was fourth in importance values of the species present. It was not detected in intermediate-aged stands (67-73 years) and was of low importance in mature (112-176 years) and old-growth (367-370 years) stands (Apfelbaum and Haney 1999). Near Hearst, Welsh and Fillman (1980) found it in uncut upland deciduous stands but not in uncut lowland coniferous stands. It occurred in upland clear-cuts 3-19 years old, lower-slope mixed clear-cuts 17 years old, and lowland coniferous cuts 3-9 years old. Welsh (1993) considered it an early successional species in the Boreal Forest Region. It occurred in clear-cuts 1 year after cutting, was most abundant in 3-8-year-old cuts, but occurred regularly in cuts as old as 16 years and irregularly in older stands to 33 years of age. It was not detected in stands 57-220 years old. Northeast of Lake Superior, it frequented new growth in burns, clear-cuts, and forest clearings (Baillie and Hope 1943). In the Clay Belt, it was most common in nutrient-rich stands and those that were wetter than average. It was most abundant in stands dominated by trembling aspen and trembling aspen with mixed conifers. Although it was most abundant in these stand types, it occurred in all stand types investigated, including those dominated by black spruce, balsam fir, jack pine–trembling aspen, and balsam poplar–trembling aspen (Welsh and Lougheed 1996).

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, James and Peck (1995a) surveyed jack pine stands near Gogama. They found the Mourning Warbler where tall deciduous shrub coverage was at least 50% and often nearly 100%. It usually occurred in areas cut or burned 5-10 years previously, but also at edges of tall pine forests where shrubs and raspberries were

common. In Algonquin Park, MacLulich (1938), Martin (1960), and Tozer (2012) concurred that it inhabits open, brushy habitats such as forest edges and open cuts. It was common in cuts in white pine stands 2-9 years old, uncommon in 10-18-year-old cuts, and absent in areas with no history of cutting. Kingsley and Nol (1999) considered it a shrub-nesting species that responded positively to most silvicultural treatments. It was most abundant in stands with a greater extent of herbaceous cover and deciduous and coniferous subcanopy. In Muskoka and Parry Sound districts, it thrived in dense, moist thickets. It nests there in disturbed areas such as margins of cottage and secondary roads, along hydro-line corridors, and in forest and river edges (Mills 1981).

South of the Shield in the Great Lakes–St. Lawrence Forest Region, Speirs and Orenstein (1975) considered it a mid-successional species in Durham Region, where it was not associated with any coniferous species. They observed it in stands with an open canopy and dense growth of shrubs such as raspberries, winterberry holly, mountain holly, and highbush blueberry. Within this forest region, it also nests in meadows dominated by large hawthorns, in grassy and herbaceous cultural meadows with residual tree cover and scattered clumps of shrubs, shrubby edges and openings in coniferous plantations, and on shrubby hydro transmission line rights-of-way passing through deciduous forest (personal observation).

In the Carolinian Forest Region, the Mourning Warbler was frequently the most common warbler in Elgin County in thickets, woodland edges, regenerating second-growth scrub, damp wooded areas, raspberry tangles, and anywhere that dense underbrush was present (Lancaster et al. 2004). In Waterloo Region, it inhabited a mature sugar maple forest for approximately 5 years after it was heavily logged (personal observation). In southern Ontario, its abundance was positively correlated with the amount of forest cover 100 m from edge, woodlot size, the amount of forest cover within 2 km, and the amount of regional forest cover. Only the relationship with the amount of forest within 2 km was significant (Austen et al. 2001).

Throughout its range, the Mourning Warbler nests in shrubby meadows, forest edges, and small openings in forests created by treefalls, wind, fire, and disease. Clear-cuts and burns in forested areas create good habitat 1-3 years after disturbance, with highest densities occurring in the east when forests are 10-15 years old and declining in older stands. It is associated mostly with deciduous and mixed stands but may occur in coniferous forests and plantations provided that an understorey of deciduous shrubs and saplings is present. It is often strongly associated with aspen stands and, in the west, prefers mature aspen stands over younger forests. Nesting may occur in both upland and wetland sites and it tends to prefer nutrient-rich habitats over nutrient-poor areas. In many areas, it is slightly more frequent in damp areas such as alder, willow, or dogwood thickets and margins of bogs and fens. It occurs at edges and in openings of lowland forests, including those dominated by spruce and balsam fir as well as deciduous riparian forests. Presence of dense deciduous shrubs is essential and it may be found in areas with a variety of shrub or sapling species such as red-osier dogwood, willow, alder, bur oak, trembling aspen, rose, highbush cranberry, raspberries, hawthorn, white birch, maple, chokecherry, winterberry holly, blue beech, and gooseberries. It may also nest in dense patches of tall herbaceous plants such as nettles, fireweed, goldenrods, thistles, and jewelweed. In most areas where it nests, there may be little to no canopy closure. The Mourning Warbler is often one of the dominant species in recent clear-cuts and burns. In Minnesota, it

occurred on all clear-cuts studied and was one of the 4 most abundant species. It was positively correlated with snag density and basal area (BA), shrub density and BA, and shrub height. It was negatively correlated with tree density, tree BA, and shrub patchiness. None of these relationships were significant. It is frequently common on roadsides, ski-hill cuts, cuts for seismic lines, and utility rights-of-way passing through forested habitat (Back 1979; Beals 1960; Bent 1953; Bielefeldt and Rosenfield 1994; Brooks 1940, 1947b; Brooks and Bonter 2010; Campbell et al. 2001; Capen 1979; Chapman 1907; Collins 1983a; Collins et al. 1982; Cox 1960; Dessecker and Yahner 1987; Faanes and Andrew 1983; Freedman and Johnson 1999; Freemark and Collins 1992; Graber et al. 1983; Gromme 1934; Haney 1999; Harrison 1984; Hoffman 1989; Hofslund 1954; Imbeau et al. 1999; Kirk et al. 1996; Lent and Capen 1995; Morgan and Freedman 1986; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991; Nadeau and Gauthier in Gauthier and Aubry 1996; Niemi and Hanowski 1984a; Niemi and Pfannmueller 1979; Noon et al. 1979; Pitocchelli 2020; Samson 1979; Schieck et al. 1995; Sinclair et al. 2003; Taylor and Taylor 1979; Thompson et al. 1999; Titterington et al. 1979; Whitaker and Montevecchi 1997, 1999).

Freemark and Collins (1992) considered the Mourning Warbler an area-sensitive species and Mossman and Hoffman (1989) concluded that it preferred larger forests in Wisconsin. These studies did not provide any supporting documentation for these conclusions. There is no indication that the Mourning Warbler is area sensitive in Ontario. Austen et al. (2001) found no significant relationship between forest size and its abundance or presence in southern Ontario. James (1984b) and Coleman et al. (2000) did not consider it an area-sensitive species. It is a common breeder in ravines and urban parks within the city of Toronto, which is highly suggestive of it not being an area-sensitive species (Zimmerling in Cadman et al. 2007). It was common in 30-m-wide buffers between water bodies and clear-cuts in Newfoundland (Whitaker and Montevecchi 1999). In Saskatchewan, there was no relationship between forest size and its abundance (Hobson and Bayne 2000).

Essentially all studies concluded that the Mourning Warbler is a forest edge species (when it inhabits forested habitat) or that it nests in small forest gaps. It is possible for it to prefer both forest edge and local landscapes with high forest coverage. In Saskatchewan, it was randomly distributed in contiguous and fragmented forested landscapes, but was more common in areas with a high percentage of forest cover within 5 km. It was an edge species. Its presence and abundance were not significantly correlated with forest size (Hobson and Bayne 2000).

Ontario nests were in or among plant stalks, raspberry canes, fern fronds, hazel stems, grasses, and garden flowers. One was in a brush pile and another was on a clump of sedges. Most were 0-15 cm from the ground, but 2 were 0.3 m up, 2 were 0.6 m up, and 1 was 0.9 m from the ground (Peck and James 1987). Mills (1981) reported a Muskoka nest that was just off the ground in a patch of raspberries and jewelweed.

Throughout its range, the Mourning Warbler places its nest on or near the ground. Raised nests are typically 15-50 cm from the ground, rarely as high as 1 m. Nests are usually well concealed in dense herbaceous vegetation or shrubs, but rarely may be completely exposed. One was on top of a vine on the ground with no cover. Most nests are in tangles of dense vegetation such as raspberries, blueberries, chokecherry, horsetails, elderberries, jewelweed, roses, goldenrods, ferns, or coppice growth around stumps. Nests are frequently on top of hummocks or clumps of grasses and

sedges and occasionally on tops of logs. One nest was 14 cm from the ground and supported by fallen tree branches. The nest site is often in a grassy area among treetops left by loggers, near paths through forests, or at forest edges and roadsides. Some nests were in very wet areas, including within clumps of skunk cabbage and marsh marigolds, but most are in drier areas (Bent 1953; Campbell et al. 2001; Chapman 1907; Cox 1958, 1960; Gromme 1934; Harrison 1984; Hofslund 1954; Pitocchelli 2020).

The Mourning Warbler is territorial and the territory appears to contain both the nest site and foraging areas. In Minnesota, interspecific aggression was directed at the Common Yellowthroat and Chestnut-sided Warbler, but there was no mutual exclusion of territories. North of Lake Nipigon, 2 territories were 0.36 and 0.61 ha, but few observations were made and they may have been larger. Ten Minnesota territories averaged 0.77 ha (range 0.49-0.97 ha). One New Hampshire pair foraged within an area of 0.5 ha. Vermont territories were smaller than 0.5 ha (Cox 1960; Kendeigh 1947; Lent and Capen 1995).

No information is available on natal philopatry or adult site fidelity (Pitocchelli 2020). It is probable that natal philopatry is very low. Site fidelity may be low because the early successional habitat that the Mourning Warbler prefers does not persist long. Lent and Capen (1995) termed it a fugitive species that was constantly shifting its distribution to find ephemeral canopy openings embedded within a forested matrix.

Limiting Factors

Eggs have been reported in Ontario nests from late May until the third week of July, with most present in the last half of June (Peck and James 1987). In Algonquin Park, eggs are present from mid-June to mid-July, nestlings are present from late June to mid-July, and dependent fledglings have been observed from mid- to late July (Tozer 2012).

Courtship begins shortly after birds arrive and nesting occurs soon thereafter. No information is available on the time it takes to build a nest and whether there is a delay between nest completion and egg laying. One egg is laid per day. Incubation may begin with laying of the penultimate or even the first egg. The incubation period was at least 11 days at 1 Ontario nest and 12 days at 3 Minnesota nests. Young leave the nest when they are 7-9 days old (Cox 1960; Hofslund 1954; Peck and James 1987; Pitocchelli 2020).

No double broods have been recorded for the Mourning Warbler. It probably raises a single brood per season throughout its range. Clutches of 2-5 eggs were reported in Ontario (mode 4 eggs, average 3.71 eggs). In the remainder of its range, clutches of 2-5 eggs have been recorded, with 4 eggs most frequent and an average of 3.7 eggs (Bent 1953; Chapman 1907; Cox 1960; Harrison 1984; Peck and James 1998a; Pitocchelli 2020).

No information is available on the age of first breeding (Pitocchelli 2020), but it is probably 1 year. The mating system is probably monogamous, but this has not been confirmed.

The Mourning Warbler forages in dense undergrowth on but usually above the ground. Males forage at higher heights than females so they can alternate between singing and foraging. Females remain lower in the underbrush near the nest. North of Lake Nipigon, males sang at heights of 0.3-18 m (average 7.9 m). In Minnesota, males sang from near the ground level to a height of 12 m. Most

singing (37%) occurred in low underbrush less than 1.5 m tall. The second-most frequently used stratum was 6.1-7.6 m (22% of the time) where males often perched and sang for long periods of time. The primary foraging technique consists of gleaning branches of shrubs and turning over leaves to find prey (Cox 1960; Kendeigh 1947; Morse 1989; Pitocchelli 2020; Sodhi and Paskowski 1995). In Wisconsin, Sodhi and Paskowski (1995) compared the foraging strategies of the Mourning, Nashville, Chestnut-sided and Canada warblers. The woody plant species used most frequently for foraging by all species were trembling aspen, large-toothed aspen, sugar maple, red maple, white birch, hazel, and white pine. The Mourning Warbler and Canada Warbler foraged more frequently in aspens than the other species. Female Mourning Warblers foraged most frequently in shrubs. Male Mourning Warblers foraged lower than males of other species. Male Mourning Warblers foraged in shrubs 19% of the time, hardwoods 25%, aspens 39%, and conifers 17%. Females foraged in shrubs 42% of the time, hardwoods 30%, aspens 18%, and conifers 10%. Substrate usage by males was 15% twigs and leaves, 68% branches, 5% limbs and trunks, and 12% air. Female substrate usage was 15% twigs and leaves, 70% branches, 5% limbs and trunks, and 10% air. Foraging techniques for males consisted of 58% gleaning, 18% pouncing, 5% hovering, and 17% sallying compared with 34% gleaning, 34% pouncing, 16% hovering, and 16% sallying for females. The differences in gleaning by sexes were significant. Male and female Mourning Warblers were more similar in their foraging behaviours to birds of the same sex of other species than they were to each other. Average foraging height was 3.07 m for males and 2.68 m for females. The high use of hazel indicated use of young disturbed forest with high light penetration and a well-developed herbaceous and shrub layer.

The Mourning Warbler is largely insectivorous during the breeding season. The male feeds the female during the incubation period, typically with large green caterpillars. Both sexes feed the young, mostly caterpillars and other small insects (Bent 1953; Cox 1960; Pitocchelli 2020). Kendeigh (1947) analyzed the stomach contents of 8 adults north of Lake Nipigon. By frequency, the diet consisted of 24.2% lepidopterans, 15.8% spiders, 13.4% beetles (including click and soldier beetles), 11.6% true bugs (including stink bugs), 5.9% sawflies and other hymenopterans, 5.6% flies (including snipe, deer, and crane flies), and 1.5% soft-winged bugs. It demonstrates no numerical response to spruce budworm abundance. Near Manitouwadge, it decreased over time as budworm numbers increased, but not significantly (Venier et al. 2009). In Maine, a severe spruce budworm outbreak opened up the forest canopy allowing a dense understorey of raspberries, deciduous saplings, and regenerating conifers to develop. The forest was colonized by the Mourning Warbler shortly after this occurred (Pitocchelli 2020).

In Ontario, 3 of 35 Mourning Warbler (8.6%) nests were parasitized by the Brown-headed Cowbird. The cowbird has parasitized the Mourning Warbler in much of its range, including Illinois, Minnesota, and British Columbia. Outside Ontario, the number of nests reported in studies is 5 or fewer, so it is not possible to make meaningful estimates of the rate of parasitism, and it is likely to vary geographically. The effects of parasitism on its reproductive success are unknown (Campbell et al. 2001; Cox 1960; Graber et al. 1983; Harrison 1984; Manolis et al. 2002; Peck and James 1998a).

Habitat loss and degradation are not significant limiting factors for the Mourning Warbler in Ontario and throughout its range. It benefitted from the deforestation that occurred due to European settlement. Practices such as road building, mining, and clear-cut logging that open vast

expanses of boreal forest may be contributing to its range expansion. Large-scale habitat alterations may have allowed it to colonize northeastern British Columbia as late as the 1970s (Campbell et al. 2001; Nadeau and Gauthier in Gauthier and Aubry 1996; Pitocchelli 2020). Large-scale conversion of forested habitat to agricultural or urban uses may be detrimental. It appears to prefer areas where there is considerable forest cover locally, even if it is not area sensitive.

The Mourning Warbler responds well to forest management and is resilient, capable of adjusting to a variety of silvicultural practices (James 1984b; Pitocchelli 2020). Vanderwel et al. (2007) reviewed 42 studies on the effects of partial forest harvesting in the Boreal Forest Region with special reference to Ontario, and concluded that there were no significant effects on it at any level of harvest. Near Sault Ste. Marie, it was essentially absent in uncut northern hardwoods stands and increased significantly after stands were selectively cut (Holmes and Pitt 2007). Jobes et al. (2004) reported similar results in Algonquin Park. It was significantly more abundant in recent cuts (1-5 years old) than in cuts 15-20 years old. In the Carolinian Forest Region of Ontario, Holmes et al. (2004) found no significant differences in its abundance in uncut forests and those that had been harvested using selection or diameter-limit thinning. In the Canadian Shield of Ontario, there was no difference in its abundance in early successional clear-cuts and burns, but it was significantly more abundant in mid-successional clear-cuts than in mid-successional burns. It was significantly more abundant in early successional than mature stands, but significantly less abundant in mid-successional than mature stands (Zimmerling et al. 2017). In New York, Webb et al. (1977) completed bird surveys in uncut forests and forests where 25%, 50%, 75%, or 100% of the merchantable timber was removed. The Mourning Warbler was 1 of 6 species that occurred in all 4 logged areas at approximately the same density but was absent in the natural forest. Haché et al. (2013) studied the effects of selection harvesting in New Brunswick sugar maple–beech–yellow birch forests. Canopy closure was reduced by 20%. The first 2 years postharvest, shrub density was 13.7% lower than preharvest, but increased steadily thereafter until it was 29.5% higher 5 years postharvest. The selection harvest method was favourable to the Mourning Warbler. It was associated with a dense shrub layer and increased in density following harvest. It was first observed 3 years postharvest and increased thereafter with shrub density. It was absent in unharvested forests. In Nova Scotia and New Brunswick, it was absent in uncut stands but present in clear-cuts, plots thinned to 45% of their previous BA in shelterwood cuts, and in strip-cuts (Freedman and Johnson 1999; Freedman et al. 1981). In strip-cuts in Quebec, it was abundant in final cuts and found adequate breeding habitat in newly created strips, but was much less abundant in older strips where regeneration formed a closed canopy (Falardeau et al. 1999). In Alberta, it increased significantly when 90% of trees were removed from mixed stands, but there were no significant changes related to tree harvesting in deciduous and coniferous stands (Harrison et al. 2005). In the same province, it had a neutral response to clear-cut edges, with no difference in the mean distance that it occurred from edge in contiguous forest and adjacent clear-cuts; Villard et al. (2007) considered it a generalist species. Tittler et al. (2001) considered the Mourning Warbler a habitat generalist in Alberta. In the first year after clear-cutting, its abundance increased significantly with increasing BA retained within the cut. Three years postharvest, its abundance was unaffected by the amount of retained timber. Titterington et al. (1979) recorded its abundance in different seral stages of clear-cuts in Maine spruce–balsam fir stands. Abundance was low in the first stage, which consisted of dense slash and abundant open ground that dominated

for 2 years after cutting; highest in stage 2, which consisted of dense raspberries and regenerating hardwoods less than 2 m tall, typically 3-5 years after cutting; and intermediate in stage 3, which consisted of hardwood regeneration taller than 2 m with a well-developed but slower growing layer of coniferous regeneration. It was absent in the last 2 stages, which consisted of hardwood regeneration 4.5 m and taller with 10-15-cm diameter-at-breast-height trees, and a dense conifer overstorey with an open forest floor. In Minnesota, it was absent in uncut forests and responded positively to all levels of timber harvesting (Hanowski et al. 2003, 2005).

In Alberta, the Mourning Warbler was equally abundant at noisy compressor stations and quiet well pads, exhibiting no response to chronic noise (Bayne et al. 2008).

In Alberta, Bayne et al. (2016) studied the effects of energy sector disturbances on the Mourning Warbler. It exhibited no response, with no difference in its abundance at seismic lines, pipelines, or well pads and forest interior adjacent to these features.

Price (2004) predicted that the Mourning Warbler might disappear as a breeding species in southern Ontario if the average summer temperature increased by 2°C.

Status

Fleming (1907) stated that the Mourning Warbler was a rare summer resident and breeder in the Toronto area, and that it had been rare even as a migrant a few years previously. Baillie and Harrington (1937) considered it fairly common, breeding north to the transcontinental railway line and west to Lake of the Woods. Breeding was not documented in Middlesex County until 1962 (Scott 1988). In Elgin County, it was unknown even as a migrant in 1891, was a regular migrant but not a breeder in 1954, and was a locally common breeder by 2000. By then, it was the most common breeding warbler at some sites. Throughout the county, it was tied for third in abundance with the Ovenbird (Lancaster et al. 2004). The first atlas determined that it bred north approximately to a line from Sandy Lake to Attawapiskat. It was sparsely distributed in the Carolinian Forest Region and essentially absent in Essex and Haldimand counties. In the Great Lakes–St. Lawrence Forest Region, it was absent in much of Prince Edward and Frontenac counties. It was a common breeder, particularly in the Great Lakes–St. Lawrence and Boreal Forest regions (Fraser in Cadman et al. 1987). James (1991) considered the Mourning Warbler a common summer resident across the province north to Sandy Lake and Fort Albany.

The second atlas indicated that there had been no substantial change in the distribution of the Mourning Warbler. It was observed in a few locations north of the previously known northward limit. There were scattered new records for Essex, Haldimand, Prince Edward, and Northumberland counties, but it still remained largely absent from these areas. There was no change in its overall probability of observation, but there was a significant decline in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, and a significant increase in the Boreal Forest Region. The decline in the southern portion of the Shield may be due to forest maturation and succession. The increase in the Boreal Forest Region is likely because of increased forest management which provides suitable early successional forest cover. It was most abundant in a band across the province between latitudes 48°N and 50°N. This corresponds roughly to the area from Thunder Bay and Rainy River north of Kenora in the west, east to Lake Nipigon and the Clay Belt area (Zimmerling in Cadman et al. 2007).

The Mourning Warbler appears to have increased considerably since the late 19th and early 20th centuries. Chapman (1907) concluded that it was more or less rare throughout its range, and it also appeared to be rare in Ontario and Quebec at about the same period. Bent (1953) concluded that it still was not common in the eastern United States. The Breeding Bird Survey indicated annual decreases of 1.31% in Canada and 1.46% in Ontario 1970-2021. The trends 2011-21 were annual decreases of 0.55% in Canada and 0.388% in Ontario. All results were highly reliable except for the short-term Ontario trend which was of medium reliability (A.C. Smith 2023).

POSTFLEDGING PERIOD

At 1 Minnesota nest, fledglings remained in thick underbrush within the general area of the territory for 3 weeks after fledging. The young were unable to fly when they left the nest but could fly about 9 m with a fluttering, uneven flight 6 days after fledging. The young were last seen 20 days after fledging. They were feeding independently but were still accompanied by the adults (Cox 1960).

The Mourning Warbler continues to be an early successional species during the postfledging period. It is most common in regenerating clear-cuts and other areas with dense growths of deciduous shrubs and saplings, but it also occurs in forests. In Pennsylvania, Stoleson (2013) mist netted Mourning Warblers in 3-6-year-old clear-cuts and 90-110-year-old deciduous forests. They captured 4 adults and 17 juveniles in clear-cuts and 0 adult and 2 juveniles in forests. Streby et al. (2011b) caught 141 in regenerating clear-cuts 2-10 years old in Michigan, including 92 adults and 49 fledglings. In Michigan, Akresh et al. (2009) reported captures of Mourning Warblers per 1,000 hours of 0.1 in upland forest and 2.5 in riparian forest, with 80% of juveniles captured in riparian forest. Upland habitat was dominated by trembling and large-toothed aspen 100 years old. The riparian habitat was dominated by trembling aspen with an open canopy and a dense understorey of alder and honeysuckle.

MIGRATION

Judging by kills at television towers and other tall structures, migration appears to be nocturnal. Males arrive a few days earlier in spring than females. Males precede females by 5.0 days in upstate New York and 3.8 days in Massachusetts (Pitocchelli 2020). At Prince Edward Point, the mean date of spring arrival for males was 26.1 May and 30.4 May for females. It was the second-last warbler to arrive. There were few recaptures, suggesting that it stayed over for only 1 or 2 days. The difference in mean arrival dates between the sexes was greatest in years when males arrived the earliest (Francis and Cooke 1986). In Massachusetts, neither sex arrived significantly earlier over time 1970-2002; the difference in arrival times between the sexes did not change. Arrival time was not significantly related to any climate variables. The sex ratio did not change over time, but more females were captured in years with higher temperatures (Bauböck et al. 2012). In southern Ontario, most pass through in the last half of May, with some arriving in the first week of May (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). In the southern Shield, average arrival is in the third week of May with the earliest birds arriving in mid-May (Mills 1981; Tozer 2012). North of Lake Nipigon, the Mourning Warbler was first seen on 7 June (Kendeigh 1947). A bird observed at Shagamu on 5 June was considered a spring overshoot, as this is north of its known breeding range (Wilson and McRae 1993).

Autumn migration usually begins in August in Ontario. In the southern Shield, autumn migration begins in mid-August and continues into September, with some remaining into early October (Mills 1981; Tozer 2012). In the south, migration is underway by early August and most have passed through by mid-September, with a few remaining until late October (Black and Roy 2010; Curry 2006; Keast 1980; LaForest 1993; Lancaster et al. 2004; Weir 2008).

During migration, the Mourning Warbler seeks out low, dense vegetation. It tends to remain in dense vegetation less than 1.5 m tall and may occur in a variety of habitats provided they have a dense deciduous understorey. During migration in Illinois, it has been observed in brushy edges, thickets, understorey vegetation in open woods, mature bottomland forests, mature upland forests, and forest edges. It may occur in wetland margins and riparian areas with dense growths of willows, alders, and other shrubs. Birds in upland forests often seek wetter areas such as lower portions of ravines, which probably afford denser shrub coverage. Autumn migrants in South Dakota used both an extensive wooded riparian corridor and a 3.5-ha farm woodlot. Birds were able to gain weight while they remained within the woodlot, suggesting that it was good habitat (Bent 1953; Campbell et al. 2001; Chapman 1907; Cox 1960; Dean et al. 2004; Graber et al. 1983; Pitocchelli 2020).

Male Mourning Warblers may exhibit territorial behaviour during spring migration. Cox (1960) noted territoriality in some migrants. One male defended about 0.4 ha in a brushy area adjacent to a small stream.

During autumn migration, the Mourning Warbler is usually solitary, but it infrequently forages in mixed-species flocks. In Rhode Island, 5 fecal samples contained fruit, 4 contained insects, and 3 contained both fruit and insects (Pitocchelli 2020).

The Mourning Warbler is frequently killed during migration by colliding with communication towers and other tall human-made structures. More than 360 were killed at television towers in Wisconsin 1960-69. At the Lennox generating station chimneys, 202 were killed 1972-82. Highest kills occurred in 1981 when 82 were killed on 6 September and 74 were killed the following night (Graber et al. 1983; Pitocchelli 2020; Weir 2008). In the United States, the Mourning Warbler was highly vulnerable to striking low-rises and was 19.3 times more likely to suffer a collision with this type of building than average. It was not on the lists of the 20 most vulnerable species for striking residences 1-3 stories high or for high-rises (Loss et al. 2014). In Toronto, it was more likely to collide with buildings surrounded by hard surfaces such as parking lots, other buildings, and roads than buildings with vegetation and more canopy cover (Pitocchelli 2020).

The Mourning Warbler may suffer mass mortality during severe weather while migrating. A large kill occurred in spring over Lake Michigan following 2 storm systems with high winds, heavy rain, and hail. It is probably affected by storms while crossing the Gulf of Mexico and in the North Atlantic. Declines in eastern populations 1967-96 were correlated with storm frequency (Pitocchelli 2020).

James (1991) considered the Mourning Warbler an uncommon migrant in Ontario. Netting and banding results in the Kingston area indicate that it is more common than sight records suggest. In other areas, it has been noted that it appears rarer than it actually is, particularly in autumn when it does not sing, because it is very secretive, skulking in dense thickets and rank herbage (Bent 1953; Pitocchelli 2020; Weir 2008).

Common Yellowthroat

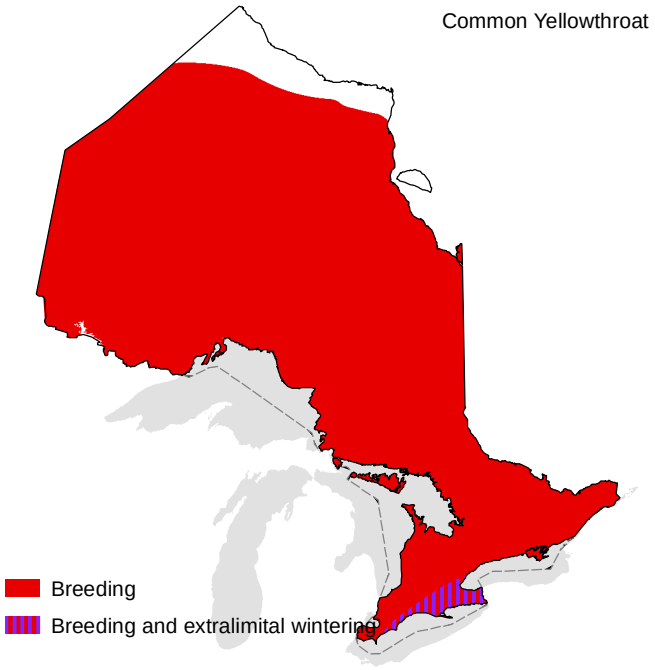
Geothlypis trichas

BREEDING SEASON

Habitat Requirements

In Ontario, the Common Yellowthroat breeds mostly in wet areas (83.1% of nests) and less frequently in dry habitats. Wet areas used for nesting included sedge, grass, and rush meadows and other types of meadow marshes (30.5% of nests); cattail and bulrush marshes (23.7%); bogs (13.6%); margins of lakes, rivers, and ponds (10.2%); and open, wooded swamps (5.1%). Dry nesting areas included brushy sites (10.2% of nests), grassy fields (5.9%), and a woodland edge at a road (0.8%). Nest sites had tall dense growths of rushes, grasses, sedges, and shrubs occurring either singly or in combination (Peck and James 1987).

In the Boreal Forest Region of Ontario, the yellowthroat occurs predominantly in wet habitats but occasionally in dry areas, and is strongly associated with the presence of deciduous shrubs and saplings. It occurs in open shrubby bogs and fens; shrub thickets along margins of lakes, rivers, and wetlands; in young clear-cuts regenerating with deciduous shrubs and saplings; and in open-



canopied forests. In the Pickle Lake area, it inhabited mostly shrub thickets, including deciduous and mixed shrubby areas. It was absent in forests, coniferous scrub, heath, and tundra (James 1980; McLaren and McLaren 1981). Near White River and Manitouwadge, it nested in regenerating stands 21 years old and younger, but not in stands 24-223 years old. It was significantly more abundant in clear-cuts 8-10 years old than those 3-5 or 13-25 years old (Venier and Pearce 2005; Venier et al. 2009). Near Hearst, Welsh and Fillman (1980) reported it in a 19-year-old clear-cut in a lower-slope mixed forest and in lowland coniferous clear-cuts 3-17 years old as well as in uncut lowland coniferous forest. It was most abundant in stands 5-13 years old, with numbers dropping off significantly in 17-year-old stands. It was the dominant species in 5- and 6-year-old clear-cuts. In the Clay Belt, it was most common in jack pine, black spruce, and balsam poplar stands. It occurred mostly in wetter, nutrient-poor stands (Welsh and Lougheed 1996). In the Boreal Forest Region of Ontario, it was associated with young, open-canopied, deciduous and mixed forests with high levels of disturbance and high interspersion of habitats, particularly between young and old forests. Stand size was the most important factor in determining its abundance, explaining 62% of variation (Rempel 2007; Rempel et al. 2007).

The yellowthroat breeds in similar habitat in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield. Near Gogama, it was common in regenerating jack pine stands where grasses and sedges covered most of the ground and deciduous shrub coverage was 25-75%. It gradually disappeared as the trees grew and shaded the ground. Maximum densities occurred when stands were 6-9 years old and few, if any, remained when trees were 20 years old (James and Peck 1995a). It was moderately common in jack pine stands near Parry Sound. These were open immature stands mixed with a variety of deciduous tree species with numerous openings due to the presence of rock outcrops and wetlands (James 1979a). In Muskoka and Parry Sound districts, Mills (1981) reported it along road and hydro line rights-of-way, in wet open areas, in bogs and alder thickets, and in shrubby fields. Three different studies examined its habitat use in Algonquin Park. MacLulich (1938) reported that it was abundant in beaver meadows, alder and willow thicket swamps, and other thickets. Martin (1960) reported it in wet and dry bogs, with lesser numbers in black spruce–white cedar stands. It was a characteristic species of bogs along with the Swamp Sparrow and these 2 species occurred in higher densities in bogs than reported for any other species in any habitat. In bogs, the yellowthroat ranged from the ground to 6 m, which represented the top of the canopy, but did not occur at the top of dead snags that extended 9 m from the ground. In black spruce–

white cedar stands, it ranged from the ground to 3 m, which corresponded to the top of the shrub layer and the bottom of the canopy. It occurred in low densities in balsam fir–spruce and balsam fir–spruce-hardwood stands and at edges of forest stands. In white pine shelterwood cuts in Algonquin Park, it was absent in 2-9-year-old cuts, present in 10% and 27.3% of plots over 2 years in 10-16-year-old cuts, and present in stands with no recent history of harvesting in 7.1% and 0% of plots (Kingsley and Nol 1999).

South of the Shield, the yellowthroat is associated mostly with marshes and thicket swamps, although it also occurs in treed swamps with open canopies and undergrowth of aquatic emergent plants. It is much less likely to use upland areas dominated by deciduous shrubs and saplings south of the Shield than further north. Cattail marshes are preferred habitat. One Ontario study found that there was no difference in its abundance in the interior and at the edge of marshes (Timmermans and McCracken 2001; Tozer et al. 2006). It usually prefers the outer portions of marshes where the water is shallow or the soil is only moist, particularly where there are scattered clumps of shrubs such as willows and dogwoods and occasional short trees. Where open-water marshes have an outer fringe of shrubs or meadow marsh communities, these are more likely to be inhabited. At Point Pelee, low numbers nested in forests with nearly complete canopy closure containing a high proportion of ash trees (Dodds and Otis 2009). In Durham Region, it nested in a very young pine plantation that was still dominated by willow shrubs and meadowsweet; in an old orchard overgrown with apples, hawthorns, and grasses; in open-canopied forests containing standing water and supporting dense shrub growth; and in a black spruce bog (Speirs and Orenstein 1975).

In Great Lakes coastal wetlands, the yellowthroat was positively correlated with wetland cover and negatively correlated with the amount of urban and agricultural land in the watershed. It was mostly unaffected by water levels but tended to decrease with higher water levels (Tozer et al. 2024).

In southern Ontario, the Common Yellowthroat was negatively correlated with organic farms and use of herbicides, but positively associated with corridors such as roads, railways, and utility rights-of-way. The negative association with organic farms may have been because conventional farms had significantly more riparian woodland, which is preferred habitat (Kirk et al. 2011).

Throughout its range, the Common Yellowthroat nests in a variety of habitats. These include all types of wetlands (bogs, fens, marshes, and thicket and treed swamps); thickets along margins of water bodies and watercourses and on dry hillsides and mountain slopes; in clear-cuts, burns, and other regenerating areas; in open-canopied forests, forest edges and forest clearings; in prairies and grasslands; in pine and oak barrens; and in agricultural lands. Despite its usage of numerous vegetation types, many authors consider the yellowthroat a habitat specialist. It occurs almost exclusively in open, early successional habitats. Presence of shrubs appears to be more significant than the moisture regime of sites. In some areas it chooses habitat based on shrub density and height.

The yellowthroat is commonly thought to be a wetland species, but it may be more abundant in wetlands because shrubs are more prevalent in these habitats. It may be one of the more abundant species in open bogs and fens and in thicket swamps. It is characteristic of marshes, but tends to inhabit edges of shallow-water marshes and meadow marshes where there is at least some woody growth. In treed swamps, it is most common in stands with an open canopy, standing water,

and patches of emergent vegetation or shrubs in the understorey. In New York, it was the most abundant species in clear-cuts 2-6 years old (Keller et al. 2003). In Wisconsin, it was abundant in cattail and bulrush marshes but nested in patches of medium-height willows (Hutto 1981). In Michigan, it nested in sites with damp or wet soils. Occupied habitat was characterized by a mixture of dense, lush herbaceous vegetation and woody plants, mainly shrubs and small trees. This habitat usually occurred along margins of streams, ponds, and lakes; in bogs; and in seepage areas below springs. Habitats ranged from savannah-like areas with scattered groups of shrubs and trees 0.9-4.6 m tall, to dense thickets of small woody plants that were usually less than 1 m tall. Habitats included marshes, sedge meadow marshes, shrub thicket swamps, and forest edges. Stewart (1953) concluded that the key habitat feature may be the dense growth of low vegetation, which is more prevalent in wet areas, rather than moisture itself. In Minnesota, Niemi and Hanowski (1984a) reported higher densities in tall than low shrub communities. It was uncommon in open spruce forests and absent in closed spruce forests and fens. In riparian willow habitat in Wyoming, the yellowthroat was significantly more abundant where willows were taller and less dense, although it used areas where willows were 0.27-2.12 m tall. It was most abundant where the willow habitat was more structurally complex (Olechnoswki and Debinski 2008). In North Dakota, highest densities were in juneberry thickets and willow shrub communities. Lowest densities were in lowland forests. It was associated predominantly with early stage deciduous habitats (Faanes and Andrew 1983). Grant et al. (2004) studied the effects of shrub invasion in mixed-grass prairies in North Dakota. Maximum vegetation height and coverage by shrubs 1 m tall or less and taller shrubs were significantly higher where the yellowthroat was present, and coverage by smooth brome was higher where it was absent. It increased as abundance of shrubs increased. Also in North Dakota, it was present in shrubby plots and absent in grassy and herbaceous plots without shrubs (Arnold and Higgins 1986). This was also the case in Georgia where it was one of the most common species in mixed grass and shrub habitats (Johnston and Odum 1956). In Great Lakes coastal marshes along Lake Michigan, increased woody vegetation improved habitat for the Common Yellowthroat. It was most abundant in wet meadows supporting more shrubs, deciduous trees, and deciduous snags and had a particular preference for wet meadows with willow shrubs. Its abundance was positively correlated with increasing shrub density; increasing abundance of alder, moss, trees, and snags; increasing shrub foliage diversity; and increasing frequency of willow. It was negatively correlated with graminoid cover, coniferous snags, and deep water. In these meadow marshes, it was one of the most abundant species (Riffell et al. 2001). In Utah, it was restricted in habitat use and preferred areas with high shrub density, moderate ground coverage, and little canopy coverage (Whitmore 1977). In Iowa, Delphey and Dinsmore (1993) studied yellowthroat usage of natural and restored prairie potholes. It was present in significantly more natural than restored potholes. All natural wetlands had zones ranging from open water in the interior to outer zones of aquatic emergents and low prairie or meadow marsh zones. The outer zone was often lacking in restored wetlands and the abrupt transition from pothole to upland habitat was less attractive to it. Also in Iowa, Fairbairn and Dinsmore (2001a) considered it associated with wet meadows and concluded that it may select wetlands based upon their vegetative structure. In Iowa, it also nests in managed grasslands planted to switch grass. In this habitat, it selected areas with higher forb abundance for nesting but this parameter was associated with lower nesting success. It selected sites with denser and more senescent vegetation for nest sites. The number of young fledged was positively correlated with the

proportion of senescent vegetation. In Wyoming, Finch (1989b, 1991a) studied its habitat use in different elevational zones and concluded that it was a habitat specialist because its use of habitat differed from habitat availability. Although it nested in both moist and dry areas, it selected areas with dense shrub coverage (more than 70% willow coverage), dense foliage cover through the shrub layer, and few trees. In Wisconsin, it was 1 of 12 species that commonly nested in tall thickets dominated by red-osier dogwood, meadowsweet, and a variety of willow species, and 1 of 13 that regularly nested in alder thickets (Hoffman 1989b). In the Boreal Forest Region, Erskine (1977) considered the yellowthroat characteristic of low shrubbery in tamarack and bog forests and one of the more numerous species in open, wet bogs dominated by sedges and low shrubs. In shrubby bogs, it is often a dominant species; it is also common in spruce bogs. In riparian habitat in Iowa, Stauffer and Best (1980) considered it a habitat specialist. It did not nest in forb, deciduous sapling, or deciduous or coniferous tree cover. Its abundance was significantly correlated with sapling richness and vertical stratification of vegetation less than 3 m tall, but negatively correlated with sapling size and shrubs. In Minnesota and Maine, it nested in open areas, marshes, bogs, and tall grasses. It was associated chiefly with high ground coverage in open marshland with few or no trees where it was codominant with the Yellow Warbler. The yellowthroat was also associated with shrub coverage (Collins 1983a; Collins et al. 1982). In New Hampshire and Maine, it was most abundant in white pine stands with numerous small deciduous trees in the understorey and in aspen stands. It was considerably less abundant in hemlock, northern hardwood, and spruce-fir stands and even less abundant in swamp hardwoods. It was absent in white birch stands. It was significantly more abundant in sapling-sized stands than in those dominated by pole-sized, sawtimber-sized, or large-sawtimber-sized trees. It was positively correlated with the number of deciduous trees larger than 10 cm diameter at breast height (DBH), the number of coniferous trees 2-10 cm DBH, and the total foliage volume of coniferous trees 2-10 cm DBH. It was negatively correlated with percent ground cover and the total foliage volume of deciduous and coniferous trees larger than 10 cm DBH (DeGraaf et al. 1998). In British Columbia, it often preferred willows but also occurred in drier habitats along edges of agricultural fields, airport runways, or damp meadows; in tall grass meadows bordered by shrubs; young cottonwood stands; and undergrowth of trembling aspen–conifer forests. More characteristic habitat included densely vegetated wetlands such as shallow lakes or ponds and similar habitat dominated by emergent vegetation such as tall sedges, reeds, cattails, or low shrub coverage of steeplebush, sweet gale, and willows; meadow marshes of sedges, grasses, and bulrushes; estuarine salt marshes, borders of rivers, beaver ponds, and sewage lagoons; ditches; permanent ponds in fields; wooded swamps; regenerating trembling aspen clear-cuts; and abandoned quarries (Campbell et al. 2001). In the Yukon, it always breeds in moist areas with shrubs, most frequently in shrubby wetlands dominated by willows and birches. Old beaver dams overgrown with shrubs provide good habitat. In forested communities, it is limited to riparian areas along back channels and sloughs rather than occurring along main rivers (Sinclair et al. 2003).

The yellowthroat may use a variety of open upland habitats. Most frequently, these are dry shrub thickets that may include shrubby fields, including those on hillsides; edges of drainage ditches in agricultural lands; hedgerows; overgrown orchards; pastures and abandoned fields; and road rights-of-way, particularly those through forests. It has also nested in Christmas tree plantations. In New Jersey regenerating fields, it occurred in fields 10-40 years old, the entire range of ages that was

studied. Along an interstate highway through forested habitat in Maine, it was significantly more abundant near the road than in forest interior. It was presumably attracted to the edge and open habitat created by the right-of-way (Brooks and Bonter 2010; Ferris 1979; Graber and Graber 1963; Gross in Bent 1953; Guzy and Ritichison 2020; Harrison 1984; Kendeigh 1947; Létourneau and Lafontaine in Gauthier and Aubry 1996; Parnell 1969; Suthers 1988). In North Carolina, it showed a preference for thickets, although it occasionally occurred in forests. Relative numbers seen were 2.89 in wet thickets, 2.59 in dry thickets, 0.55 in floodplain forests, 0.43 in pine-hardwoods forests, 0.20 in oak-hickory forests, 0.10 in pine forests, and 0 in beech forests. It was most common where the greatest proportion of vegetation was between 0 and 60 cm (Parnell 1969).

The Common Yellowthroat is characteristic of large open habitats created by clear-cuts or burns, and is often a dominant species in these habitats. It may also be common to abundant on utility rights-of-way where the vegetation is managed to keep it in an early successional stage. It usually inhabits clear-cuts about 3 years after cutting once a dense growth of raspberries and deciduous saplings becomes established. Populations tend to peak 5-10 years after cutting, and then decline rapidly with few remaining once trees reach pole size. How long a cut remains suitable depends upon how fast the regeneration grows and how much of the cover is coniferous, with conifers being less suitable. Clear-cuts where patches of trees are retained support lower densities because the retained areas are not used. Young burns are less suitable than similarly aged cuts. Burns tend to have lower densities of shrubs and saplings and very hot burns may affect productivity of the soils. Although regeneration may take longer on burns, they are valuable habitat and may remain suitable longer than cuts. Historically, fires would have been the principal means of establishing yellowthroat habitat in the Canadian Shield (Dessecker and Yahner 1987; Erskine 1977; Falardeau et al. 1999; Freedman and Johnson 1999; Hanski et al. 1996; Harrison and Kilgo 2004; Hoffman 1989a; Imbeau et al. 1999; Keller et al. 2003; Kirk et al. 1996; Lent and Capen 1995; Morgan and Freedman 1986; Thompson and Capen 1988; Titterington et al. 1979; Tittler et al. 2001; Yahner 1993, 2003). Yahner et al. (2002) examined avian assemblages on power-line rights-of-way through deciduous forests in Pennsylvania. The yellowthroat did not occur within the adjacent forest habitat, but was sixth in abundance on the right-of-way. It was ubiquitous and common in all treatment areas, which included areas where vegetation was hand cut, sprayed, mowed, or a combination of these techniques. It was most common in areas bordering the forest which were a combination of shrub cover types mixed with forb, grass, or tree cover. It was also common under the hydro wires where vegetation was mostly forbs and ferns.

The yellowthroat has nested in a variety of forest types, but is not a forest-dependent species. In almost all cases, it is associated either with very early successional stages of forest, shrubs at edges of forests, or openings within forests. In most cases, it is not attracted by the forest cover, but by open, shrubby areas associated with them. In Illinois woodlots, it had a strong negative association with distance to edge and the percentage of urban coverage within 1 km. An exception may be red maple swamps, where it is one of the most abundant breeding species in southern New England. It has the potential to occur in most swamps and lowland forests where there are openings in the canopy and deciduous shrubs and saplings in the understorey. In upland forests, it is associated with stands dominated by early successional species such as poplar and birch. It is absent from climax upland forests dominated by sugar maple and beech. In riparian forests in Michigan, it was much

more abundant in the outer upland band of forest, where it was presumably associated with edge shrubs, than in the contiguous floodplain forest. In Pennsylvania, it demonstrated a negative affinity for old-growth forests and was significantly more abundant in younger stands. Virtually all studies demonstrated that it is more abundant in stands with an open canopy (Back 1979; Beals 1960; Capen 1979; Dawson 1979; Fitch 1958; Golet et al. 2001; Graber and Graber 1963; Grant and Berkey 1999; Haney 1999; Inman et al. 2002; Mossman 1988; Niemi and Pfannmuller 1979; Noon et al. 1979; Robbins et al. 1979; Rumble and Gobeille 1998; Samson 1979; Schneider and Miller 2014; Taylor and Taylor 1979; Temple et al. 1979). In very open forest habitat in Indiana, its density was highest where coverage by low ground vegetation was 80+-100%. High densities were also associated with high shrub and low tree density. Fire in these communities was beneficial and it reached peak abundance when fire frequency was 7.3 fires every 15 years, the maximum frequency of fires (Grundel and Pavlovic 2007a).

Askins et al. (2007) stated that the yellowthroat was not an obligate grassland bird but that it was commonly found in tallgrass prairies where it was associated with low to moderate amounts of woody vegetation. In Illinois, it exhibits a preference for prairie-marsh ecotones and reaches its highest density in prairie, marsh–wet prairie, and meadow habitats. Its occurrence was positively correlated with mean grass height and shrub density and negatively correlated with density of live vegetation and grasses (Graber et al. 1983; Herkert 1994a). In Iowa, it was one of the most abundant species in Conservation Reserve Program fields. It was most abundant in fields with high coverage by forbs such as alfalfa, Canada thistle, dandelions, and prickly lettuce. It rarely occurred in fields with homogeneous grass cover, but was abundant in plots with patches of weedy forbs. Reed canary grass planted in waterways provided attractive habitat, and it was most abundant in grassed waterways in fields dominated by other grasses such as smooth brome, orchard grass, and red fescue. Its abundance was positively correlated with horizontal patchiness and percent coverage by forbs. It was negatively correlated with percent coverage by grasses (Patterson and Best 1996). In grasslands managed for waterfowl in Saskatchewan, it was more abundant in dense nesting cover plots than in native grasslands, and was absent in wheat fields. Dense nesting cover consisted of a mix of native and introduced wheat grasses, brome grass, alfalfa, and sweet clover (Hartley 1994).

In many areas, the Common Yellowthroat is a common inhabitant of pine and oak barrens. In Massachusetts, it is 1 of the 3 most common species in pine barrens. These areas are characterized by well-drained sandy soils supporting stands of open-canopied pitch pine with a dense shrub layer. Deciduous trees are uncommon in this habitat and consist primarily of black and white oaks. The ground cover is dominated by wintergreen and bearberry (Morimoto and Wasserman 1991a, 1991b). In New Jersey pitch pine barrens, it was the most common species in pine swamps. It was also common in upland forests with a dense, low shrub layer and uncommon on unburned plains (Brush 1987). In Wisconsin, it was one of the most common and regular species in pine and oak barrens. It occurred in every barren type except oak savannah. It was abundant in brush prairie; common in diverse barrens and clear-cuts; fairly common in open aspect barrens, almost forest, and coniferous plantations; and uncommon in open aspect and river terrace barrens (Mossman et al. 1991).

The yellowthroat rarely nests in low densities in agricultural crops. It is most likely to occur in fields of red clover, alfalfa, and mixed hay and is rare and infrequent in grain fields (Fitch 1958; Graber and Graber 1963; Graber et al. 1983).

Some studies examined the habitat requirements of the Common Yellowthroat at the landscape level. In Iowa, Fairbairn and Dinsmore (2001b) concluded that habitat features outside a wetland could be important in determining its presence. Its presence was positively correlated with the amount of semi-permanent wetland within 3 km, but negatively correlated with the amount of seasonal wetlands. In Connecticut, its probability of occurrence was negatively correlated with the amount of forest cover within 2 km (Askins et al. 1987). Austen et al. (2001) observed a similar relationship in southern Ontario, but it was not significant. In Illinois at the 400-m scale, it was positively associated with agricultural land (Glass and Eichholz 2023).

Other studies examined the yellowthroat's microhabitat requirements. In open habitat in Minnesota, its average habitat characteristics were 98.2% ground cover, 39% shrub cover, 12.4% canopy cover, 5.2 m tall canopy, 6.8% conifers, and 0.9 tree per 0.04 ha (Collins et al. 1982). In Vermont clear-cuts, habitat characteristics were 86.4% ground coverage by green vegetation, 7.9% ground coverage by slash, 30.9% canopy closure, 8.5 m tall canopy, 5.7 m canopy depth, 30 m^2 basal area (BA) deciduous trees, 0.4 m^2 BA conifers, and average DBH of 5.1 cm for deciduous species and 4.4 cm for conifers (Thompson and Capen 1988). In forests in the mid-Atlantic states, its abundance was positively correlated with moisture, percent ground cover, percent coverage by conifers, and number of trees smaller than 3 cm DBH. It was negatively correlated with canopy closure and the number of trees within a 0.04-ha circle (Robbins et al. 1989). In Illinois, its density was negatively associated with shrub density, which was an indicator of the abundance of nonnative shrubs, particularly common buckthorn (Schneider and Miller 2014). In Arizona, it nested in low dense shrubs. It tended to nest close to water and distant from trees. It occurred mostly in marshy habitat with dense foliage from the ground to 2 m. Brown and Trosset (1989) considered it a habitat specialist.

In Illinois, Rodewald and Vitz (2005) examined edge effects on the yellowthroat by netting in 3-7-year-old clear-cuts at differing distances from a mature forest edge. More were captured 50 and 80 m from edge than at 20 m from edge, but the difference was not significant. It exhibited no avoidance of edge. In Illinois, nests closer to edge had lower survival rates. It did not avoid edges or roads and nest density was higher in grasslands with a greater proportion of roads around the perimeter (Glass and Eichholz 2023).

The Common Yellowthroat is not an area-sensitive species in any of the habitats it uses. It was not area sensitive in Great Lakes coastal marshes (Riffell et al 2001) and Golet et al. (2001) reached the same conclusion for red maple swamps in Rhode Island. In Illinois, Lehnen and Rodewald (2009a) found no evidence of area sensitivity of it in shrub patches. Capture rates did increase with patch size, but not significantly. In the same area, Rodewald and Vitz (2005) captured more yellowthroats in large (13-16 ha) than small (4-8 ha) clear-cuts, but the difference was not significant. Two studies in Michigan and Iowa determined that its occurrence was positively correlated with wetland size. Both studies examined very small wetlands that were below its minimum territory size. The authors of the Michigan study concluded that analyzing their data from a finer or coarser scale could yield

different results (Crozier and Niemi 2003; Fairbairn and Dinsmore 2001a). The maximum sizes of wetlands investigated in these 2 studies were 9.42 and 20.5 ha, with means only slightly above 2 ha. It is unlikely that the yellowthroat was truly area sensitive in these areas. Studies conducted in grassland habitat concluded that it is not area sensitive. In Illinois, Walk and Werner (1999) and Herbert (1994a) observed no evidence of area sensitivity in grasslands. In Massachusetts, Vickery et al. (1994) determined that its abundance was significantly negatively correlated with grassland area. It was positively correlated with the density of tall shrubs and trees. The proportion of shrubby habitat decreased with increasing grassland area, which probably explained the negative relationship with area. Johnson and Igl (2007) examined its area sensitivity in grasslands in Montana, South Dakota, North Dakota, and Minnesota. In most areas, field size had no effect on it. At 3 sites, it was negatively affected by field size, but its density was positively associated with size at 1 site. They concluded that there was a greater tendency for area sensitivity in regions with high densities of yellowthroats. Studies in forested habitat demonstrated that it is either unaffected by forest size or that it declines with increasing forest size. In North Dakota and Pennsylvania woodlots, size had no effect on it (Grant and Berkey 1999; Keller and Yahner 2007). In riparian forests in Maryland and Delaware, there was no difference in its probability of detection in forests 50, 100, 200, 300, and 800 m wide (Keller et al. 1993). In South Dakota, it was much more abundant in isolated woodlots 0.7-3.5 ha in area than in large, contiguous riparian woodlands (Gentry et al. 2006). In southern Ontario and the mid-Atlantic states, its abundance and probability of occurrence were significantly negatively correlated with woodlot size (Austen et al. 2001; Robbins et al. 1989).

Half of Ontario nests were on the ground and the remainder were 0.2-1.4 m above ground, mostly 0.2-0.3 m up. Nests were usually well concealed: among sedge or grass stems (54.1% of nests), among shrub stems (17.8%), attached to cattail or bulrush stems (11.1%), attached to both grasses and shrubs (5.9%), under boughs of shrubs or small trees (5.9%), among plant stalks (3.0%), beside fallen logs (1.5%), and near the top of a shrub (0.7%). Nests were in 9 species of deciduous shrubs and 1 coniferous tree species (Peck and James 1987).

Throughout its range, the yellowthroat places its well-concealed nest on or near the ground, usually within 7.6-10 cm of the ground, but occasionally as high as 1.8 m and rarely as high as 3 m. Higher nests tend to occur later in the season or be above water among emergent vegetation. Nests are typically in clumps of grasses or sedges, among herbaceous vegetation or shrubs, and, less frequently, above water in emergent vegetation. Nests are occasionally at the base of a tree or shrub, but these nests are also typically within clumps of grasses or sedges. Elevated nests may be simply wedged between dense stalks of vegetation without being attached to them. One nest was in a shoe on an exposed rafter under a house (Campbell et al. 2001; Chapman 1907; Graber et al. 1983; Gross in Bent 1953; Guzy and Ritichison 2020; Mousley 1916a; Stewart 1953).

Males establish territories immediately upon arrival and are aggressive toward other species such as Black-capped Chickadee, Yellow Warbler, Field Sparrow, and Henslow's Sparrow, but only until the females arrive. Latecomers have to be aggressive to obtain a territory, which typically involves a reduction in size of established territories and boundary shifting. In Wisconsin, larger dominant males established territories in coniferous bog communities with dense herbaceous cover and many small and dead trees. Smaller males established territories in areas dominated by

grass. Once territorial boundaries are established, trespassing seldom occurs, but intruders are quickly dispatched. Birds raising a second brood may adjust the territory boundaries after the first brood fledges. Territory boundaries are relaxed when the adults are feeding nestlings and when fledglings are present. Territoriality ceases with the onset of the postnuptial moult during the first half of August. Family groups may range unchallenged over boundaries while they are foraging. In Algonquin Park, territory size averaged 0.14 ha (range 0.02-0.64 ha) with a depth of 4.9 m. Five Illinois territories averaged 0.23 ha (range 0.01-0.44 ha). Eleven other Illinois territories averaged 0.57 ha and 3 others averaged 0.36 ha. In a 0.20-ha Illinois swamp, 17 nests were found, suggesting an average territory size of 0.01 ha. In Michigan, the territories of 10 monogamous males averaged 0.51 ha (range 0.32-0.73 ha). One Kentucky male defended 1.38 ha, but the habitat may have been marginal. Territory sizes of 0.8 ha were reported elsewhere in Kentucky. Other territory sizes include 0.2-2.9 ha in Michigan, 0.16-0.6 ha in Minnesota, 0.5 ha in Rhode Island, 0.29 ha in Maine, 0.5-0.93 ha in California, 0.1 ha in Texas, 2.20 ha in Colorado, and 0.3-0.4 ha in New York. Over 3 years in Massachusetts, territory densities were 1.8-1.9 per ha, suggesting territory sizes of 0.53-0.55 ha. A polygynous male in New York had a territory of 1.2 ha, approximately twice the size of those of monogamous males. In Michigan, a polygynous male had a territory of 1.38 ha; the average size for monogamous males was 0.51 ha. The 2 females in the polygynous mating had home ranges that were entirely separate and they were probably unaware of each other (Brewer 1955; Fitch 1958; Graber et al. 1983; Gross in Bent 1953; Guzy and Ritichison 2020; Kendeigh 1945; Létourneau and Lafontaine in Gauthier and Aubry 1996; Martin 1960; Morimoto and Wasserman 1991a; Morse 1977; Powell and Jones 1978; Stewart 1953).

In Ohio clear-cuts, 3 of 131 juveniles (2.3%) returned to their natal site. In Michigan and Minnesota, 1 of 85 nestlings (1.2%) was found 2 years later approximately 100 m from where she was banded. Another female bred the year after banding about 1,500 m from the natal site. In New Jersey, 1,083 yellowthroats were banded, but the number of juveniles and adults was not specified. Overall, 164 (15.1%) were recovered at the same area, including 125 adults and 39 juveniles (Guzy and Ritichison 2020; Lehnen and Rodewald 2009b; Suthers 1988). Schlossberg (2009) reported an average return rate of 2% for juveniles based on 216 birds and 2 studies. In a resident population at Brownsville, Texas, genetic analyses determined that young dispersed and did not defend territories near their natal area, and relatives did not appear to defend territories near each other (Roy et al. 2013).

Adult site fidelity appears to be low for migratory populations, possibly because the early successional habitat that it prefers is transitional. In Ohio, 41 of 128 adults (32.0%) returned to the same site. In Michigan and Minnesota, 1 male and 1 female of 11 adults (18.2%) returned the following year to the same territory. Adult return rate was 55% in the Rio Grande Valley where the yellowthroat is a year-round resident; 59% of males and 43% of females returned to breed at the same site. Between-year territory retention rates in 2 subpopulations of the resident subspecies in Texas were 45% and 89% (Guzy and Ritichison 2020; Lehnen and Rodewald 2009b). Schlossberg (2007) reported an average adult return rate of 47% based on 160 birds and 2 studies. In Texas, most males defended the same territory that they held the previous year. Birds defending another territory settled an average of 168 m from the previous year's territory (Roy et al. 2013).

Limiting Factors

Eggs have been reported in Ontario nests from mid-May to the end of July, with most present in the last 3 weeks of June (Peck and James 1987). In Algonquin Park, nests are under construction from early to late June, eggs are present from early June to late July, nestlings are present from late June to late July, and dependent fledglings have been observed from late June to late August (Tozer 2012).

Courtship begins as soon as females arrive and extends over 6-7 days. Females chose their mate within 1 or 2 days and select a nest site. Nest building may be completed in as little as 2 days or take as long as 7-10 days. Egg laying typically starts 2-4 days after the nest is complete, but as many as 8 days may elapse before an egg is laid. One egg is laid per day, but some days may rarely be skipped during periods of cold weather. Incubation begins with the laying of the last egg. The incubation period has been reported as 12 days, with a range of 11 days 3 hours to 12 days 19.75 hours in Michigan. The incubation period of 1 Ontario clutch was approximately 14 days. The nestling period is 8-9 days and is usually 7.8-9 days (Gross in Bent 1953; Guzy and Ritichison 2020; Kendeigh 1945; Peck and James 1987; Stewart 1953).

The Common Yellowthroat routinely raises 2 broods per season in southern Michigan and Texas, but is single brooded in northern Minnesota. Egg dates suggest that second broods may be common throughout its range. No second broods have been confirmed in Ontario or Quebec. Replacement clutches are common if a nest is lost. One Michigan pair made 3, and possibly 4, nesting attempts before successfully rearing a brood, which consisted of 2 cowbirds. It builds new nests for replacement clutches and second broods, with subsequent nests placed in the territory. The shortest reported interval between nest loss and building a new nest was 10 days and the interval between the start of 2 consecutive nests when the first was successful was 28 days in 1 case. Clutches of 2-5 eggs were reported in Ontario (average 3.97 eggs, mode 4 eggs). Elsewhere, clutches of 2-6 eggs were reported. The average size of 675 clutches, excluding those from Ontario, was 3.99 and 4 was the most frequent clutch size. In Michigan, early clutches were larger than later ones, with an average of 5.0 eggs in June and 4.2 in July. In other areas, no difference in clutch sizes occurred between early and late nests (Campbell et al. 2001; Chapman 1907; Graber et al. 1983; Guzy and Ritichison 2020; Hofslund 1957; Létourneau and Lafontaine in Gauthier and Aubry 1996; Gross in Bent 1953; Peck and James 1987; Stewart 1953).

The age at first breeding is 1 year. Both sexes can breed in their first year, but the incidence of this may vary individually and geographically. The yellowthroat is typically monogamous, but rare cases of polygyny have been documented. Polygyny is likely to occur only where there is a shortage of males so individuals can defend a larger than normal territory. Females exhibit no fidelity to their mates and may copulate with other males. The frequency of extra-pair copulations and paternity is unknown (Ford 1996; Guzy and Ritichison 2020; Powell and James 1978; Stewart 1953).

The yellowthroat is selective regarding the heights it forages at, and males forage at greater heights than females. In Massachusetts, females avoided foraging at heights of 1.5-3 m and above 6 m. Males foraged more opportunistically and used vegetation at different heights in proportion to their availability. Females foraged lower because they were associated with the nest, which was usually no more than a few centimetres from the ground. Males foraged and sang at a variety of

heights above 0.5 m. In June in Wyoming, mean foraging height was 0.18 m and this increased to 1.41 m in August. The increase in foraging height was attributed to the fact that other shrub-nesting warblers had left by this time. This study did not separate the sexes when calculating foraging heights. The increased height of foraging in August could also have been because females no longer had to tend to nests. In Massachusetts, there was no difference in plants used for foraging by the sexes. They exhibited a preference for feeding in scrub oak, used pitch pines and deciduous species according to their availability, and used ericaceous shrubs and herbaceous species less than their availability. There is no difference in the foraging techniques of the sexes and gleaning is the most frequent foraging technique, representing 93-100% of prey searches. Other less frequently used techniques include taking food from the ground, hovering, and hawking. Foraging occurs mostly at heights of 0-6.2 m, but occasionally as high as 15 m, predominantly on leaves, but also on the ground, on branches less than 1 cm in diameter, on bark, and on flowers and fruit. One study found that most prey captures were in the distal half of branches. Other studies found that it foraged equally on the inner and outer portions of trees. It prefers areas of dense vegetation for foraging. In Wyoming, 7% of foraging occurred where vegetation density was 50-85%, 27.3% at density of 85-100%, 22.7% at density of 15-50%, and 0% at density of 0-15%. In North Carolina, strata used for foraging included 6.2% in the canopy, 21.9% in low trees, 68.8% in shrubs, and 3.1% on the ground. In the canopy, 3.1% of all foraging occurred at the top of the crown, 3.1% in the lower crown, and 0% in the inner crown and on the bole. In low trees, 12.5% of foraging was at the top of the crown, 3.1% in the inner crown, 6.3% in the lower crown, and 0% on the bole. On shrubs, 12.5% of foraging occurred at the top of the crown, 3.1% in the inner crown, 0% in the lower crown, 43.8% in dense thickets, 3.1% in brush piles, and 6.3% in grasses. On the ground, 3.1% of foraging occurred in dense thickets and 0% occurred in grasses, at water's edge, or in the open (Guzy and Ritichison 2020; Hutto 1981; Lent and Capen 1995; Morimoto and Wasserman 1991b; Parnell 1969).

Young are initially fed small insects and larvae. By the age of 6 days, they are provided spiders and adult insects such as small moths, beetles, and grasshoppers. Food brought to an Iowa nest over an entire nesting season consisted of 22.2% unidentified insects, 20.5% moths, 17.1% larvae of various types, 16.5% spiders, 6.9% mayflies, 5.4% unrecognizable material, 3.6% flies, 3.2% damselflies, 1.2% caterpillars, 0.8% beetles, 0.8% chrysalises, 0.7% butterflies, 0.6% seeds, 0.4% grasshoppers, and 0.2% caddisflies. The adult diet consists of mostly insects and spiders. In Arizona, stomachs of 10 birds contained, in decreasing order of frequency, spiders, true bugs, flies, beetles, ants and termites, various larvae, hymenopterans, grasshoppers, and soft-winged bugs. In Illinois, 4 yellowthroats had consumed 80% lepidopterans (mostly cankerworms, but also other families), 8% beetles (weevils and rove, minute brown scavenger, and long-horned beetles), 4% flies (mostly gnats), 5% true bugs (mostly ash-gray leaf bugs), and a single hymenopteran, spider, and harvestman. It also eats katydids, gypsy moths, fall webworms, leafhoppers, aphids, grubs, plant lice, leafroller moths, dragonflies, locusts, insect eggs, and pokeweed (Graber et al. 1983; Gross in Bent 1953; Guzy and Ritichison 2020; Létourneau and Lafontaine in Gauthier and Aubry 1996; Stewart 1953; Suthers 1988; Whelan et al. 1989).

The yellowthroat is a common host of the Brown-headed Cowbird. It occasionally rejects cowbird eggs by abandoning the nest or building a second or even third nest over the cowbird eggs. In most cases, it accepts cowbird eggs. Most parasitism occurs in the first yellowthroat nest

with little to no parasitism of replacement and second clutches. Cowbird parasitism greatly reduces yellowthroat productivity and may be a limiting factor in some areas. At 1 Michigan study area, only 1 of 9 parasitized nests (11.1%) produced a yellowthroat fledgling. The average number of yellowthroat fledglings produced was 0.1 per parasitized nest compared with 1.9 per unparasitized nest. Another Michigan study determined that 3 of 20 parasitized nests (15%) produced yellowthroat fledglings. Fifty-eight percent of the total egg loss of yellowthroats was attributed to the cowbird. Of losses due to cowbirds, 33% were from removal of the host egg, 20% because of punctured eggs, 13% due to nest desertions caused by cowbird activity, and 33% to loss of incubation heat to the larger cowbird eggs. There was a direct relationship between hatching success and the number of cowbird eggs in the nest. No more than 2 cowbird eggs or 1 cowbird and 2 yellowthroat eggs hatched in any nest. If more than 1 cowbird egg was present, no yellowthroat eggs hatched. The heat of incubation each cowbird egg received was enough to prevent the hatching of 2 yellowthroat eggs. If yellowthroats successfully raise a cowbird, they do not renest. No loss of nestlings was attributed to cowbirds, and yellowthroat nestlings developed at the same rate in parasitized and unparasitized nests. Nine of 20 parasitized nests (45%) produced cowbirds. An average of 1.3 cowbirds fledged per successful nest, but only 0.6 were produced per parasitized nests. In Ontario, 36 of 187 nests (19.3%) were parasitized; 1 nest contained 2 yellowthroat eggs and 6 cowbird eggs. Parasitism rates vary considerably geographically: 7% in southern Quebec but 18.3% of all nests in Quebec; 18% of 35 British Columbia nests; 31.4% of 35 nests in Iowa; 10 of 22 (45.5%) and 20 of 52 nests (38.5%) in Michigan; 15 of 67 nests (22.4%) in Illinois; 19.7% of 84 Minnesota nests; 5 of 9 nests (55.6%) in Arizona; 42.0% of 88 nests in the Great Plains; and 0 of 7 nests in South Carolina (Campbell et al. 2001; Graber et al. 1983; Gross in Bent 1953; Guzy and Ritichison 2020; Hofslund 1957; Kilgo and Moorman 2003; Létourneau and Lafontaine in Gauthier and Aubry 1996; Lowther 1985; Peck and James 1987, 1998a; Sodhi 1995; Stewart 1953).

Habitat loss is not a significant limiting factor for the yellowthroat. Extensive deforestation in the mid-19th and early 20th centuries probably increased the amount of habitat available for it, although some forests that were removed were probably swamps that were suitable habitat. Significant wetland losses continued until the mid-1980s and this undoubtedly reduced habitat availability. Overbrowsing by deer and clearing of shrubs on cottage lots may render some habitats unsuitable. The replacement of shrub-lined drainage ditches with underground tile drainage results in habitat loss. Early mowing of hayfields, particularly those planted to alfalfa, usually results in the loss of nests, although this is poor habitat that is seldom inhabited (Guzy and Ritichison 2020; Létourneau and Lafontaine in Gauthier and Aubry 1996; Olechnowski and Debinski 2008; Stauffer and Best 1980).

Timmermans and McCracken (2001) examined population trends of the yellowthroat in relation to Great Lakes water levels. It was more abundant when lake levels were low and declined as levels increased. Higher water levels result in more open water, fewer emergents, and often a decrease in the amount of transitory meadow marsh between open-water marsh and upland habitats.

Forest thinning and clearing is beneficial for the yellowthroat and often creates habitat where none existed previously. Diseases, windstorms, ice storms, and other factors that reduce canopy closure are beneficial. The suitability of these habitats is short-lived, becoming unsuitable once the

canopy closes or young forests reach large sapling or pole size. Clear-cuts are most beneficial, followed by strip-cuts, shelterwood cuts, and selective thinning. In Pennsylvania timber improvement cuts where dead, dying, diseased, suppressed, and low-quality trees were removed, stands where snags were retained supported significantly higher densities of yellowthroats than those where snags were removed. Snag-retention areas had a more patchy and open canopy (52.9% canopy closure compared with 71.7% closure) and significantly more woody vegetation less than 1.5 m tall. In New York clear-cuts, it was the most abundant species and represented 30-40% of the entire avian population. It became abundant immediately after cutting and remained the dominant species until the study was terminated 6 years postharvest (Guzy and Ritichison 2020; Keller et al. 2003; Stribling et al. 1990). In the Canadian Shield of Ontario, there was no difference in its abundance in early successional and mid-successional clear-cuts and burns in the same seral stages. It was significantly more abundant in early successional than mature stands and equally abundant in mid-successional and mature stands (Zimmerling et al. 2017).

Two studies examined the effects of spraying clear-cuts with glyphosate, which suppresses deciduous woody species. In Nova Scotia and New Brunswick, there was no significant difference in the abundance of the yellowthroat on sprayed and control plots. It exhibited somewhat lower abundance on sprayed plots until the second postspray year but recovered by the fourth postspray year. In Maine, it was the most abundant species in untreated areas and second in abundance in treated areas. Its mean density was significantly less in treated sites than in control areas. Territories on treated sites were in areas where some uncontrolled shrubby vegetation remained, areas missed during the herbicide application. This was particularly evident 2-3 years after application. Invertebrates were much less abundant after spraying and were mostly in untreated skipped areas. Its density was positively correlated with the number of hardwood stems, vegetation height, total foliage density, and the foliage density contributed by each stratum (Freedman and Johnson 1999; Santillo et al. 1989).

The use of grasses for biofuel production may be beneficial to the yellowthroat. It is known to nest in fields planted to switch grass, reed canary grass, and Chinese silver grass (Robertson et al. 2012). It occasionally nests in hayfields dominated by alfalfa. In Iowa, density in that habitat was low. Males deserted their territories after mowing and never returned (Frawley and Best 1991).

Agricultural chemicals may be detrimental to the yellowthroat. One was found dead after granular carbofuran, an insecticide, was applied to a field. Poisoning can occur from direct ingestion of the granules or by consuming poisoned insects (Guzy and Ritichison 2020).

In Alberta, there were no significant differences in the yellowthroat's abundance at seismic lines, pipelines, or well pads than in forest interior adjacent to these facilities (Bayne et al. 2016). In West Virginia, it was significantly more abundant near well pads, access roads, and pipelines than in areas distant from these facilities (Farwell et al. 2019).

In Massachusetts, Zuckerberg and Vickery (2006) examined the effects of burning and mowing shrublands on the Common Yellowthroat. Shrubby areas were mowed 1-3 times or burned once in treatment areas, management that is undertaken to maintain habitat for grassland and shrubland species. It preferred control and burned shrublands and avoided shrublands that had been mowed. It was more abundant than expected in shrublands that had not been mowed, less abundant than

expected in shrublands that had been mowed once, and absent in shrublands that had been mowed 2 or 3 times. Shrublands that were left unmanaged or burned once were not noticeably different and were characterized by tall shrubs. Habitat preferred by the yellowthroat consisted of areas having shrubs 1-2 m tall and no litter cover. In North Dakota mixed-grass prairie, it was most abundant in grasslands that had not been burned for more than 80 years. Fire increased the amount of grasses and decreased shrub coverage. It showed a consistent and distinctly negative reaction to fire; it started to recover 7-8 years postfire (Madden et al. 1999). In grassland habitat in Indiana, Grundel and Pavlovic (2007a) found that it benefitted from burning at a frequency of about a fire every other year. In Illinois, daily nest survival was positively associated with distance to shrubs and negatively associated with vegetation height and density, suggesting that the reduction of woody vegetation and plant biomass by prescribed burns may benefit nest success (Glass and Eichholz 2023).

Drought may have adverse effects on the yellowthroat. In Wisconsin, its abundance decreased with increasing drought indices, with a 1-year time lag. In North Dakota, numbers fluctuated considerably over a 25-year period and were significantly associated with the number of ponds present in May (Blake et al. 1992; Niemuth et al. 2009).

In Pennsylvania and New Jersey over a 15-year period, hemlock declined from 56% of the total basal area to 46% due to mortality from the hemlock woolly adelgid. The amount of woody understorey increased as a result of the more open canopy. The yellowthroat increased because of these habitat modifications (Toenies et al. 2018).

Status

The Common Yellowthroat has always been common in Ontario and may be locally abundant. McIlwraith (1894) reported that it was widely but irregularly distributed, being an abundant breeder in some locations and mysteriously absent in other areas of suitable habitat, such as in Hamilton. Baillie and Harrington (1937) reported that it was a common breeder north to southern Kenora and northern Sudbury districts, and that it occurred sparingly further north to Moose Factory. The first atlas demonstrated that it bred from the southern boundary of the province north throughout the Boreal Forest Region and sparingly in the Hudson Bay Lowland where it was found in a few inland locations near Hudson Bay. It was the most abundant warbler in the province (McLaren in Cadman et al. 1987). In certain habitats, such as bogs and young clear-cuts, it may nest in high densities and be one of the dominant species (Martin 1960; Welsh and Fillman 1980). In large marshes in the south, it is often fourth in abundance (Tozer et al. 2006). James (1991) considered the yellowthroat a common breeder across the province north to Big Trout Lake and Attawapiskat, and probably occasional further north in the western portion of the province.

The second atlas confirmed that the range of the Common Yellowthroat included the entire province except for the northern portion of the Hudson Bay Lowland and Tundra Region. Although individual singing males were detected along the Hudson Bay coast, few occur within 100 km of the northern coast. It was detected in several squares north of Attawapiskat, which may represent a modest range expansion. Its probability of observation was similar province-wide during both atlases, although the tendency was toward an increase. Significant increases in its probability of observation occurred in the Boreal Forest Region and Hudson Bay Lowland. It attained its highest

abundance in the eastern portion of the Boreal Forest Region, north and east of Georgian Bay, and in a broad band along the southern edge of the Shield (McLaren in Cadman et al. 2007).

Marsh Monitoring Program results indicate that the Common Yellowthroat increased at a rate of 1.2% per year in the Great Lakes basin from 1995 to 2012 (Tozer 2013). In Great Lakes coastal wetlands, it decreased at an annual rate of 2.3% 2011-21 (Tozer et al. 2024). Breeding Bird Survey data indicate that it decreased at annual rates of 0.256% in Canada and 0.351% in Ontario 1970-2021. Trends 2011-21 were an annual increase of 0.438% in Canada and an annual decrease of 0.304% in Ontario. All results were highly reliable except for the Canadian long-term trend, which was of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Recently fledged young do not move far unless they are disturbed, initially remaining within 1-2 m of the nest before moving to adjacent woods or thickets. One brood was still within a few feet of the nest 3 weeks after fledging. The parents and young may move in search of food and travel as far as 300 m from the territory (Guzy and Ritichison 2020). In Michigan, adults that nested in riparian forests remained there after the young fledged, and fledglings also remained there (Akresh et al. 2009). The adults continue to feed the young approximately 2 weeks after fledging. Fledglings continue to beg from the parents and may not be completely independent until 22-28 days after fledging. Young from second broods may be fed until it is time for autumn migration (Guzy and Ritichison 2020).

In Michigan, both adults and juveniles were captured in upland mature forests dominated by trembling aspen and large-toothed aspen, and in riparian trembling aspen forests with an understorey of honeysuckle and alder. Both age classes were significantly more abundant in riparian forests, where 79% of fledglings were captured (Akresh et al. 2009).

Both adults and juveniles frequently inhabit young regenerating clear-cuts during the postfledging period. In West Virginia clear-cuts, abundance of the yellowthroat was negatively correlated with increasing BA of retained trees. Residual trees inhibited understorey growth and limited stem density. Residual trees provided perches for raptors but did not offer protection from raptors. Within clear-cuts, it avoided residual trees and captures were greater in areas with few nearby trees. In Pennsylvania, it was 1 of the 5 most frequently caught species in clear-cuts that were considered early successional species. It was also 1 of the 10 most abundant species captured in forests during the postfledging season (McDermott and Wood 2010; Stoleson 2013; Streby et al. 2011b; Vitz and Rodewald 2006). In Missouri, Porneluzi et al. (2014) netted during the postfledging period 2-15 years after an oak-hickory-pine forest was clear-cut. Numbers captured were quite low and yellowthroats were netted in only years 3 and 4 after cutting.

On Pennsylvania hydro transmission line corridors through forested habitat, the yellowthroat was abundant during the postfledging period. In August, it was absent within the adjacent forest habitat, but occurred at densities of 200-347 per km^2 on the rights-of-way. In 1 year, an average of 2.50 families per day was observed; 5.83 per day were seen the following year. One year it was the most abundant species in this habitat; it was third in abundance the other year (Yahner et al. 2002).

MIGRATION

The Common Yellowthroat is a nocturnal migrant. All North American populations are migratory except for resident populations in Florida, along the Gulf Coast, in Texas, and in the southwest (Guzy and Ritichison 2020; Harrison 1984). Birds appear to migrate singly rather than in flocks (Campbell et al. 2001). Encounters of banded birds indicate a predominantly north-northwest-south-southeast orientation in Ontario. Two birds banded in Ontario were recovered in Florida during autumn migration (Brewer et al. 2018). Atwood (1992) used morphological measures to identify discrete breeding populations. Most birds measured at Toronto were associated with breeding populations along the Ottawa and St. Lawrence rivers near the Ontario-Quebec border, the Georgian Bay area, northeast of Sault Ste. Marie, and western Quebec. A few were associated with breeding populations in Newfoundland, Nova Scotia, and Anticosti Island. Toronto migrants represented predominantly birds breeding in southern Ontario and southwestern Quebec, and orientation appeared to be mostly north-south. The destinations of spring migrants were not confirmed.

Males arrive in spring before females. At Prince Edward Point, the mean date of arrival was 18.8 May for males compared with 23.0 May for females. Few birds were recaptured, indicating that most remained on site only 1 or 2 days (Francis and Cooke 1986). In Michigan, most females arrived about a week after the first appearance of males (Stewart 1953). In Massachusetts, the average difference in arrival by the sexes was 5.5 days. There were no significant changes in arrival times over a 33-year period or in the relative timing of arrival of the sexes. There were no significant relationships with any climate variables and timing of spring migration (Bauböck et al. 2012). In Maine, males arrived significantly earlier than females by 5.0 days. After-second-year birds arrived significantly earlier than second-year birds. Stopover lengths were not significantly different: 2.0-4.3 days for males and 1.8-6.1 days for females (Morris et al. 2003).

In southern and central Ontario, the yellowthroat typically arrives in early to mid-May, with the earliest migrants arriving in late April. Migration is mostly over by the end of May, but a few may remain into the first week of June (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). At Long Point, the spring midpoint of migration is 20 May (Mills 2005).

During autumn, there is no difference in timing of migration by juveniles and adults. Woodrey and Chandler (1997) compared autumn migration timing of the 2 age classes at Long Point Bird Observatory (LPBO) and in Pennsylvania and Alabama in 1990 and 1991. In 1990, there were no differences in timing of migration of juveniles or adults at any of the sites. In 1991, the median passage of juveniles preceded that of adults by 14 days in Pennsylvania, but there was no difference in timing at the other sites. They concluded that timing of migration of adults and juveniles varied annually and by site.

At Ekwan, Wilson and McRae (1993) observed single migrants on 7, 9, and 11 September. In the southern Shield, the peak of autumn migration is in September and most are gone by the second or third week of October (Mills 1981; Tozer 2012). In southern Ontario, migration begins by mid-August and continues through September and much of October. Some remain into the first week of November, but there are numerous January and a few February records in the Hamilton area

(Black and Roy 2010; Curry 2006; Keast 1980; LaForest 1993; Lancaster et al. 1981; Weir 2008). At Long Point, the autumn midpoint of migration is 14 September (Mills 2005a).

Mills (2005b) compared timing of migration at Long Point from 1974 to 2002 in relation to climate change. When first date of arrival was considered, birds arrived earlier in spring in 2002 than in 1974, but not significantly. There were no differences when spring quartiles were examined. In autumn, it departed earlier in 1974, but not significantly. In spring, vanguard individuals may respond disproportionately to climate change, especially males in good condition. The yellowthroat may be breeding earlier and leaving earlier, but differences over time are not significant. In Pennsylvania, the average spring temperature did not change over an 18-year period, but the amount of precipitation received in May increased. It arrived earlier with time at a rate of 2.8 days per decade (R.J. Smith et al. 2023).

In spring, the yellowthroat is more restricted in its habitat use and may simply show up on breeding territories in the north. During spring,it is found mostly in habitats similar to those used for breeding, although a wider variety of habitats may be used at more southern stopover sites. In autumn, it occurs regularly away from wetlands and may be found in patches of dense vegetation and shrubs, such as raspberries, that retain leaves later into autumn. It also occurs along open creeks, at sewage lagoons, at forest edges, in bottomland forests, in flower gardens, along stagnant ditches and drains with emergents, in trembling aspen groves, in dense grassy areas, and even in upland forests (Campbell et al. 2001; Curry 2006; Graber et al. 1983; Guzy and Ritichison 2020; Sinclair et al. 2003; Tozer 2012).

Several studies examined habitat preferences of the yellowthroat during migration. In Illinois, Graber et al. (1983) did not examine marsh habitats, but found it to be most numerous in forest edges and shrubby areas. It also occurred in mature bottomland forests, but in inconsequential numbers. During spring migration in Wisconsin and Minnesota, it was significantly more abundant in floodplain forests than upland forests (Kirsch et al. 2013). During spring migration in North Carolina, it was most common in shrub habitat. Average numbers seen per hour were 3.28 in wet thickets, 2.00 in dry thickets, 1.55 in floodplain forests, 0.19 in pine and oak-hickory forests, 0.08 in pine-hardwoods forests, and 0 in beech forests (Parnell 1969). During spring migration in Pennsylvania, it was significantly more abundant in shrubs than forests. Detections per 100 m of transect were 0.08 in forests and 0.84 in shrubs; captures per 1,000 net-hours were 3.7 in forests and 32.8 in shrubs (Smith and Hatch 2008). In New Mexico, capture rates in willows shorter than 3 m tall were 4-fold greater than in any other habitat (agricultural edges, cottonwood–Russian olive stands, and cottonwood-mixed stands; Kelly et al. 2000). During autumn migration in Pennsylvania, its abundance was significantly higher in shrub-sapling-stage forests than forest-agricultural edge habitat. It was not observed in forest interior, suburban forests, or pole-stage forests. The shrub-sapling stage had the highest number of stems in the 0.25- and 2.5-8-cm diameter classes. In forest-agricultural edges, it usually used shrubby habitat at edges (Rodewald and Brittingham 2004). In open-canopied forests in Indiana, migrating yellowthroats were associated with low ground vegetation, high shrub density, and low tree density and were most abundant where there were frequent fires (Grundel and Pavlovic 2007a). During spring migration in Pennsylvania, it was more

likely to be detected in large than small patches, but there was no relationship between its abundance and patch size during autumn migration (Keller and Yahner 2007).

During migration, the yellowthroat usually forages singly and is seldom seen in mixed-species flocks of warblers (Campbell et al. 2001). During spring migration in North Carolina, 3.0% of foraging occurred in the canopy, 20.5% in low trees, 72.2% in shrubs, and 4.2% on the ground. In the canopy, 0% of foraging occurred at the top of the crown, 1.2% in the inner crown, 1.8% in the lower crown, and 0% on the bole. In low trees, 1.8% of foraging occurred at the top of the crown, 13.9% in the inner crown, 4.8% in the lower crown, and 0% on the bole. In shrubs, 8.4% of foraging occurred at the top of the crown, 10.8% in the inner crown, 2.4% in the lower crown, 51.0% in dense thickets, 6.6% in brush piles, and 3.0% in grasses. On the ground, 1.8% of foraging occurred in dense thickets, 0% in grasses, 1.2% at water's edge, and 1.2% in the open (Parnell 1969). In New York, Lebbin et al. (2007) observed yellowthroats foraging at night among the foliage of low shrubs in an area illuminated by football-stadium lights.

The yellowthroat is vulnerable to being killed by extremely adverse weather during migration. These may include cold fronts with headwinds, heavy rains, and tornados (Guzy and Ritichison 2020).

During migration, the yellowthroat is frequently killed by striking buildings, communication towers, and other human-made structures. From 1972 to 1982, 1,995 were killed at the Lennox generating station chimneys near Kingston, including 1,002 on the night of 6 September 1981. There is a record of 2 being killed by striking a fire tower in central Ontario. It is one of the species most vulnerable to striking high-rise buildings in Toronto. In Florida, 2,710 were killed at television towers over 3 years during autumn migration. In Illinois, it represented 5.1% of all warblers killed at television towers and was 11.4% of all birds killed at human-made structures in the United States and Canada (Chapman 1907; Colling et al. 2022; Graber et al. 1983; Gross in Bent 1953; Guzy and Ritichison 2020; Mills 1981; Weir 2008). Loss et al. (2014) examined bird-building collisions across the United States and determined that the yellowthroat was more vulnerable to striking buildings than average. For all types of buildings, it was 10.9 times more likely to strike a building than average. At low-rises, it was 18.4 times more likely to strike a building than average compared with 20.4 times at high-rises.

In Pennsylvania, an outbreak of the viburnum leaf beetle resulted in almost complete mortality of the southern arrowwood, which was formerly the third most abundant shrub species. Prior to the infestation, spring migrating yellowthroats gained significant mass after sunrise, but no weight gains occurred after the infestation (Smith and Hatch 2017).

James (1991) considered the yellowthroat a common to locally abundant migrant.

At LPBO, migration monitoring determined that the yellowthroat declined at a rate of 1.6% per year 1961-88. Trends by period were: −1.8% 1961-70, −1.9% 1970-79, and −1.1% 1979-88. All trends were nonsignificant, suggesting that populations were stable (Hussell et al. 1992).

WINTER

The winter range of the Common Yellowthroat covers most of the area where the frost-free period is longer than 240 days, generally north to the Virginia area in the east. Densest populations occur where the average minimum January temperature is higher than 7°C (Root 1988). Ontario is considerably north of its normal winter range. It is only occasional and rare during winter from Point

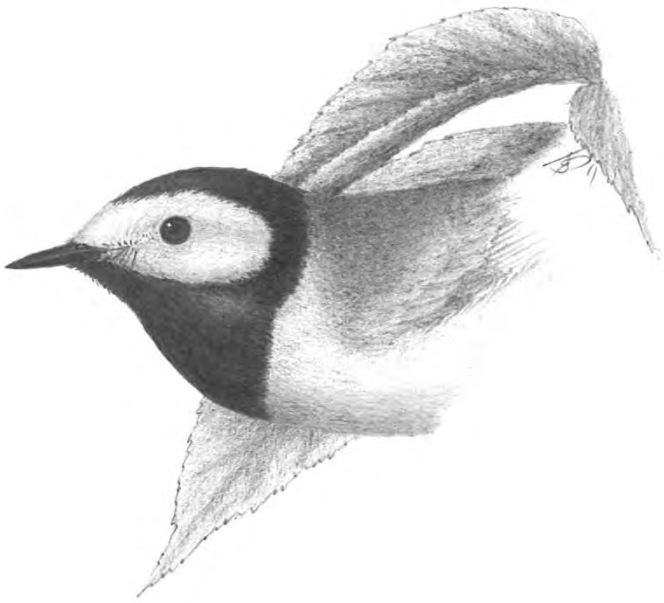
Pelee to Toronto (James 1991). The proportion of birds that attempt to overwinter that survive is unknown.

In the Hamilton area, the yellowthroat may successfully overwinter on occasion, and is usually observed among cattails in lakeside marshes (Curry 2006). Wintering birds in Ohio were also seen in cattail marshes (Gross in Bent 1953).

The yellowthroat commonly defends a territory in winter (Guzy and Ritichison 2020; Morse 1989). Due to its rarity in the province in winter, it is unlikely that any territorial defence is required.

Hooded Warbler

Setophaga citrina



BREEDING SEASON

Habitat Requirements

Ontario Hooded Warbler nests were in mixed (50.5% of nests), deciduous (47.3%), and coniferous (2.2%) forests. The coniferous stands were mature white pine plantations. Most forests it used for nesting were dry and all had characteristic understories of dense saplings, shrubs, and vascular plants (Peck and James 1987, 1998a). It occurs predominantly in tracts dominated by white oak, hickory, red maple, sugar maple, beech, and white pine. Common habitat associations that it uses include sugar maple–beech, oak-hickory, oak–sugar maple, and oak-pine stands. It occurs in white pine plantations only if they are mature and have an understorey of deciduous shrubs or saplings. It occurs less frequently in silver or red maple swamps and hemlock–yellow birch ravines (Austen et al. 1994; Page and Cadman 1994b; Sutherland and Gartshore in Cadman et al. 1987; Walters and Nol 2011b).

Potential occupancy of Ontario woodlands by the Hooded Warbler is affected by factors at the landscape level, by characteristics of the forest, and by microhabitat features. Habitat is not occupied if there are deficiencies at any level.

There appear to be 2 important factors at the landscape level that determine if a given woodlot has potential to support the Hooded Warbler. These include the amount of forest cover within the landscape and presence of sandy soils. In the Long Point area, the amount of forest cover within the local landscape was a significant predictor of Hooded Warbler occupancy. At the 3 major sites supporting it in southwestern Ontario, forest cover is 61-77% within 1 km of nest sites. Eastern Elgin County and Norfolk County, where the core of the population occurs, have 16-25% forest cover. In sand plains in western Chatham-Kent and Lambton where forest cover is as low as 3%, it was originally absent in otherwise suitable forest patches (Friesen et al. 2012; Gartshore 1988; Melles et al. 2012). With its recent range expansion, some forested areas in Chatham-Kent and Lambton have become occupied (Badzinski in Cadman et al. 2007).

Sutherland and Gartshore (in Cadman et al. 1987) and Gartshore (1988) were the first to notice that most occupied woodlands were on sand plains. Other records can mostly be explained by local sand deposits. Much of Haldimand County is dominated by the Haldimand Clay Plain, but a nest near Cayuga was at the end of the Oriskany sandstone formation where there is rich sandy soil. Even with the expanding population, the relationship with sandy soils appears to ring true. The recent expansion into the Ganaraska Forest occurred in areas of sandy soils (Heagy and Badzinski 2012; Walters and Nol 2011b).

In addition to having the appropriate dominant tree cover, forests must be mature and large or very close to a large forest to be occupied. Forests with trees smaller than timber size are avoided. At St. Williams and South Walsingham, forest maturity was an important factor in determining nest-site selection. Nesting areas had a higher basal area (BA) of large trees than unoccupied areas. Nest sites have a significantly lower BA of trees 7.5-15 cm diameter at breast height (DBH). Presence of large trees is essential because the Hooded Warbler relies on gaps in the canopy for nest sites. In undisturbed forests, these are created primarily by treefalls so presence of large trees is required to create large enough gaps. It is unlikely to use woodlots that lack mature growth (Bisson and Stutchbury 2000; Whittam et al. 2002).

The Hooded Warbler appears to be area-sensitive in Ontario. Extra-pair copulations are an important component of its mating system, so forests have to be large enough to support more than a single pair. It occasionally uses smaller woodlots, but only if they are close to larger tracts that support additional breeding pairs. The amount of habitat required to support it in Ontario is

uncertain, and is probably evolving as it increases in abundance. When a species is rare, it typically is restricted to the largest patches of optimum habitat, but may use smaller patches and those of somewhat lower quality as it becomes more common. The degree of isolation and the amount of local forest cover may also influence the size of forest required. Initially it was thought that contiguous woodlands exceeding 100 ha in size were required to support the Hooded Warbler in Ontario and 95% of known occurrences are still within forests of that size. It was subsequently concluded that 30 ha or more were required to support a viable population and later that it was consistently absent from woodlots smaller than 20 ha. More recently, it has been documented nesting in woodlots 8-10 ha in area, but only where they are near larger forests. Both forest size and connectivity are important (Friesen and Stabb 2001; Friesen et al. 2012; Heagy and Badzinski 2012; James 1984b; Page and Cadman 1994b).

Large, mature forests on sandy soils with suitable tree species composition are unlikely to be occupied unless they have canopy openings that promote growth of deciduous shrubs and saplings. Although the Hooded Warbler nests within mature woodlots, it does not nest within mature portions of woodlots and selects small patches of early successional habitat. It is a forest-gap specialist that nests in small openings in the canopy created by treefalls, windthrow, insect damage, diseases, or forest management. The importance of shrubby gaps has been demonstrated in the South Walsingham Forest in Norfolk County and the Springwater Conservation Area in Elgin County. It declined significantly or disappeared from these areas once forest gaps matured and filled in. Gaps used for nesting in Ontario range from 5 to 1,178 m^2. Gaps may be occupied 1-5 years after they are created until they are 12 or 13 years old. Gaps are abandoned once saplings reach 5-10 m in height. At this stage of succession, the ground is usually devoid of vegetation. Common shrub and sapling species found in gaps used for nesting include raspberries, red elderberry, maple-leaved viburnum, grape, gooseberry, chokecherry, red maple, sugar maple, white ash, and beaked hazel. Sixty-six woody species were found at nest sites in southwestern Ontario. To be suitable, gaps must have a high density of deciduous woody plants at the height that nests are usually placed, usually 0.5-1.3 m from the ground. Because gaps provide suitable nesting habitat for only a short period, the location of breeding territories and nests may be constantly shifting in large forests, and the number of breeding pairs may fluctuate considerably depending upon availability of suitable gaps. Populations in small woodlots may be ephemeral, being occupied for a few years after disturbance and absent when the canopy is closed (Allaire and Badzinski 2004; Bisson and Stutchbury 2000; Friesen et al. 2012; Gartshore 1988; Heagy 2008; Heagy and Badzinski 2012; Melles et al. 2012; Page and Cadman 1994b; Walters and Nol 2011b; Whittam 1999; Whittam et al. 2000, 2002). Although presence of suitable gaps for nesting is critical, presence of suitable nesting habitat within high-quality forests does not ensure occupancy. Occupancy declines with increasing distance from core populations indicating that connectivity at the landscape level is important. Forests with suitable nesting areas within the maximum gap-crossing distance for this species (50 m for females and 500 m for males) are frequently selected for nesting (Melles et al. 2012).

Several Ontario studies described the habitat characteristics of gaps used for nesting and compared them with unused areas within the same forest. Gartshore (1988) described the habitat at 6 nests in the Long Point area as having 88% canopy cover, 87% shrub cover, and an average of 10.5 shrub stems per m^2 (range 3.3-27.9 per m^2). In the same region, Melles et al. (2012) determined

that nest locations had fewer saplings with a DBH of less than 2.5 cm and more large saplings (2.5-9.9 cm DBH) than pseudo nest sites. Bisson and Stutchbury (2000) sampled 23 nest sites and 23 unoccupied sites in 7 woodlots in the Long Point area. Nest sites had a higher percentage of cover at all 4 vegetation profile heights (0-0.3 m, 0.3-1 m, 1-2 m, and 2-3 m) and a lower BA of trees in the smallest size class (7.5-15 cm DBH) than unoccupied areas. The percent vegetative cover at the 4 height intervals for occupied and unoccupied sites respectively were: 0-0.3 m, 90.4% and 79.8%; 0.3-1 m, 83.9% and 56.5%; 1-2 m, 72.2% and 46.8%; and 2-3 m, 65.3% and 49.6%. The BA of trees 7.5-15 cm DBH was 1.9 m^2 per ha at occupied sites compared with 3.0 at unoccupied sites. Nest sites had a lower percent canopy cover than unoccupied sites (79.0% compared with 89.0%), but the difference was not significant. The probability that a site would be occupied increased with height of the subcanopy and percent coverage by vegetation at the 1-2-m level. Whittam et al. (2002) examined 52 nest sites in South Walsingham Forest and 57 in St. Williams Forest and compared their vegetative structure to unoccupied sites and found that they were significantly different. Nest sites in both forests differed from controls by having denser vegetation (mostly raspberries, but also some herbaceous cover) 0-0.3 m from the ground and by having fewer tree stems per ha. In South Walsingham Forest, nest sites had denser vegetation at the other 3 levels above ground, more snags per ha, less BA of small trees, and greater BA of large trees than controls. In St. Williams Forest, nest sites had taller canopy, more stumps, and more BA of stumps than controls. In both forests, vegetation density below 1 m above ground discriminated nest sites from controls. At St. Williams Forest, 86% of nest sites were in gaps averaging 43 m^2 and 196 m^2 over 2 years, and 84% of gaps were created by timber harvesting. Nest gaps averaged 6.2 years old (range 1-13 years) in 1999 and 7.6 years (range 4-14 years) in 2000. Nests were found in coniferous stands more than expected due to more recent and widespread logging in plantations. Hooded Warblers were found in areas of low, moderate, and high logging intensity more than expected by chance. Significant habitat variables at St. Williams Forest compared with control areas were: canopy height, 25.9-27.9 m compared with 22.9 m; cover 0-0.3 m from ground, 90.8-91.3% compared with 78.6%; cover 0.3-1 m from ground, 68.5-76.1% compared with 57.5%; cover 1-2 m from ground, 40.4-61.0% compared with 46.8%; 564-614 tree stems per ha compared with 861 stems per ha; 17-139 logs per ha compared with 24 logs per ha; stump BA, 9.8-18.5 m^2 per ha compared with 35 m^2 per ha; and 46-93 stumps per ha compared with 27 per ha. Significant habitat variables at South Walsingham Forest nests compared with control areas were: cover 0-0.3 m from ground, 84.2% compared with 66.0%; cover 0.3-1 m from ground, 61.8% compared with 39.6%; cover 1-2 m from ground, 57.9% compared with 37.1%; cover 2-3 m from ground, 56.2% compared with 39.5%; tree stems per ha, 1,005 compared with 1,319; snags per ha, 105 compared with 177; BA of small trees, 13.3 m^2 per ha compared with 17.3 m^2 per ha; and BA of large trees, 12.3 m^2 per ha compared with 8.8 m^2 per ha. Walters and Nol (2011b) reported similar habitat at nest sites in the Ganaraska Forest. Nests were mostly in deciduous forest but 2 of 12 (16.7%) were in managed coniferous forests regenerating to mixed forest. Similar to the Long Point area, nests were in forest gaps and habitat of these gaps was also similar. Most nest sites had 26-75% coverage 0.5-1.3 m from the ground; most unoccupied sites had 1-25% coverage in this height range. Fifty percent of nest sites had 26-50% coverage 2.5-10 m from the ground; 71% of unused sites had 1-25% coverage at this height. At nest sites, there were significantly more living woody stems (27.9 compared with 9.3 per 50 m^2) and fewer dead stems (0.8 compared with 1.3 per 50 m^2) than at unoccupied sites. There were significantly more shrubs at nest sites (43, range 7-66)

than at unoccupied sites (3, range 0-125) per 50 m^2. Similar to the St. Williams Forest, canopy closure was less at nest sites than unoccupied sites, but not significantly.

Throughout its range, the Hooded Warbler nests in habitat similar to what it uses in Ontario. In addition, it frequently nests in deciduous swamps and this appears to be preferred habitat. In New Jersey, it was significantly more abundant in hardwood swamps than in oak-pine forest. It rarely nests in mature coniferous plantations in Wisconsin and pine barrens in New Jersey, where it nests at the interface between cedar and pine swamps. Nonetheless, it shows a decided preference for deciduous forests. Forests that it uses are intermediate in age or mature so that a treefall creates a large enough gap for nesting. In Pennsylvania, it occurred in 36.4% of old-growth forests, 28.8% of woodlots state-wide, and 31.3% of woodlots on the Appalachian Plateau. It had neutral affinity for old-growth forest, being neither more nor less likely to occur in old-growth stands. It is a gap specialist throughout its range, nesting in small canopy openings with dense deciduous shrubs and saplings. In North Carolina, its relative abundance was 3.19 in pine-hardwoods, 2.11 in beech forests, 1.76 in floodplain forests, 1.37 in pine forests, 0.95 in oak-hickory forests, and 0 in wet and dry thickets. Mist-netting during the breeding season resulted in captures per 100 net-hours of 2.1 in gaps, 4.0 in edge, and 2.0 in forest. Forest habitat was used most during the breeding season, but it was never the dominant habitat used. It nested and foraged in the mature forest, but often foraged in gap habitat in all seasons, and young remained in gaps during the postfledging period. In the mid-Atlantic states, habitat variables that defined suitability for the Hooded Warbler were identical to those identified in Ontario. Its abundance was significantly correlated with canopy height, the amount of forest within 2 km, foliage density 0.3-1.0 m from the ground, and percent ground cover. Habitat characteristics of nest-site gaps in Pennsylvania were: 23.7 stems per m^2; 19.7 branches per m^2; overall visibility, 50.4%; 57.9% visibility at nest height; 39.0% visibility at 1.5 m; and 31.0% visibility from above with considerable variation in all parameters. The dominant nest substrate corresponded to the dominant shrub species in the forest and included blackberry, beech, prickly gooseberry, and black cherry. In Tennessee, it was significantly negatively correlated with foliage, branch, and bole biomass of trees 1.2-8.4 cm DBH. The Hooded Warbler was closely associated with the Cerulean Warbler and Carolina Chickadee. The 3 species were separated vertically with the Cerulean Warbler inhabiting the canopy, the chickadee the subcanopy and understorey vegetation, and the Hooded Warbler with the layer closest to the ground. In Ohio, 7 of 23 vegetation variables varied significantly between nest sites and perches. Nest sites were characterized by a greater density of small coniferous and deciduous trees, a lower canopy closure percentage, more deciduous woody plants 1.0 cm and 1.1-2.5 cm DBH, and significantly more conifers smaller than 1.0 cm, 1.1-2.5 cm, 15.1-23 cm, and 30.1-38 cm DBH than perch sites. Both nest sites and perches were significantly correlated with percent ground cover and trees larger than 53 cm DBH. The Hooded Warbler exhibited a high degree of selectivity for nest sites, but nest sites and perches became more similar with increasing sample area. The difference between nest sites and perches may be related to the requirement to conceal nests compared with the desire of the male to sing from a conspicuous area. When selecting a nest site, it responds to vegetation in an area of less than 0.04 ha and more specifically to a 1-m radius, or 3 m^2 (Anderson and Shugart 1974; Bent 1953; Bielefeldt and Rosenfield 1994; Bowen et al. 2007; Brooks 1940; Brush 1987; Buffington et al. 1997; Bushman and Therres 1988; Graber et al. 1983; Haney 1999; Harrison 1984; Howlett and Stutchbury

1996; Kilgo et al. 1996; Mossman and Hoffman 1989; Mumme et al. 2023; Noon et al. 1979; Parnell 1969; Petit et al. 1988a; Powell and Rappole 1986; Rich et al. 1994; Robbins et al. 1989; Sargent et al. 1997).

In a Connecticut woodlot over a 59-year period, there was a progressive shift to larger trees, a sparser shrub layer, and a less diverse tree canopy dominated more by oaks and maples due to a severe decline in hemlock. The Hooded Warbler declined within the woodlot but populations increased statewide. The decline was likely due to the reduction in the shrub layer (Buchanan et al. 2016).

The Hooded Warbler appears to be area sensitive in some areas, but inhabits very small woodlots in other areas. Area sensitivity may vary considerably even in areas close to each other. In western Maryland, where it is uncommon, it is found only in woodlands larger than 4,000 ha, but it nests in woodlots as small as 5 ha in central Maryland (Bushman and Therres 1988). Robbins (1979) concluded that 30 ha were required to support a viable population, but Robbins et al. (1989) found that its abundance and occurrence were not related to forest size in the mid-Atlantic states, which include Maryland. Mumme et al. (2023) stated that it inhabited forests larger than 15 ha. In Pennsylvania, it regularly breeds successfully in woodlots smaller than 2 ha. Forest fragments where it was studied averaged 1.2 ha (range 0.7-1.8 ha). All fragments were close to larger habitat patches, and this probably contributed significantly to their habitat suitability. Only 19% of isolated forest fragments 0.5-5 ha were occupied (Norris and Stutchbury 2002; Norris et al. 2000). The degree of its area sensitivity probably depends on a number of factors such as its local abundance, the amount of suitable habitat in the landscape, and the proximity of suitable woodlots to each other. In Pennsylvania, both males and females regularly flew across open habitat into adjacent larger woodlots. No females crossed open gaps wider than 50 m, but males crossed gaps as wide as 465 m. In some cases, there were wooded corridors connecting the fragment to the larger forest patch. Only 1 of 3 females that had a corridor available to them used it. When males had corridors available, most (62.5%) used the corridor when leaving the woodlots but not when returning (16.7%). Seventy-seven percent of all forays to adjacent woodlands occurred despite the absence of corridors. Protection of corridors linking patches may not be as important as limiting the degree of isolation between forested areas. The added time and energetic costs of making forays in fragmented landscapes could explain the low occupancy rate of small woodlots (Norris and Stutchbury 2001, 2002).

Numerous authors considered the Hooded Warbler a forest-interior species that avoided edge habitat. Edges were considered detrimental due to anticipated higher levels of predation and parasitism by the Brown-headed Cowbird. Few of these studies based their conclusions on empirical data. Early status reports prepared for the Committee on the Status of Endangered Species in Canada (COSEWIC) emphasized the importance of forest interior to the Hooded Warbler. The first COSEWIC report suggested that the distance required from edge was probably closer to 600 m than 60 m and that large forests dominated by edge were of little use to it. It was thought that it rarely wandered to forest edge. The second COSEWIC report stated that it was unlikely to persist without large blocks of forest where much of their area was more than 200 m from edge. An earlier Environment Canada factsheet concluded that nesting success was often greater in forest interior

than at the edge. The third COSEWIC report acknowledged that it uses forest edges (Freemark and Collins 1992; Friesen and Stubb 2001; Heagy and Badzinski 2012; James 2000; Page and Cadman 1994b). Even prior to the preparation of the first COSEWIC report, the Hooded Warbler was known to nest at the edges of Vanessa Swamp and the St. Williams Forest (personal observations).

Some studies specifically examined presence of the Hooded Warbler in relation to forest edge. Although a few studies observed an apparent edge-avoidance reaction, more studies determined that it was either indifferent to edge or even more likely to occur near edge. Lynch (1987) mapped territories in Maryland and found that no territories included edge; 30 m was the closest it was observed to edge. In New Jersey, it was consistently more abundant in forest interior than at forest edge (Rich et al. 1994). In the St. Williams Forest, nest sites tended to be further from forest edge than pseudo nest sites. Nonetheless, it tended to nest in the northern and southwestern portions of this forest, fairly close to forest edges that bordered on roads and trails (Melles et al. 2009, 2012). Kroodsma (1984) examined the relationship between edge and the Hooded Warbler in Tennessee. It exhibited no edge-avoidance behaviour, with 7 pairs detected 0-268 m from edge and 0 pairs 268-488 m from edge. It was most abundant 40 m from edge, which consisted of a power-line right-of-way. Moorman et al. (2002) examined nest distribution and success relative to group selection and clear-cuts in South Carolina. Nests were clumped near edges of both types and there were approximately 2 times as many nests 0-50 m from edge than 51-100 m or further than 100 m from edge. Very few nests were further than 200 m from edge. Nest success was unrelated to distance from edge. In Pennsylvania, Howlett and Stutchbury (1996) found 1 nest within 10 m of a forest-field edge and 77% of 75 nests were near microedges such as deer trails, old logging roads, path edges, and gas well roads. In Pennsylvania, Norris et al. (2000) radiotracked males in small isolated woodlots and in a 150-ha woodland. Edge was defined as the area 0-20 m from the outer limit of the forest for birds in small fragments and the same distance from the territory edge for birds in contiguous forest. In fragments, males spent 34.5% of their time in edge, less than expected by chance. The amount of time spent by males at edges in contiguous forest was only 11.3%, significantly lower than for birds in fragments. Males in both habitats spent more time than expected in the core of their territory, consistent with the strategic-centre hypothesis that males should spend more time in the core of the territory because loss of this area is more likely to result in complete territory loss. Males with high numbers of neighbours in the large forest spent more time in the core of the territory. The single male that had only a single neighbour exhibited the highest use of territory edge (26%). The authors concluded that it avoided edges because of social factors and not because of higher predation or a reduction in prey availability. Males in isolated woodlots spent over a third of their time in edge. In the Birds of the World species account for the Hooded Warbler, Mumme et al. (2023) concluded that individuals do not avoid edge habitat.

Of nests reported to the Ontario Nest Records Scheme (ONRS), 79.5% were in deciduous saplings and shrubs, 8.4% were in conifers, 8.4% were in ferns, and 3.6% were in herbaceous plants: horse balm, mayapple, and sweet cicely. Nest height ranged from 0.2 to 1.5 m, with most 0.4-0.7 m from the ground. Two nests were in maple saplings, 2 were in crotches of maple-leaved viburnum, 2 were in raspberry canes, 1 was in the crotch of a sensitive fern, and 1 was joined to 3 basswood saplings (Peck and James 1987, 1998a). Several other nests have been described in the province. Nests are typically in or on the edge of a forest gap and may be in the middle of regenerating

logging roads, at edges of footpaths, and near lanes cut for mist nets. Nests are usually in the crotch of the supporting plant or on a platform created by branches. One nest was placed where a dead branch touched a sapling. Average height of 23 nests in Norfolk County was 46.3 cm and 10 nests in the Ganaraska Forest averaged 56 cm from the ground. In Norfolk County, 69.6% of nests were in raspberries, 13.0% in red elderberry, 4.3% in chokecherry, 4.3% in wild grape, 4.3% in sensitive fern, and 4.3% in gooseberry. In the Ganaraska Forest, 50% of nests were in sugar maple saplings, 25% in red elderberry, 17% in raspberries, and 8% in beaked hazel. In Elgin County, 1 nest was in a beech sapling (Baillie 1962; Bisson and Stutchbury 2000; Gartshore 1988; Lancaster et al. 2004; Walters and Nol 2011b).

Throughout its range, the Hooded Warbler nests a short distance above ground. Nests have been reported 0.15-5.5 m from ground, with the highest nest in a slender upright shoot growing from the trunk of a large beech tree. Excluding this nest, the highest other nests have been reported is 1.8 m, but most nests are 0.3-1.5 m from the ground. Nests higher from the ground are often just over the edge of a ravine such that the nest is just below the level of adjacent upland ground. Most nests are in a fork of the supporting vegetation and they often include a dead branch that has fallen across the fork. Nests are rarely in dead branches of fallen trees or in piles of debris. Most nests are in deciduous saplings or shrubs, but a few are in ferns and herbaceous species. In addition to the plant species reported in Ontario, it has nested in giant ragweed, jewelweed, swamp currant, Ohio buckeye, honeysuckle, buttonbush, huckleberry, Manitoba maple, oak, ash, spicebush, and blue cohosh, which is a preferred nest substrate in some areas. Selection of the species for nesting is site specific, with the local species that offers the best protection from weather and predators selected. Nests tend to be well concealed laterally and from above, but are fairly conspicuous from below. Nests built earlier in the season are rarely reused (Bent 1953; Chapman 1907; Mumme et al. 2023; Fall 1989; Graber et al. 1983; Harrison 1984; Howlett and Stutchbury 1997; Kilgo et al. 1996; Odum 1931; Powell and Rappole 1986).

The Hooded Warbler is territorial, with both sexes defending a territory. Some females nest at territory boundaries and appear to not have an extensive territory. Both sexes nest and feed within the territory, but may make extensive and frequent trips off the territory, apparently to seek extra-pair copulations. Birds nesting in small woodlots may visit adjacent larger woodlots, but the territory is confined to the smaller woodlot and movements to other woodlands are extra-territorial. Territories tend to be clumped and it has been considered semicolonial by some authors. Some areas of forest are inhabited by high densities of Hooded Warblers whereas nearby areas of apparently identical habitat are left almost vacant. At St. Williams Forest, nests were significantly clustered at the scale of 360-900 m. Above and below this scale, nests were randomly distributed, and nest clustering occurred specifically between 360 and 480 m. Clustering was not related to the distribution of suitable habitat or to the distribution of unmated males. Just below the 900-m scale, unmated males were more clustered than mated males, providing evidence that unmated males cluster their territories, but at a larger scale than mated males. Territories are non-overlapping, so nest avoidance occurs at the 30-m scale. Females nested randomly within available habitat at scales approximately equal to that of a male's territory (60-240 m), but there was clustering at 120 m and nests were clustered between 240 and 420 m. Nests may be selected to be closer to other females and their associated nests to facilitate obtaining extra-pair copulations from mated males. Nest

distribution was not associated with the distribution of unmated males because they are presumably lower-quality potential mates. In Pennsylvania, nearest-neighbour distances were 50-75 m where territories were close together, but 60-600 m when territories were spaced apart. Outside Ontario, territories tend to be 0.5-1.0 ha in larger forest patches that support several pairs, but may be as large as 2.2 ha in small forest fragments supporting a single pair. Territories in Ontario are much larger than reported elsewhere. The average size of 33 Ontario territories was 3.2 ha (range 0.3-11.4 ha). The complete range of territory sizes occurred at the St. Williams Forest. Territories were 1.1-2.4 ha in woodlots smaller than 50 ha. The larger territories in Ontario may be because the habitat is inferior or because the density of birds is low. The habitat in Ontario is typical for the species, so it is most likely that the large territories are a function of the habitat not being saturated. Territories are still clumped, but each male can defend a larger than normal territory because male density is low (Bent 1953; Evans Ogden and Stutchbury 1997; Friesen et al. 2012; Heagy and Badzinski 2012; Melles et al. 2009; Mumme et al. 2023; Neudorf et al. 1997; Norris 2000; Norris and Stutchbury 2002; Tarof et al. 1998).

Home ranges are consistently larger than territories. Throughout the breeding season, males leave the territory on a daily basis. In small woodlots in Pennsylvania, 85% of males left their woodlot at least once and some made extra-territorial forays more than once every 2 hours and spent an average of 16.5% of their time off territory. Twenty percent of males spent more than one third of their time off territory. Males travelled 40 m to 2.5 km from their territory. Over 50% of forays were less than 200 m, but 20% were further than 500 m and 5% were further than 1 km. In isolated woodlots, all forays involved flying over open habitat on a daily basis, with the maximum gap crossed being 465 m. Woodlots that the Hooded Warbler visited were significantly closer than woodlots that were not visited (213 m compared with 394 m). Approximately half of forays were to other territories. During these intrusions, 91% of males were silent and 71% visited the nest vicinity while the neighbouring female was fertile. Some males visited the same territory repeatedly and rarely or never visited other territories an equivalent distance away. Approximately 10% of males visited more than 1 woodlot during a foray and in all cases visited intervening woodlots to reach further destinations rather than flying over woodlots. Females also leave the territories, mostly when they are fertile. In Pennsylvania, 77% of fertile females left the territory compared with 10% of nonfertile females. Fertile females visited 1-4 territories of immediate neighbours. Nonfertile females visited neutral areas undefended by any males. The maximum open gap that females crossed was 50 m. Females travelled as far as 300 m from their territories (Neudorf et al. 1997; Norris 2000; Norris and Stutchbury 2001, 2002; Stutchbury et al. 2005b; Tarof et al. 1998).

Natal philopatry rates are fairly high in Ontario but low elsewhere. At the South Walsingham Forest, 11.0% of juvenile males and 10.8% of juvenile females returned. One male occupied its natal territory the following year. There were several instances of recruitment of birds banded as nestlings at other sites within 20 km. It is likely that dispersal of young and adults occurs at greater distances, but this has not been confirmed. In Pennsylvania, 2 of 232 nestlings (0.9%) returned to the natal area to nest. Juvenile birds banded later in summer away from the natal territory had higher return rates: 16.0% in Ontario and 15.4% in Pennsylvania. Juveniles may seek and select suitable nesting areas prior to migrating in autumn (Evans Ogden and Stutchbury 1996; Gartshore and Agro 1994; Heagy

and Badzinski 2012; Mumme et al. 2023). One Pennsylvania fledgling was captured 3 years later during the breeding season 50 km from his natal site (Mumme et al. 2023).

For Ontario adults, the return rates were 61.8% for males and 42.1% for females. There was no significant difference in the return rate of the sexes, although returning males always outnumbered females in every age class. Males tended to return to the same territories in subsequent years and one used the same general area in 6 consecutive years. One male occupied a territory from 1988 to 1991. His son, hatched in 1988, occupied the same territory in 1992 and in 1993, a grandson, hatched in 1992, occupied the territory. In each case, the male of the previous generation had disappeared. When the son occupied the territory in 1992, he had not been seen since 1988 and it was unknown where he had spent the intervening years. Several birds banded as adults nested 5-15 km away, which may be a reflection of the ephemeral nature of the habitat the Hooded Warbler occupies. Females appeared to have higher dispersal rates than males. The population in southwestern Ontario appears to be maintained by frequent dispersal into and out of the population, and this is probably typical of many populations (Gartshore and Agro 1994; Heagy and Badzinski 2012). In Pennsylvania, the overall return rate for adults was 47%, with 52% of males and 43% of females returning. Males exhibited greater territorial fidelity than females, with 58% of returning males occupying the same territory compared with 29% of females. Females that returned to the same area tended to have fledged more young the previous year than those that occupied different areas, but the difference was not significant. Birds that remated had higher territory fidelity (84.6%) than birds that divorced, with 47.1% of divorced males and 5.9% of divorced females occupying their previous territory. For birds whose mate from the previous year did not return, 50.8% of males and 22.2% of females occupied their previous territory, significantly less than for reunited pairs. Females that had extra-pair young the previous year were slightly more likely to return to their previous territory. Although prior nesting success and occurrence of extra-pair young had a positive effect on female site-fidelity, territory and mate fidelity was not influenced by these factors for males. Some females may disperse to improve breeding success or their chances for extra-pair copulations. Males may disperse to better habitat or to areas that are not as densely occupied (Howlett and Stutchbury 2003). In the same study area, females returning in a subsequent year nested significantly further from their previous nest (mean 239 m, median 151 m) than males (mean 93 m, median 51 m; Mumme 2024).

Limiting Factors

In Elgin County, males are on territory as early as the first week of May, and adults have been observed feeding nestlings in the first week of June. Eggs have been found in Ontario nests from mid-May to early August, but most contain eggs from mid-June until the first week of July (Allaire and Badzinski 2004; Lancaster et al. 2004; Peck and James 1998a).

The female settles on a male's territory within a few days of arrival. She selects the nest site and builds the nest in 2-7 days, typically 5-6 days. Egg laying commences once the nest is complete; eggs are laid at the rate of 1 a day. Incubation begins with laying of the last egg. The incubation period at 12 Ontario nests was 11-12 days, consistent with reports from elsewhere, with most eggs taking 12 days to hatch. In Ontario, most young leave the nest when they are 8 days old. The nestling period is 8 or 9 days throughout the Hooded Warbler's range (Baillie 1962; Bent 1953; Evans Ogden

and Stutchbury 1997; Friesen et al. 2012; Gartshore 1988; Harrison 1984; Mumme et al. 2023; Niven 1993; Odum 1931; Page and Cadman 1994b; Peck and James 1998a; Powell and Rappole 1986).

Some birds are double brooded and triple broods have been reported in Ontario. At St. Williams, 20% of pairs successfully raise 2 broods per year. In Pennsylvania, 43.9% of females with a successful first brood began a second brood. Double-brooded females nested significantly earlier than single-brooded females, with the average date of the first egg 26 May for those rearing 2 broods compared with 31 May for those raising a single brood. Eighty-two percent of females that began laying by 23 May and did not experience predation laid second clutches. Of birds that initiated laying by 31 May, 46% did not attempt a second brood. Yearlings are significantly less likely to attempt a second brood than older females. Time appears to be the main constraint to raising a second brood. Birds that attempted a second brood produced 63% more fledglings than those that raised a single brood. Raising a second brood has costs, with adults having to care for young well into August. They also have to delay their moult by approximately 3 weeks and are still on the breeding grounds while other birds are establishing winter territories. Having a second brood may reduce the likelihood of successfully establishing a winter territory. The average interval between young fledging from the first nest and laying eggs in the second nest was 11 days in Pennsylvania (range 3-22 days). Successful females that initiate a second nest did so in the same territory with the same mate, but nested significantly further from the first nest (60 m) than females laying replacement clutches after the first nest was depredated (48 m). Successful females may move their second nest further away to avoid their fledglings from the first nest. The Hooded Warbler is a persistent renester, renesting as many as 3 times in an attempt to raise young. Females usually remain within the same territory and retain their mate while renesting. In Pennsylvania, only 3 of 184 females (1.6%) deserted the territory to renest. A more recent study at the same location determined that 7 of 567 females (1.2%) changed mates and territories within a season. Usually a new nest is built for each nesting attempt, but 1 Ontario pair raised 2 clutches in the same nest. Nests reported to the ONRS contained 3-5 eggs (average 3.64 eggs, mode 4 eggs); there was only one 5-egg clutch. Twenty-three nests in Norfolk County had an average clutch size of 3.5 eggs and a mode of 4 eggs. In another sample of 43 nests from St. Williams and South Walsingham forests, overall clutch size averaged 2.81 and 3.47 eggs over 2 years. Mean clutch size for parasitized nests was 2.27 and 3.25 eggs compared with 3.40 and 3.60 eggs for unparasitized nests. Throughout its range, it lays 3-5 eggs per clutch, but mostly 4 eggs. Clutch size declines with season. In Pennsylvania, mean clutch size in late May was 4.0 eggs (range 2-5 eggs) compared with 3.5 in June (range 3-4 eggs); all July nests had 3-egg clutches (Allaire and Badzinski 2004; Bent 1953; Bisson and Stutchbury 2000; Chapman 1907; Evans Ogden and Stutchbury 1996, 1997; Friesen et al. 2012; Gartshore 1988; Graber et al. 1983; Heagy and Badzinski 2012; Howlett and Stutchbury 1997; Mumme 2024; Mumme et al. 2023; Peck and James 1998a; Whittam et al. 2002).

The age at first breeding is 1 year for both sexes and all yearling females apparently nest. There are some nonbreeding males in most populations, mostly yearlings that failed to attract a mate. At St. Williams Forest, an average of 25% of males was unmated (range 10-40%). In smaller Ontario woodlots near the St. Williams Forest, 17-24% of males were unpaired. In Pennsylvania, 25-27% of males were unmated in small woodlots but less than 1% were unmated in a 150-ha forest. Overall, about 6% of males remain unmated. Once a bird has bred, it presumably nests every year thereafter

(Bisson and Stutchbury 2000; Heagy and Badzinski 2012; Mumme et al. 2023; Norris 2000; Norris and Stutchbury 2002). The Hooded Warbler is typically monogamous but approximately 4% of males are polygynous. Polygyny has been documented in Ontario (Mumme et al. 2023; Walters and Nol 2011b). Pairs remain together for an entire breeding season, including for second broods and replacement clutches. In Pennsylvania, 60 of 175 returning birds (34.3%) had mates that also returned. Of the 60, 26 (43.3%) paired with the same mate to form 13 pairs that had been previously mated. Eleven of the 13 females (84.6%) remated with a former mate that was defending their previous territory. In the other 2 cases, the male was defending a new territory (Howlett and Stutchbury 2003; Mumme et al. 2023). Cooperative breeding by the Hooded Warbler is rare. At 1 of 60 Pennsylvania nests (17%), a second male helped feed nestlings. The second male had been mated with the female the previous year on a nearby territory, but was genetically unrelated to his offspring that year (Tarof and Stutchbury 1996). In 2 of 17 cases (11.8%) in Pennsylvania, males fed young on their own territory that had fledged from a neighbour's territory. In both cases, the social father was no longer on his territory at the time of adoption and the social mother had renested in an attempt to raise a second brood. Both males were unrelated to their adopted fledglings, but 1 male was the genetic father of 2 of 3 nestlings in the social mother's second brood. By adopting fledglings, males increase the availability of fertile females on neighbouring territories by increasing the likelihood that females will renest. Fledgling adoption may be a widespread behaviour (Stutchbury and Evans Ogden 1996).

Extra-pair copulations are an important component of the Hooded Warbler's mating system. It is likely that territories are clustered to facilitate extra-pair copulations. Even in isolated woodlots supporting only a single pair, young in the nest may be extra-pair. Both males and females seek extra-pair copulations. All females mated to younger males moved off their territories, presumably to seek extra-pair copulations, compared with 50% of females mated with older males. A similar proportion of young (60%) and old (99%) females left their territory. In Pennsylvania, 55 of 57 intrusions (96.5%) by males were to adjacent territories, but males occasionally travelled as far as 150 m to intrude. Seventy-six percent of intrusions occurred when the resident female was nest building; only 2% occurred in territories where there was no female or when the female was egg laying (8%) or incubating (14%). In 78% of intrusions, the male entered a territory when the female was chipping, and females chip only 20% of the time. One of 10 males made only 2 intrusions within 10 hours, both to a single territory. Another male made 9 intrusions in 12 hours into 4 different territories. The mean rate of intrusion of males into adjacent territories was 0.4 per hour. Males with the highest intrusion rates into adjacent territories had the lowest intrusion rates into their own territories. In a high-density population in Pennsylvania, 66.7% of broods contained at least 1 extra-pair young and 53.7% of nestlings were extra-pair. In a low-density population, 26.1% of broods contained extra-pair young and 22.0% of nestlings were extra-pair. The frequency of extra-pair young declines with the season, with 40% of nestlings being extra-pair in late May compared with 15% in late June. There was no difference in the frequency of extra-pair fertilizations between replacement clutches (14.0% of young and 22.2% of broods) and second broods (19.6% of young and 31.3% of broods). Over 95% of extra-pair fathers were adjacent neighbours, but some birds travelled as far as 600 m for extra-pair copulations. For broods with more than 1 extra-pair young, all young had the same genetic father in 13 of 17 cases (76.5%). Eighty percent of males were not known to father extra-pair young,

but 5.7% of males had 3 or more extra-pair young per year. Younger females had significantly more extra-pair young in their broods than older females: 41.9% for yearlings, 17.7% for 2-year-olds, and 6.2% for 3-year-olds. Younger females arrive later in spring and might be expected to obtain lower-quality mates and be more likely to seek extra-pair copulations. The proportion of extra-pair young per nest ranged from 0% to 100% with a strongly bimodal distribution. Females either had no extra-pair young or most of the brood was extra-pair. It appears as though females are actively selecting genetically superior males to sire their young (Evans Ogden and Stutchbury 1997; Mumme et al. 2023; Neudorf et al. 1997; Norris and Stutchbury 2001; Stutchbury 1988; Stutchbury et al. 1994, 1997, 2005b; Tarof et al. 1998).

Parnell (1969) observed foraging locations of the Hooded Warbler during the breeding season in North Carolina. Of all observations, 24.5% were in the canopy, 51.0% were in low trees, 24.5% were in shrubs, and 0% were on the ground. In the canopy, 0% of observations were in the top of the crown, 6.1% in the inner crown, 18.4% in the lower crown, and 0% on the bole. In low trees, 2.1% of observations were in the top of the crown, 20.8% in the inner crown, 20.8% in the lower crown, and 0% on the bole. In shrubs, 0% of observations were in the top of the crown, 16.3% in the inner crown, 0% in the lower crown, 6.1% in dense thickets, 2.1% in brush piles, and 0% in grasses. Singing males occurred at heights of 0-15 m (average 6.0 m). Other birds were seen at heights of 0-15 m (average 3.0 m). Males forage higher because they use the canopy for singing and the females remain lower in association with the nest. The Hooded Warbler is an excellent flycatcher that obtains much of its prey from the forest subcanopy, including aerial insects it captures in flight. It captures a high proportion of prey by hovering or gleaning insects from leaves and stems. While foraging, it flicks its tail to reveal the white tail spots. This flushes prey and enhances the foraging performance of warblers. Females with experimentally darkened tail spots had significantly reduced foraging success related to decreased frequency of aerial prey attacks. These females delivered significantly fewer winged insects to nestlings and proportionately more insect larvae than control females (Bent 1953; Harrison 1984; Mumme 2014; Mumme et al. 2023).

Young are fed crane flies and other flies, moths and their larvae, beetles, and spiders. In Pennsylvania, the mean size of prey fed to nestlings was greater than those found by sweep netting; 16.0% of prey delivered to nestlings was more than 20 mm long. Females initiating a second brood discontinue feeding their first fledglings once they begin incubation, leaving care of the fledglings to the male. When first learning to feed on their own, fledglings attack moths most frequently. Adults feed exclusively on arthropods. It eats spiders, weevils and other beetles, and adult and larval lepidopterans in proportion to their abundance. Other food items include grasshoppers, locusts, plant lice, flies, ants, wasps, bugs, caddisflies, and nematodes (Bent 1953; Buehler et al. 2002; Evans Ogden and Stutchbury 1997; Mumme et al. 2023; Odum 1931).

The Hooded Warbler is a frequent host of the Brown-headed Cowbird. It appears to be preferentially selected as a host, possibly because of the chipping calls made by the female while building the nest. In Pennsylvania, 54% of Hooded Warbler nests were parasitized in 1 year compared with 3% of nests of other songbirds nesting within 3 m of the ground. Females respond aggressively toward cowbirds, but this appears to be ineffective given the high rate of parasitism. It usually accepts cowbird eggs, but occasionally abandons a parasitized nest. Despite the high rate

of parasitism throughout its range, most authors concur that cowbird parasitism has little effect on the reproductive success of the Hooded Warbler. This is because replacement clutches and second broods are seldom parasitized. Experimental removal of cowbirds at a Pennsylvania site drastically reduced parasitism, but did not result in a significant increase in reproductive success. Cowbird removal resulted in an average increase of only 0.12 young fledged per nest, or about 5 extra fledglings from a breeding population of 40 pairs. The reason for the minimal increase in productivity was that many unparasitized nests were depredated. Cowbird parasitism in Norfolk County resulted in warbler clutches that were 0.8 egg smaller than unparasitized nests. Nesting success was 35.0-58.3% for unparasitized nests compared with 18.2-41.5% for parasitized nests. Nestling survival rate was 55% in parasitized nests compared with 81% in unparasitized nests. In South Carolina, the costs of parasitism were clutches 0.8 egg smaller and 0.9 fledgling fewer per nest. In Ontario, parasitism rates are significantly higher in recently logged sites and in forests smaller than 75 ha. In South Carolina, the probability of parasitism was greater near clear-cut edges and at nests with less ground cover. Female cowbirds concentrated their nest-searching activities near edges of openings that were larger than 0.26 ha. Gaps created by group-selection harvesting did not increase parasitism rates. In Ontario, 54 of 114 nests (47.4%) reported to the ONRS were parasitized. Over a 2-year period in St. Williams Forest, 11 of 21 nests (52.4%) and 13 of 33 nests (39.4%) were parasitized. In South Walsingham Forest, a parasitism rate of 45% was reported compared with 18% at other scattered sites in southern Ontario. Annual parasitism rates are highly variable, ranging from 13-52% 1999-2010 at St. Williams. Over this period, 35% of 497 nests were parasitized. At the Ganaraska Forest, 1 of 13 nests (7.7%) was parasitized 2006-10. Parasitism rates reported from other areas include 61.5%, 64.3%, and 62% in Pennsylvania; 13.1%, 14.4%, and 18.2% in South Carolina; 75% in Illinois; 18%, 30%, and 50% in Ohio; and 5% and 39% in Arkansas (Bent 1953; Bisson and Stutchbury 2000; Heagy and Badzinski 2012; Kilgo and Moorman 2003; Mark and Stutchbury 1994; Moorman et al. 2002; Mumme et al. 2023; Peck and James 1998a; Rush and Stutchbury 2008; Sargent et al. 1997; Stutchbury 1997; Walters and Nol 2011b; Whittam 1999; Whittam et al. 2002).

Predation appears to be the greatest limiting factor for the Hooded Warbler. Ontario nest predation rates vary considerably annually, but are typically high at 30-50%. Predation is the primary cause of nest failure in Ontario and most other locations, and has a much larger influence on overall productivity than parasitism or any other factor. Predation rates during the egg and nestling periods are around 50% in much of its range. A high proportion of fledglings are also lost to predation, with most losses occurring within the first 5 days after fledging. In Ontario, 49% of fledglings survived to independence compared with only 19% in Pennsylvania. Even in large contiguous forests, females only produce 0.2-0.4 females per year and would have to live 4 seasons to replace themselves. There appear to be no differences in predation rates in small woodlots compared with large woodlots, with distance from edge, or from recent logging. Most authors found no relationships between predation rates and nest-site parameters. In a Pennsylvania experiment, vegetation was removed around some nests and the degree of concealment did not affect predation rates. The least visible nest (90% concealed by vegetation) was depredated while the most visible nest (22% concealed) was successful. Two South Carolina studies found vegetation variables at nest sites that affected predation. In 1 study, successful nests had a higher percent coverage by ferns than unsuccessful

nests. In the other study, nests that were better concealed from below were more successful. Snakes were the primary predators in this area (Allaire and Badzinski 2004; Bisson and Stutchbury 2000; Bowen et al. 2007; Evans Ogden and Stutchbury 1996; Heagy and Badzinski 2012; Howlett and Stutchbury 1996, 1997; Kilgo et al. 1996; Moorman et al. 2002; Mumme et al. 2023; Rush and Stutchbury 2008; Sargent et al. 1997; Whittam 1999).

Several studies concluded that the greatest threats to the Hooded Warbler in Ontario are habitat loss and fragmentation, and that this resulted in a significant decline in the species (Friesen et al. 2012; James 2000; Mumme et al. 2023; Page and Cadman 1994b). Bushman and Therres (1988) cited the same factors as being detrimental in Maryland. In the eastern United States, only about 20% of detections of the Hooded Warbler on Breeding Bird Survey (BBS) routes were in fragmented landscapes (Donovan and Flather 2002). The risk from habitat loss and fragmentation appears to be minimal in Ontario, and the amount of available habitat is stable or increasing. In general, the amount of forest cover is increasing and woodlands are becoming more mature. More coniferous plantations are maturing and being thinned, thereby creating suitable potential habitat (Heagy 2008; Heagy and Badzinski 2012). Loss of forests supporting it is unlikely as larger woodlots are typically designated significant woodlands by municipalities and development is usually prohibited in them. At greater risk are smaller woodlots that support the species because they may not be afforded the same level of protection. Isolation of smaller woodlots that support small populations may be detrimental. Females may avoid settling in small fragments due to lowered chances of receiving extra-pair copulations. For those that must leave the woodlot where the nest is located to seek extra-pair copulations, gaps between woodlots greater than 50 m will inhibit female movement and gaps greater than 500 m will inhibit males. Creating larger open gaps may result in smaller woodlots being abandoned (Norris 2000; Norris and Stutchbury 2002).

Diameter-limit tree cutting is usually detrimental because this removes the large trees that the Hooded Warbler requires. One Ontario study found no difference in its abundance in uncut forests and those than had been harvested using standard thinning practices and diameter-limits cuts; densities were low in all stands. Clear-cutting does not occur within its range in Ontario, but this practice can provide suitable postfledging habitat, albeit for a short period. Suitable nesting gaps within the canopy are a limiting factor and single-tree and group-selection harvesting is highly beneficial. In Norfolk County, it declined over time in a lightly logged forest and increased significantly in a nearby heavily logged forest. Eighty-four percent of gaps used for nesting were created by timber harvesting. In small woodlots, the entire area is typically logged at once, so the benefits may last only a decade at most. In larger woodlands, staggering the harvest over several years can create more permanent habitat. Management suggestions for Ontario include creating gaps no larger than 0.05 ha (a diameter of 25 m), leaving the shrub layer intact, retaining at least 12 m^2 per ha BA of trees larger than 38 cm, and creating 2-3 group-selection gaps per ha. The importance of selective harvesting for the Hooded Warbler has been identified throughout its range and in some areas it nests only in sites that have been harvested. In Illinois, openings of 0.02-0.4 ha were created in a 2,000-ha forest using group- and single-tree selection. It was absent in uncut forest, common in cuts 1-2 years old, and absent to rare in cuts 11-12 years old (Allaire and Badzinski 2004; Bisson and Stutchbury 2000; Bushman and Therres 1988; Friesen and Stabb 2001; Friesen et al. 2012; Gartshore 1988; Heagy 2008; Heagy and Badzinski 2012; Holmes et al. 2004; McCracken 1999a;

Mumme et al. 2023; Page and Cadman 1994b; Robinson and Robinson 1999; Walters and Nol 2011b; Whittam 1999; Whittam et al. 2000, 2002).

Timber harvesting may be discouraged or prohibited in some woodlands that support endangered species, and this could be detrimental to the Hooded Warbler. Page and Cadman (1994b) recommended that timber harvesting not take place in forests occupied by the endangered Acadian Flycatcher, and the 2 species often occur in the same woodland. Similarly, the presence of the endangered Jefferson salamander may inhibit or prevent timber harvesting in woodlands inhabited by the Hooded Warbler.

In New Jersey and Pennsylvania over a 15-year period, hemlock declined from representing 56% of the total basal area to 46% due to the hemlock woolly adelgid. This resulted in an increase in deciduous understorey. The Hooded Warbler increased, probably in response to the increase in deciduous shrubs and saplings (Toenies et al. 2018).

Farwell et al. (2019) examined the effects of shale gas infrastructure in West Virginia. These included pipelines, access roads, and well pads. The Hooded Warbler increased significantly with distance from well pads. In West Virginia, it was more abundant in intact forests than remnant forests near strip mines. Remnant forests were bordered by strip mines on 3 sides but were not directly affected by them (Margeneau et al. 2019).

Severe weather events that create gaps in the forest canopy may be beneficial. Insects and diseases (emerald ash borer, hemlock woolly adelgid, beech bark canker fungus, dogwood anthracnose fungus) may be beneficial provided that the canopy is not opened up too much and that some large trees remain (Friesen et al. 2012; Heagy and Badzinski 2012; Heckscher 2000).

Factors that reduce shrub coverage in woodlands are detrimental. Prescribed burns in forests may kill the low deciduous layer. This is a standard practice in pine stands in the southeastern United States. In North Carolina pine-oak forests, the Hooded Warbler occurred most frequently at points that had not been burned for more than 15 years following low severity fires, and longer following high severity fires. Woodlots grazed by sheep in Illinois were abandoned by the Hooded Warbler. Sheep grazing is not an issue in southern Ontario, but overbrowsing by white-tailed deer could have deleterious effects (Gartshore 1988; Graber et al. 1983; Rose and Simons 2016).

In Arkansas, Nagy and Smith (1997) examined the effects of spraying the larvicide Bt to eradicate gypsy moths, which results in a reduction in the number of all caterpillars. An 85% reduction in the amount of caterpillars affected few aspects of the Hooded Warbler's reproductive biology. Nest success was not affected by food limitation. Nestling mass was lower in the treatment zone for birds that hatched shortly after application, so survivorship may be reduced for these individuals. There were no differences in feeding rates between control and treatment areas. Bt application appeared to have minimal effects.

Deforestation of winter habitat is occurring to create pasture for cattle, and burning occurs regularly. This results in habitat loss and habitat that is burned becomes unsuitable. Loss of winter habitat may be a significant limiting factor (Mumme et al. 2023; Powell and Rappole 1986).

All-terrain vehicles and snowmobiles could introduce invasive species and destroy the understorey vegetation required by the Hooded Warbler (Friesen et al. 2012).

The effects of climate change on the Hooded Warbler are uncertain. Melles et al. (2011) examined factors that led to its increase in Ontario. There has been a significant and gradual lengthening of the growing season in Ontario, with the number of growing-degree days above 5°C at northern breeding sites increasing by 162 since 1940. Its mean probability of occurrence in Ontario has been increasing since 1975. Seventy-seven percent of variation in its probability of occurrence was related to increasing mean temperature and the growing season length. An additional 14% in variation was correlated with reduced amounts of precipitation. Changes in climate over the past 20 years were a better predictor of range expansion than were gradual shifts in distribution due to immigration. Forest connectivity was only marginally significant and amount of forest cover was not significant. Establishment probability, based on the number of occupied neighbouring atlas squares, and immigration from the south, estimated from BBS results, were also important predictors of range expansion. Increased growing season and July temperatures and decreased precipitation were the most important predictors. Price (2004) predicted that the Hooded Warbler could become extirpated as a breeding species in southern Ontario if the average summer temperature increased by 2°C.

Status

The status of the Hooded Warbler prior to European settlement is uncertain. It was originally thought that it probably inhabited most of the Carolinian Forest Region and portions of the southern Great Lakes–St. Lawrence Forest Region prior to deforestation of the southern portion of the province. It was postulated that it was virtually extirpated from the province as a result of forest clearing and that its recent increase in population represents recovery of the species within its original range. There were no early records from the province to substantiate this theory, but there were few ornithologists present during this era and there are also few to no records of some species that clearly were here prior to European settlement. The only evidence to support the hypothesis that it originally occurred in Ontario is that it was abundant prior to settlement at similar latitudes in southern Michigan, where it declined precipitously due to deforestation and subsequently recovered at approximately the same time frame as in Ontario. The alternate theory is that the Hooded Warbler is a recent immigrant to Ontario. This appears to be more plausible because there were very few records of the species in the late 19th and early 20th centuries. In addition, the entire range of the species increased in the mid- to late 20th century, consistent with its first breeding records in the province and subsequent increase. BBS data indicate that the northern margin of the breeding range shifted 115 km north over a 26-year period. The currently accepted explanation is that the Hooded Warbler is a recent colonist to the province rather than a species that was extirpated and is now recovering. A review of its status in the province in 1925 concluded that it was a rare migrant but acknowledged that an observation of a young bird in autumn suggested breeding (Austen et al. 1994; Baillie 1925; Heagy and Badzinski 2012; Page and Cadman 1994b).

The first record of the Hooded Warbler for the province was a spring migrant seen at Hamilton prior to 1860. It would be another 60 years before another one was seen in Hamilton during the spring of 1920. The first breeding season record came from Chatham-Kent in 1878, followed by

records from Essex in 1912; Elgin in 1940, Hamilton in 1941 and 1953; York in 1947, 1951, and 1953; Lambton in 1947 and 1957; Halton in 1954 and 1955; Niagara in 1954; and Oxford in 1957. The first nest was found in the province on 27 July 1949 in the Springwater Conservation Area in Elgin County and additional nests were found there in 1950 and 1952. Records from Elgin County give a good historical perspective of its breeding status. In 1891, it was unknown to have occurred in the county. By 1954, it was known only from the Springwater area. By 2000, it was essentially extirpated from the main forest at Springwater due to the lack of timber harvesting, but occurred near there in recently logged woodlots. At that time, it was a local breeder that was becoming increasingly common and widespread. In 1957, the first nest for Oxford County was discovered near Tilsonburg. Prior to the first atlas, the Hooded Warbler was considered a straggler that bred only occasionally in Ontario. The second atlas and intensive studies on the Norfolk Sand Plain in 1985 and 1986 revealed that it was uncommon on this geographic feature in Elgin, Oxford, and Norfolk counties, and rare elsewhere with scattered records in Chatham-Kent, Elgin, Middlesex, Niagara, Hamilton, and York. Because much suitable habitat remained uninvestigated, it was concluded that the province could potentially support 100 breeding pairs. For the next 10-15 years, breeding records increased substantially, but it was difficult to determine if it had actually increased or if the apparent increase was an artifact of more observers and more targeted searches (Austen et al. 1994; Baillie 1962, 1967; Curry 2006; Gartshore 1988; James 2000; Lancaster et al. 2004; McIlwraith 1894; Page and Cadman 1994b; Sutherland and Gartshore in Cadman et al. 1987).

Between the atlases, several targeted inventories were completed for the Hooded Warbler, and these highlighted the dramatic increase during this period. Estimates of numbers of breeding pairs were: 80-176 in 1988, 144-207 in 1998, 150-210 in 2001, and 242 in 2002. At the St. Williams Forest, which now supports much of the core population, it was apparently absent in 1994, 8 pairs were present in 1995, and there were 43 pairs in 1999 (Friesen and Stabb 2001; Gartshore 1988; Heagy 2008; James 2000; McCracken 1999a; Whittam 1999; Whittam et al. 2002).

The second atlas showed an expansion in the range of the Hooded Warbler, with several breeding records in the Great Lakes–St. Lawrence Forest Region south of the Canadian Shield and one in the Shield. It expanded its range within the Carolinian Forest Region, with concentrations in Norfolk County and Niagara Region and lesser numbers in Hamilton, Chatham-Kent, and Lambton. It was detected in 81 squares compared with 21 during the first atlas. Its probability of observation increased significantly by almost 400% between atlases (Badzinski in Cadman et al. 2007).

Numbers continued to increase after the second atlas. In 2006, a small population was detected in Ganaraska Forest, about 200 km north of its previously known range. As of 2011, this population remained stable at approximately 5 pairs. In 2007, at least 436 territorial males were detected at 89 sites in Ontario and the population increased by more than 300% from 1997 to 2007. The 2011 population was estimated at 1,000-2,000 mature birds. The population continues to be concentrated in Norfolk County where counts have at least doubled every 5 years. Numbers have also increased in Hamilton and Niagara, but not in other areas of southwestern Ontario. A small isolated population near Midland has persisted at low levels for 20 years and the Hooded Warbler has expanded in the Greater Toronto Area, especially in Durham Region, and Northumberland County. In 2012, it was concluded that there was no reason to expect that the population would

not continue to grow, at least over the next decade. There is a high probability of regular immigration from northern United States populations and this is considered essential because Ontario populations may be unable to sustain themselves without continued immigration. Small changes in the large United States population could have a significant ripple effect on the small Canadian population (Heagy 2008; Heagy and Badzinski 2012; Walters and Nol 2011b).

Early status reports assumed that the Hooded Warbler had been widespread in southern Ontario prior to European settlement and subsequently extirpated due to deforestation. At the federal level, it was first ascribed a status of special concern in 1994. A review in 1994 resulted in its status being upgraded to threatened, and this status designation was reaffirmed in 2000. At this time, it was also designated special concern provincially. A recovery strategy and another status report were prepared in 2012. The recovery strategy identified the population objective as increasing the number of breeding pairs to 500, but the status report observed that this objective had already been realized. In 2012, the status of the Hooded Warbler was downgraded to not at risk nationally and provincially (Friesen et al. 2012; Heagy and Badzinski 2012; James 2000; Page and Cadman 1994b).

BBS data indicate a nonsignificant continental increase from 1966 to 1991. During this period, there was a significant increase of 1.58% per year in the east and a nonsignificant decline of 5.43% per year centrally (Mumme et al. 2023). The global population of the Hooded Warbler has doubled since the 1970s, due in part to climate change (Mumme et al. 2023). There are insufficient BBS data to estimate population trends in Canada and Ontario (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Brood division by the adults occurs once the young fledge, with the female taking care of the extra chick in broods with odd numbers. The 2 sub-broods remain distant from each other except when the female attempts a second brood. When this occurs, the female's portion of the first brood reunites with those being cared for by the male once she starts incubating the second clutch. The young are unable to fly when they first leave the nest but can fly about 3 days later. They seek dense cover near the nest for the first 6 days out of the nest. This may consist of fallen treetops, tangles of decaying logs, or dense deciduous shrub or sapling cover. The vertical cover of vegetation 2-4 m from the ground is significantly greater at sites used by fledglings than at nest sites. Once the young are capable of flight, they follow the adult that is caring for them and move further from the nest site. During the first 6 days after fledging, the mean distance moved from the nest in Pennsylvania was 37 m compared with 70 m during days 7-15. Those that hatched in small woodlots never left the forest fragment. During days 7-28 after fledging, young in small fragments used locations with a greater proportion of cover 0-2 m and 2-4 m from the ground than those in large forests. In Pennsylvania, males and their fledglings averaged 104 m from females with their charges. Fledglings attended by females were led an average of 155 m from the centre of the territory compared with 46 m for males. Females took their broods as far as 650 m from the territory. Males usually remained within the territory or very close to it. Young first attempt to feed themselves 5 days after fledging, usually unsuccessfully, and may not be independent for 5-6 weeks after fledging. In southern Ontario, adults attend young into early September (Bent 1953; Evans Ogden and Stutchbury 1994, 1997; Mumme et al. 2023; Rush and Stutchbury 2008).

Within forests, adults with fledglings seek dense deciduous growth either in small woodland gaps or in forest edges. They are also common in non-forested early successional habitats such as clear-cuts. Juveniles, adults, and family groups have inhabited young clear-cuts during the postfledging period in Ohio, Pennsylvania, Virginia, Missouri, and West Virginia. In Ohio, the Hooded Warbler was the fourth-most abundant forest-breeding species captured in clear-cuts. It was twice as abundant in small (4.0-9.3 ha) than large (13.3-18.1 ha) clear-cuts and there was no significant difference in the number of captures 20, 50, or 80 m from the edge of adjacent mature forest. In West Virginia, its abundance in clear-cuts declined with increasing BA of retained timber. Retained trees inhibit understorey growth, limit stem density, and provide perches for raptors. Capture rates increased with increasing understorey stem density, total arthropod biomass, and total lepidopteran larvae biomass. During the postfledging period in South Carolina bottomland forests, 2% of mist-netted birds were in forests, 47% were in forest gaps, and 51% were in forest edges (Bowen et al. 2007; Evans Ogden and Stutchbury 1997; Friesen et al. 2012; Marshall et al. 2003; McDermott and Wood 2010; Porneluzi et al. 2014; Stoleson 2013; Vitz and Rodewald 2006, 2007).

In Missouri, Porneluzi et al. (2014) netted during the postfledging period 2-15 years after an oak-pine-hickory forest was clear-cut. The Hooded Warbler was the second-most abundant species captured. Its numbers increased gradually to a peak 7-9 years after cutting and then declined.

Juvenile males that immigrate to new areas outside the natal site sing and appear to establish territories. These birds may return to the same site to breed the following year (Mumme et al. 2023).

In late August and September, Ontario birds join mixed flocks before migrating (Friesen et al. 2012).

MIGRATION

Although the Hooded Warbler is a nocturnal migrant, it rarely strikes tall structures (Graber et al. 1983; Mumme et al. 2023).

Males typically arrive a week earlier than females in spring and occasionally as much as 2 weeks in advance of females. Adult females arrive 7-10 days before yearlings. In Louisiana, the average length of stopover was 2 days after birds had crossed the Gulf of Mexico. In Norfolk County, males are on territory as early as 9 May, but typically arrive 11-18 May. Elsewhere in the south, early migrants arrive in late April, but most arrive in mid-May (Black and Roy 2010; Curry 2006; Gartshore 1988; LaForest 1993; Lancaster et al. 2004; Moore and Kerlinger 1987; Mumme et al. 2023; Page and Cadman 1994b; Stutchbury et al. 1997; Weir 2008).

Autumn migrants occur throughout September and rarely into the first week of October. The latest autumn records are often of birds that are still on their breeding territories (Curry 2006; Gartshore 1988; Lancaster et al. 2004; Weir 2008).

During both spring and autumn migration, the Hooded Warbler occurs most often in edge habitat within logged forests. During spring migration in South Carolina, 5% of mist-netted birds were captured in forest, 47% were in forest gaps, and 48% were in forest edge. During autumn migration, 8% were captured in forest, 40% in gaps, and 52% in forest edge. Relative abundance in North Carolina habitats during spring migration were 1.98 in oak-hickory forests, 1.60 in floodplain

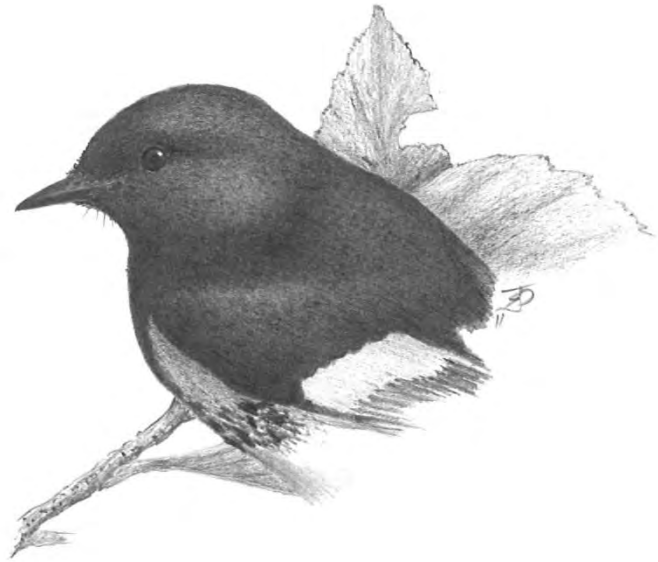
forests, 1.54 in pine forests, 1.42 in pine-hardwood forests, 0 in wet and dry thickets, and 0 in beech forests (Bowen et al. 2007; Kilgo 2005; Mumme et al. 2023; Parnell 1969).

In New York, Lebbin et al. (2007) suspected that Hooded Warblers were foraging at night under artificial lights, but could not confirm this. During spring migration in North Carolina, 18.6% of foraging occurred in the canopy, 48.3% in low trees, 30.9% in shrubs, and 2.2% on the ground. In the canopy, 0% of foraging was at the top of the crown, 2.3% in the inner crown, 16.3% in the lower crown, and 0% on the bole. In low trees, 4.5% of foraging was at the top of the crown, 11.2% in the inner crown, 32.6% in the lower crown, and 0% on the bole. In shrubs, 3.9% of foraging was in the top of the crown, 10.1% in the inner crown, 4.5% in the lower crown, 10.1% in dense thickets, 2.3% in brush piles, and 0% in grasses. On the ground, 1.1% of foraging was in dense thickets, 0% in grasses and at water's edge, and 1.1% in the open (Parnell 1969).

The Hooded Warbler is a rare migrant and is occasionally observed considerable distances from the breeding range. It has been observed during spring and autumn migration in areas such as Moosonee (James 1991). Although it continues to be a rare migrant, numbers are increasing significantly. During the mid-1990s, approximately 50 were seen at Long Point Bird Observatory (LPBO) during spring migration. During 1961-2010, numbers of spring migrants at LPBO increased significantly at a rate of 3.4% per year. The rate of increase is augmenting. The increase 1970-2010 was 2.7% per year compared with 6.2% for 2000-10. The 10-year trend indicates an 80% increase in spring migrants (Heagy and Badzinski 2012; Page and Cadman 1994b).

American Redstart

Setophaga ruticilla



BREEDING SEASON

Habitat Requirements

Most Ontario American Redstart nests were in woodlands (75.0% of nests). The remainder were in shrubby fields (19.0%), dense stands of deciduous shrubs (5.0%), and in a garden (1.0%). Of nests in woodlands, 52.1% were in deciduous stands, 37.0% were in mixed stands, 2.7% were in coniferous stands, and 8.2% were in unspecified stands. It preferred second-growth woodlands and those with a dense deciduous understorey of shrubs or saplings to mature forests. Many nests were near woodland or swamp edges, or beside roads or shorelines (Peck and James 1987). A nest in Grey County was in a small urban apple orchard (Peck and Peck 2010). James (1984b) reported that it bred in deciduous and mixed woods where it requires a closed canopy. The canopy may consist of only tall shrubs or dense young trees but may also include mature forests with dense shrub coverage within the forest or at its edges. The redstart may occur in either dry or wet forests, usually where there are some trees amongst growth close to the ground.

The range of the American Redstart barely extends into the southern portion of the Hudson Bay Lowland. It is a fairly common breeder in the Moosonee area where it inhabits riparian lichen-rich spruce forests (Wilson and McRae 1993).

In the Boreal Forest Region, the redstart nests both in forested and shrubby areas, including regenerating clear-cuts and burns. Clear-cuts may provide important habitat in extensively forested landscapes. Near Hearst, Welsh and Fillman (1980) reported it in 3-17-year-old clear-cuts in upland mixed forests and in 3- and 24-year-old clear-cuts in lowland coniferous forests. Near White River in jack pine stands, it was most abundant in clear-cuts 13-15-years old and occurred in all stand ages from young clear-cuts to mature forests (Venier and Pearce 2005). Welsh (1993) considered it a mid-successional species in the Boreal Forest Region. It occurred in stands 6-27 years old but not those 1-5 or 33-220 years old. In the Clay Belt, it occurred in all forest types, but was most abundant in those dominated by balsam poplar, followed by trembling aspen, white birch–white spruce, tamarack or white cedar, jack pine, and white spruce. It was significantly associated with nutrient-rich stands. It occurred throughout the moisture regime, from the wettest to driest stands and averaged near the midpoint on the moisture axis (Welsh and Lougheed 1996).

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield near Gogama, the redstart was common in younger mixed woods where some deciduous trees reached a height of 6-7 m. It also occurred in dense deciduous groves. It avoided older forests where the trees formed a closed canopy. It was restricted to mixed forests 17-20 years old (James and Peck 1995a). In northern hardwoods near Sault St. Marie, it increased after single-tree selection harvesting occurred. The increase occurred 6-7 years after harvest once a shrub layer became established (Holmes and Pitt 2007). Near Parry Sound, it was absent in pure jack pine stands, but occurred in low densities in young, open-canopied, mixed jack pine–deciduous stands (James 1979a). In Muskoka and Parry Sound districts, it was most abundant in deciduous or mixed forests or in the deciduous understorey of more mature forests (Mills 1981). In Algonquin Park, it was most abundant in poplar-birch stands, followed by balsam fir–spruce-hardwood stands, poplar-birch-fir-spruce stands, and hardwoods. It was also common in shrubby plots at forest edges; it was the most abundant species in border plots. It was absent in bogs, young white pine stands, and hemlock stands. In poplar-birch stands, it restricted its activities from the ground upward to the lower tree branches, a height of approximately 6 m. In hardwoods, it ranged from the ground to 8.8 m, just below the bottom of the canopy. In balsam fir–spruce forests, it occupied the central portion of the canopy. Martin (1960) considered it a species of pioneer deciduous forests. In white pine stands in Algonquin Park, Kingsley

and Nol (1999) found it in all age classes that they examined: 2-9-year-old shelterwood cuts, 10-16-year-old cuts, and forests with no recent history of cutting. It was most abundant in 10-16-year-old cuts, but not significantly. In Algonquin Park, it was associated with sapling density in the 2-5-m stratum (Jobes et al. 2004). In Muskoka District and Haliburton County, nest sites were associated with moderate canopy volume, moderate tree density, and high densities of woody understorey (Clark et al. 1983).

In Presqu'ile Park, the redstart nests in deciduous forests, especially in areas with a thick understorey (LaForest 1993). In Durham Region, Speirs and Orenstein (1975) observed it in a mature maple-oak forest on a floodplain rising to rocky ridges. Most of the plot had a full canopy, but trees were sparse on the ridges.

In the Carolinian Forest Region, the redstart was a significant indicator of diameter-limit cuts and was more abundant in heavily harvested forests than those that had been selectively cut or had no recent history of cutting. It was more abundant in recent than older cuts and was absent in selectively thinned and uncut forests (Holmes et al. 2004).

Throughout its range, presence of deciduous shrubs or saplings appears to be the most important component of the redstart's habitat requirements. In forested habitat, it is associated with edges, gaps in the canopy, or open-canopied woodlands where light penetration promotes growth of a woody understorey. Breeding habitat is not restricted to woodlands and it may be locally abundant in shrubby areas, particularly those dominated by willows and alders. Regenerating clear-cuts may provide high-quality habitat from the young sapling and shrub stage until the trees become pole-sized. Clear-cutting and other types of timber management that promote shrub and sapling growth can be beneficial, especially in forest-dominated landscapes where habitat is limited. Less frequently or rarely used habitats include orchards, fencerows, pine and oak barrens, and suburban parks and woodlots.

Because the presence of a woody understorey is the key habitat parameter, the redstart inhabits a variety of forest types. Virtually every type of deciduous forest may be used. In the northeast, it occurs equally in deciduous treed swamps and dry forests such as those dominated by maple-oak or maple-beech. In the southern and western portion of its range, it is more restricted to treed swamps, bottomland forests, and riparian thickets of willow and alder or, to a lesser extent, red-osier dogwood. It occurs in a variety of mixed forests provided that there are suitable patches of deciduous trees and undergrowth. In most mixed forests, its abundance declines with increasing coverage by coniferous species. One study concluded that it was associated with increasing abundance of pine or spruce-fir, but this does not appear to be the norm. It avoids pure coniferous forests and plantations. On islands dominated by spruce in Maine, most male redstarts failed to attract a mate. Where deciduous cover was available, it was used significantly more than its abundance. In New Hampshire and Maine, it was not recorded in balsam fir–spruce stands, but occurred in all other forest types. It was most abundant in northern hardwoods and aspen stands, followed by stands dominated by swamp hardwoods, white birch, hemlock, and white pine. In North Carolina, its relative abundance during the breeding season was 1.81 in floodplain forests, 1.41 in beech forests, 0.43 in pine-hardwoods, 0.20 in oak-hickory forests, and 0 in pine forests and wet and dry thickets. In British Columbia and Quebec eastward, it frequently breeds in coniferous

forests where it is restricted to riparian areas that support deciduous shrubs such as willows and alders. Examples of forest types that it has nested in include white pine or spruce mixed with hardwoods, almost pure spruce or balsam fir stands, sugar maple–basswood-hackberry, sugar maple, trembling or large-toothed aspen, balsam poplar, maple-beech, red maple–birch-conifers, bur oak, sycamore, white cedar–balsam fir, oak-pine, hardwood swamp, white birch–red oak, silver maple swamp, yellow birch–white birch–white cedar, sugar maple–yellow birch, hemlock–yellow birch, ash-basswood lowland forest, red maple swamp, white spruce–trembling aspen, pin oak swamp, and lowland white spruce interspersed with aspen, poplar, and white birch. In the west and northeast, the redstart shows a preference for stands dominated by trembling aspen or balsam poplar, or riparian thickets of willow and alder along margins of ponds, lakes, rivers, and wetlands. In the Boreal Forest Region, it is typical of aspen-birch stands and may be a dominant species in these stands where there is a dense subcanopy at a height of 3-9 m; elsewhere it may be scarce or lacking. In many areas, it nests predominantly in forests along streams and rivers. In Illinois, some of the highest densities occurred on wooded islands (Beals 1960; Campbell et al. 2001; Capen 1979; Chapman 1907; DeGraaf and Chadwick 1987; DeGraaf et al. 1998; Erskine 1977; Faanes and Andrew 1983; Ficken and Ficken 1967; Golet et al. 2001; Graber et al. 1983; Gross in Bent 1953; Harrison 1984; Hobson and Bayne 2000; Howe 1974; Hunt 1996; Kirk et al. 1996; LaRue et al. 1995; Morse 1973; Mossman 1988; Mossman and Hoffman 1989; Parnell 1969; Rich et al. 1994; Robbins et al. 1989; Sabo 1980; Sherry and Holmes 1997; Sinclair et al. 2003; Sturm 1945; Temple et al. 1979; Wiebe and Martin 1998).

The redstart is an adaptable species that may use different habitats in different regions. On a broad scale, this is evident in its preference for forested swamps in the south and poplar stands and willow or alder thickets in the west. Collins (1983a) compared its habitat usage in Maine and Minnesota. Maine birds occurred in areas with a high percent canopy cover, variable coniferous cover, and many trees in smaller size classes. Minnesota birds occurred in areas with dense shrub cover, moderate canopy cover, and low percentage of conifers in the canopy. Its habitat structure was significantly different from random for shrub cover, canopy cover, number of tree species, and number of trees 7.5-23 cm diameter at breast height (DBH). It selected the most optimal habitat at each site from what was available. Ficken and Ficken (1967) observed habitat differences in areas used by the redstart in New York and Maine. The New York study area was a deciduous swamp with a nearly closed canopy and an understorey of saplings 6 m tall. There were dense stands of saplings where the canopy was interrupted and it nested within both habitat types within the swamp. The Maine landscape was dominated by coniferous forests, and it selected 5 distinct habitats for breeding. The first was deciduous forest with some trees taller than 9 m, understorey saplings as tall as 6 m, and occasionally as much as 10% coverage by conifers (white pine and spruce). The second habitat type was immature deciduous forest with trees taller than 9 m, but with the understorey not as well developed and often more open. The third habitat was dense alder thickets growing to a height of 4.6 m, often with willows and some deciduous growth. The fourth habitat was mixed forest with 10-60% coverage by white pine and/or spruce and the remainder deciduous coverage. The final habitat used was coniferous cover with more than 60% coverage by conifers, including some stands that were pure spruce.

In New Hampshire, Hunt (1996) investigated areas that were defended first in spring and by adult males, which are socially dominant to yearling males, to assess which areas were preferred habitat. The site supported 3 habitats: early successional stands 4-22 years old (mean 10.8 years), mature deciduous stands 20-122 years old (mean 72.4 years), and mature coniferous stands 36-102 years old (mean 73.0 years). Early successional areas were characterized by high redstart densities; a high proportion of adult males; high mating success, even of yearling males; and smaller territories. Coniferous stands were occupied last in spring, and the proportion of adult males decreased with increasing stand age. Early successional stands were important to the redstart. It could decline as these stands matured. Coniferous stands may support lower densities.

The redstart has been variously described as an early, mid-, or late successional species or preferring early to late seral stages. This is due in part to the broad habitat range that it occupies, but also to the varying manners in which successional and seral stages have been defined. There is good evidence for it being associated with early successional areas because it occurs in recent clear-cuts, regenerating old fields, and shrubby utility rights-of-way, particularly those passing through forested habitat. Its response to habitat succession in Maine clear-cuts is typical of its usage of this habitat type. It was absent in the first 2 years after cutting when cuts were dominated by open ground covered with slash. It was most abundant 3-6 years after cutting when habitat consisted of dense coverage by raspberries and regenerating hardwoods less than 2 m tall. It was slightly less abundant in the next stage of succession, but was one of the dominant species. At this stage, the hardwood regeneration was taller than 2 m and there was a well-developed but slower growing softwood regeneration layer. It was even less common once hardwood regeneration was taller than 4.5 m and trees were 10-15 cm DBH. The final seral stage was a dense coniferous canopy with an open forest floor; it was absent in this stage. Its abundance was positively correlated with the number of deciduous trees less than 10 cm DBH that were 2.1-4.5 m tall and the number of dead tree stems larger than 10 cm DBH. It was negatively correlated with the number of conifers larger than 20 cm DBH. In many other areas, it exhibits an absence immediately after cutting, high populations during the early shrub and sapling stages, and a decline once trees become larger and shade out the lower layers of woody vegetation. In Vermont, territories included mostly forests, but some included forest and clear-cut and some were entirely in clear-cuts (Back 1979; Falardeau et al. 1999; Freedman and Johnson 1999; Hanowski et al. 2005; Lent and Capen 1995; Morgan and Freedman 1986; Sabo 1980; Thompson and Capen 1988; Titterington et al. 1979; Yahner 1993). On hydro transmission line corridors in Pennsylvania, the redstart was one of the most abundant species during the breeding season. It occurred in all types of management plots, which included combinations of hand cutting, mowing, and herbicides, but was uncommon directly under the wires where there were few shrubs. Yahner et al. (2002) considered it adapted to both early succession and forested habitat.

Most authors consider the redstart a mid-successional species associated with second-growth hardwoods or medium-aged stands. Presence of woody growth in the 1.5-6-m range is important. On South Bass Island in western Lake Erie, it was more abundant in a second-growth woodland dominated by sugar maple, basswood, and hackberry than in a mature forest of the same composition a short distance away. In New Hampshire and Maine, it was significantly more abundant in sapling-sized stands than in other tree-size classes. It was next in abundance in large

sawtimber stands with trees averaging larger than 60 cm DBH followed by sawtimber-sized and pole-sized stands (Baker 1944; Collins et al. 1982; Cyr and Darveau in Gauthier and Aubry 1996; DeGraaf and Chadwick 1987; DeGraaf et al. 1998; Ficken 1962a; Hoffman 1989a; Litwin and Smith 1992; Noon et al. 1979; Sturm 1945). Long-term studies in New York and New Hampshire found that the redstart declined significantly with time and it became extirpated at 1 site. For both sites, the declines were a result of forest maturation. During this period, areas of low shrub and sapling growth disappeared or declined, rendering the habitat less suitable (Holmes and Sherry 2001; Litwin and Smith 1992). Bond (1957) examined the distribution of birds in Wisconsin in a series of woodlots that spanned the entire successional range, a wide range of age classes, different sizes, and a range of moisture regimes. The redstart exhibited one of the most striking curves along the vegetational gradient. It reached a definite peak in the middle portion of the gradient and was uncommon in all other continuum intervals. The trend was marked regardless of the size of woods, although it was more pronounced in large than small woods. Small woodlots appeared to present more pioneer conditions to avifauna than larger woodlands with a similar continuum interval, possibly due to more light and wind penetration. It was most abundant in stands midpoint on the moisture scale where saplings were dense and well branched.

In western Canada, the redstart is significantly more abundant in mature stands, but these are typically early successional stands dominated by aspen or aspen birch. In these stands, it is associated with high shrub density and large, sparse trees. It was also present where there were large numbers of snags larger than 20 cm DBH; conifers were avoided (Kirk et al. 1996; Schieck et al. 1995). In Pennsylvania, it had a negative affinity for old-growth forest. It occurred in 18.2% of old-growth stands, 60.7% of stands within the state, and 79.6% of forests on the Appalachian Plateau (Haney 1999).

Several studies identified microhabitat preferences of the redstart, and virtually all confirmed the importance of deciduous shrubs or saplings in the understorey. In Illinois, its abundance was associated with silver maple trees larger than 10 cm DBH and a shrub understorey. In the mid-Atlantic states, its abundance was correlated with trees larger than 38 cm DBH and percent ground cover. In Iowa, it was correlated with shrub coverage and negatively correlated with grass cover (Graber et al. 1983; Robbins et al. 1989; Stauffer and Best 1980; Vanderwel et al. 2009). In Alberta, Sodhi et al. (1999) compared habitats of trembling aspen forests that were occupied and unoccupied by the redstart, and habitats within and outside territories. Unoccupied woodlots and areas outside territories contained larger trees and higher densities of trembling aspen, accompanied by prickly rose, red-osier dogwood, and honeysuckle. Areas within territories were characterized by high densities of willow trees and shrubs, cherries, Saskatoon, and balsam fir saplings, as well as a tall shrub layer. Nest sites were associated with a high density of white birch trees and saplings, willows, cherry, and balsam poplar saplings, as well as viburnums that contributed to a tall shrub layer. Territories were not established randomly and were characterized by a high abundance of willow and other tall shrub species. Nest sites also supported high densities of white birch. Trembling aspen was underrepresented in occupied sites, even though this was the dominant tree in the community. It preferred early successional forests or disturbed areas embedded within older stands, but might also choose territories based on soil moisture or food availability. In Vermont, average habitat variables for the redstart were 37.2% green ground cover,

8.7% cover by slash on the ground, 77.0% canopy closure, 22.9 m canopy height, 12.5 m canopy depth, 17.0 m^2 per ha basal area (BA) of deciduous species, 3.5 m^2 per ha BA of coniferous species, 16.4 cm DBH for deciduous species, and 15.9 cm DBH for conifers. It was in the closed-canopy deciduous association (Thompson and Capen 1988). In Minnesota, average habitat characteristics were 67.7% ground coverage, 70.7% shrub coverage, 66.3% canopy cover, 14.5 m canopy height, and 4.7% coniferous cover. It was in a guild with the Black-and-white Warbler, Nashville Warbler, Magnolia Warbler, and Canada Warbler. It was separated from other warblers in this guild by preferring more medium-sized deciduous trees and conifers (Collins et al. 1982). In subalpine areas of New Hampshire, it preferred areas midway between sheltered valleys and exposed slopes, areas with wet depressions, average canopy height 10.4 m, 74% canopy closure, 38% coniferous foliage volume, and an average DBH of 10 cm for live trees (Sabo 1980). In New Hampshire and Maine, it was positively associated with the number of coniferous trees larger than 10 cm DBH, the number of deciduous trees 2-10 cm DBH, the number of woody stems per ha, and total foliage volume of both deciduous and coniferous trees larger than 10 cm DBH. It was negatively correlated with the number of coniferous trees 2-10 cm DBH (DeGraaf et al. 1998).

Several authors considered the redstart a forest-interior species, but provided no data to support this (Freemark and Collins 1992; Grant and Berkey 1999; Hobson and Bayne 2000; Sherry et al. 2020). It does not avoid edge in New Hampshire or Alberta (Sherry et al. 2020). In southern Ontario, it was negatively correlated with the amount of forest further than 100 m from edge, although this relationship was not significant (Austen et al. 2001). There appears to be no evidence that the redstart is a forest-interior species. If anything, the opposite is more likely because shrubby areas at edges of woodlands may provide superior habitat to forest interior.

The American Redstart appears to be area-sensitive in some areas and not in others. Area sensitivity in this species may be complex, with sensitivity being exhibited where it is uncommon, where there is limited forest cover in the landscape, and where woodlots are isolated from each other. Where woodlots are close together or the landscape is largely forested, area sensitivity may completely break down. Extra-pair fertilizations are an important component of its mating behaviour and the requirement for neighbours to accomplish this may be 1 factor that affects area sensitivity. Because of the variables that affect area sensitivity, various studies have concluded that the redstart is mildly or highly area sensitive, or unaffected by forest size. Certain authors (Freemark and Collins 1992; Mossman and Hoffman 1989; Robbins 1979) considered the redstart an area-sensitive species without providing any supporting documentation. Some studies determined that it is not area sensitive. In Alberta, Sodhi et al. (1999) found it nesting in woodlots as small as 2 ha. In Pennsylvania, it was not area sensitive during the breeding season (Keller and Yahner 2007). In North Dakota, it was not influenced by forest size or isolation, and was present in woodlots smaller than 2 ha (Grant and Berkey 1999). In Wisconsin, it was not restricted to larger islands (Beals 1960). Robbins et al. (1989) did not find a relationship between redstart abundance or occurrence and forest size in the mid-Atlantic states, but it was positively correlated with the percent forest coverage within 2 km. In red maple swamps in Rhode Island, there was no significant difference in its abundance in swamps smaller than 1 ha and those 11-20 ha. These swamps were surrounded by upland forests, so this may not have been a true test of area sensitivity (Golet et al. 2001). In Maine, it nested on islands where the forest cover was only 0.16-1.50 ha (Morse 1973). Other studies concluded that the

redstart is area sensitive. In Saskatchewan, it was significantly correlated with forest size and only occurred in woodlots 15 ha or larger (Johns 1993). Also in Saskatchewan, it was significantly correlated with forest size and amount of forest cover within 5 km (Hobson and Bayne 2000). In western Maryland, where it is uncommon, it was found only in forests larger than 4,000 ha and, in other areas of the state, it was not found in woodlots smaller than 70 ha (Bushman and Therres 1988). In South Dakota, it was absent in 3.5-ha woodlots, but common in large riparian woodlands. Gentry et al. (2006) were uncertain if woodlot size precluded usage by the redstart or if other factors contributed such as vegetation structure or distance from other wooded areas. In Wisconsin, Bond (1957) found the redstart in woodlots as small as 6.5 ha, near the minimum woodlot size that he examined. Its frequency of occurrence increased with forest size: 7.3% in woodlots 6.1-14.2 ha, 16.6% in woodlots 16.2-32.4 ha, and 29.0% in woodlots larger than 32.4 ha. It was at least 50% more common in large than small woodlots. There are 4 studies relevant to redstart area sensitivity in Ontario. James (1984b) did not identify it as being area-sensitive but Coleman et al. (2000) concluded that it was highly area sensitive and required forests 100 ha or larger. No fieldwork was undertaken as part of these studies. South of the Canadian Shield, its presence was positively correlated with woodlot size, but not significantly. It was negatively correlated with the amount of forest cover within 2 km and the amount of regional forest cover, but these relationships were also not significant (Austen et al. 2001). A study in Grey County on the Niagara Escarpment found redstarts in small woodlots 1-2 ha in size. This area was extensively forested and all woodlots were very close together (personal observation). The distribution map in the second atlas (McLaren in Cadman et al. 2007) indicates that it occurred in most squares in southern Ontario, except for a few in Essex, Lambton, Chatham-Kent, and Haldimand. This suggests that it is not particularly area sensitive in Ontario, but this needs more study.

Adult-plumaged males are socially dominant to males with juvenile plumage, so yearling males may be forced to breed in suboptimal habitat that differs from that of adult males. Some woodlands may be split into 2 neighbourhoods, one occupied by adult males and the other by yearlings. As individuals age, they tend to move from the yearling to the adult neighbourhood, thereby keeping the age classes separate. In New Brunswick, territories of adult males had high density of ground cover, large black cherries and poplars, and many deciduous trees taller than 8 m. Territories of yearlings had high contributions of deciduous trees in the 2.5-m layer. There were highly significant differences in the floristic features of territories of adults and yearlings, but there were also differences within age classes. Redstarts selected territories in a variety of habitats and which were better was not readily identifiable by which age class used it. Studies on the distribution of age classes in New York, Maine, and Michigan had conflicting results. All study areas contained deciduous forests and alder thicket swamps. In Maine, yearlings were least common in alder thickets and mature deciduous forests and more common than older adults in immature deciduous, mixed, and coniferous forests. The distribution of age classes appeared to be related to the amount of deciduous foliage, with the frequency of adult males higher where deciduous foliage density was higher. Highest deciduous foliage density occurred in alder and mature deciduous stands. The percentage of yearling males in Maine habitats were 7% in alder, 21% in mature deciduous forest, 71% in immature forest, 60% in mixed forest, and 82% in coniferous forest. In Michigan, 0% of males in deciduous forest were yearlings compared with 25% in alder thickets. The Michigan deciduous

forest was more mature than the one in Maine which might explain why yearlings were more common in this habitat type in Maine than Michigan. Complete separation of the age classes has also been documented in New Hampshire (Ficken and Ficken 1967; Howe 1974; Lemon et al. 1996; Morris and Lemon 1988a; Sherry and Holmes 1988).

Ontario nests were in saplings, shrubs, mature trees, and vines, predominantly in live woody vegetation but 8 nest trees or shrubs were dead. The redstart greatly preferred saplings and shrubs to mature trees for nesting, and deciduous species (22 species, 92.5% of nests) were used more often than coniferous species (6 species, 7.5%). The species chosen most frequently were maples (53 nests), birches (28 nests), ashes (15 nests), hawthorns (12 nests), alders (12 nests), and white cedar (8 nests). On the Bruce Peninsula, 42 of 55 nests (76.4%) were in coniferous species: 42 in white cedar, 5 in balsam fir, and 2 in American yew. This was markedly different to the preference shown for deciduous species elsewhere. The DBH of 9 trees and saplings supporting nests ranged from 3.8 to 17.8 cm, mostly 5-10 cm. A total of 93.9% of nests were in upright crotches, 5.1% were on horizontal branches, and 1.0% were between 2 upright trunks. They were mostly placed against the main trunk, but 4 were 0.6-1.8 m from the trunk. Nest heights ranged from 0.3 to 15 m, with most 1.8-3.7 m up (Peck and James 1987, 1998a). Near Kingston, 1 pair renested for the second time in an old Red-eyed Vireo nest. This was the latest redstart nest attempt that season, and usage of an existing nest may save time. Usage of other species' nests appears to be rare. This was the only observed case out of more than 750 nests (McKellar 2010). Nests in Algonquin Park were in vegetation ranging from shrubs to tall trees at an average height of 2.8 m (Tozer 2012).

Throughout its range, the redstart typically nests in tree saplings, less frequently in shrubs and mature trees, and seldom in vines. Nests are at the juncture of 3 or more small branches, usually at the trunk of the nest tree. Where nests were built on horizontal limbs, they were almost always where several branches grew upright. It rarely builds in crotches formed by 2 branches. These nests are vulnerable to being blown out of the tree. In New Brunswick, nests were at an average of 52.0% of the nest-tree height (range 41.8-58.7%). Nest height did not appear to be influenced by seasonal foliage development. Nests were often built in deciduous species before they fully leafed out despite the presence of coniferous trees. Most tree species are used according to their availability, but some are underutilized. Trembling aspen, balsam poplar, and striped maple are seldom used, possibly because the bark is too smooth and the branch structure is inadequate to support a nest. Conifers other than white cedar are seldom used, possibly because the branch structure is unsuitable. In New Brunswick there was a difference in nest-tree selection by adult and yearling males. Nests of yearlings were located more often in chokecherry and a variety of other tree species than those of adults; 4.2% of yearlings' nests were in white cedar compared with 14.8% of adults' nests. Nests are frequently placed in grey alder, beaked willow and other willow species, white birch, yellow birch, sugar maple, beech, white cedar, cherry, and hawthorns. Other species that have supported nests include ash, dogwood, gooseberry, elm, hackberry, hazelnut, silver maple, white oak, bur oak, raspberry, sycamore, hophornbeam, balsam poplar, trembling aspen, hobblebush, striped maple, spruce, and tamarack. In New Hampshire, 37.8% of nests were in sugar maple, 31.0% were in yellow birch, and 28.4% were in beech. Overall, nests have been reported 0-28 m from the ground. Ground nests are rare, and most nests are 2-5 m up. In Maine, 4% of nests were 0-1.5 m from the ground, 12% were 1.5-3 m up, 36% were 3-4.6 m up, 22% were 4.6-6.1 m up, 10% were 6.1-9.1

m up, 12% were 9.1-12.2 m up, and 4% were higher than 12.2 m from the ground. In New Brunswick, nest height averaged 3.5 m but differed by plant species: 2.7 m in alder, 5.3 m in white birch, 3.9 m in white cedar, 2.2 m in cherry, 3.4 m in hawthorn, and 3.4 m in other species. In New Hampshire, mean nest height was 8.2 m with a strong mode at 1.5-3 m and a second shallow mode 10-20 m from the ground. Nests were higher in yellow birch (median height 15 m) and only 1-4 m in other species. In the western and southern portion of the redstart's range, the nest is often built over or near water. The redstart has used old nests of the Yellow-throated Vireo, Red-eyed Vireo, and Yellow Warbler. These nests may be used as is or additional material may be added to the interior to bring the cup to the proper dimensions. Material from old redstart nests may be incorporated into a new nest, but there are no records of redstart nests being reused. Several unusual nests have been reported. One was built on a metal bracket at the front door of a house; one was in a lilac shrub 30 cm from a front window of a house; one was partially sunken into the ground at the base of a gooseberry between 2 logs; one was 1.5 m up in the fork of a dead branch that had fallen and was leaning against a sapling; and one was on a U-shaped grapevine hanging from a tree, saddled on the vine at the bottom of the U where it swung 1.5 m with the wind (Baker 1944; Campbell et al. 2001; Chapman 1907; Cruickshank 1956; Ficken 1964; Graber et al. 1983; Gross in Bent 1953; Harrison 1984; Morris and Lemon 1988a, 1988b; Mousley 1916a; Sherry et al. 2020; Sodhi et al. 1999; Stauffer and Best 1980; Sturm 1945; Yezerimac 1993).

The male does not tolerate any other males in his territory. Males are also aggressive toward females and females defend the territory from both sexes, except when accepting extra-pair copulations. Territories may be defended from spring arrival until autumn migration. Territory size shrinks during the nestling period and expands again during the fledgling period. At this time, territoriality may be somewhat relaxed. Most activity is confined to the territory, although both sexes make occasional off-territory forays. When densities are high, all suitable habitat is defended but when densities are low, there may be an undefended gap of about 15 m between territories. There are no differences in territory sizes of yearling and adult males or in the size of area used by females. Yearling males that are unsuccessful in attracting a mate abandon their territories after about 2 weeks and may travel several kilometres to establish a new territory. When adults shift their territorial boundaries later in the nesting season, yearlings may be successful in defending a territory. Occasionally a female builds a nest at or outside the boundary of the male's territory and he is forced to try and shift the boundaries. The American Redstart may maintain multiple territories simultaneously when it mates polygynously. These areas are not contiguous and individuals may have as many as 3 discrete advertising areas 120-450 m apart. Other polygynous males have large territories that can accommodate 2 nesting females. Nests of females mated to the same male may be as close together as 120 m; nests of different pairs may be separated by only 9 m. Territories near Quebec City were significantly clustered at scales of 250, 350, 450, and 550 m. The purpose of this may be to facilitate extra-pair copulations. This may also contribute to area sensitivity. In Algonquin Park, territories averaged 0.15 ha (range 0.03-0.74 ha). Most territories are 0.4-0.6 ha, but some are quite small and others are twice this size. In Illinois, territories averaged 0.57 ha in 1 area; another single territory was 1.29 ha. In New York, territories averaged 0.30 ha or less than 0.4 ha; most Maine territories were larger than 0.4 ha. In New York, average territory size in the early stages of nesting was 0.41 ha and declined to 0.07 ha during the nestling period. On South Bass Island in western Lake

Erie, most territories were 0.2-0.4 ha, but one was only 0.06 ha. Average territory size in subalpine areas of New Hampshire was 0.6 ha. In New Hampshire, territory sizes averaged 0.17 ha in 8- and 22-year-old stands and 0.54 ha in mature forest. Quebec territories averaged 0.64 ha (range 0.35-0.93 ha); average size in maple stands was 0.39 ha (range 0.17-0.61 ha). A polygynous male in New York had a territory that was 1.25 ha (Bourque and Desrochers 2006; Cyr and Darveau in Gauthier and Aubry 1996; Ficken 1962a; Ficken and Ficken 1967; Ford 1996; Graber et al. 1983; Hickey 1940; Hunt 1996; Kendeigh 1945; Martin 1960; Sabo 1980; Secunda and Sherry 1991; Sherry et al. 2020; Sturm 1945; Yarrow 1970).

In Ontario, 26 of 632 nestlings (4.1%) returned to the natal area (Sherry et al. 2020). In New Brunswick, 9 of 172 nestlings (5.2%) returned, including 5 males and 4 females. Three of the 5 males remained on the study area briefly and were not seen again, probably having been unsuccessful in attracting a mate. The other 2 males established territories 0.5 km from their natal site. Three of the returning female yearlings nested 300 m from their natal site (Lemon et al. 1996). In New Hampshire, 1 of 161 nestlings (0.6%) returned (Sherry et al. 2020). Using stable isotopes in Maryland, Rushing et al. (2015) determined that long-distance dispersal of yearlings was rare. Long-distance natal dispersal was influenced by habitat quality experienced during the previous winter. Birds were more likely to disperse northward following years of low food abundance and habitat quality. Yearlings were more likely to disperse southward in years when cherry trees blossomed early. The quality of an individual's winter territory did not affect long-distance dispersal. The long-distance immigration rate of yearlings to the site was 18.1%.

Adult site fidelity varies geographically, annually, by sex, by age class, and may be affected by how late birds remain in autumn and if they were successful in raising young. In Saskatchewan, Bayne and Hobson (2002b) found no difference in survival rates of males and females, and 55% of birds returned the following year. In New Hampshire, 49 of 182 adults (26.9%) returned the following year. Males returned at a significantly higher rate (30%) than females (19%). Yearling males banded in the year of their first breeding season returned at a lower rate than older males (16% compared with 39%). Returning males nested significantly closer to their previous year's territory (average 68 m, range 17-617 m) than females (average 171 m, range 22-236 m). There were no significant differences in the distances between subsequent territories for returning yearling and older males. There was a tendency for successfully returning individuals of all sexes and ages to return more frequently than unsuccessful birds (Holmes and Sherry 1992). In New Brunswick, 44% of adult birds returned compared with 26% of yearlings. Males that were banded as yearling breeders returned to their previous territory significantly less (26.7%) than returning adult males (84.6%). Over half of returning yearlings settled on the same or an adjacent territory. Reproductive success of males the previous year was not a significant predictor of territory change and some previously successful males switched territories. Twenty-four of 119 females (20.2%) returned. Of returning females, 5 returned to the same territory, 8 to an adjoining territory, and 3 no further than 2 territories from the original territory. One female that returned 5 years nested as far as 400 m from the original territory some years, but returned to it in the final year. Breeding success was a strong predictor of return of females, with 30.8% of successful and 21.0% of unsuccessful females returning. The date that a bird was last seen on the study area was a significant predictor of return for both yearling and adult males, suggesting that the decision to return is made in the autumn of the previous year (Lemon et

al. 1996). Fifteen percent of Maryland redstarts made long-distance movements between breeding sites or natal sites and first breeding sites. In 3 of 4 years, 78.4% of immigrants to the site originated from the north; 70% originated from the south in the other year. The odds of birds originating from the south increased with earlier cherry blossom dates. The rate of long-distance dispersal to the site was less for adults (11.2%) than for yearlings (18.1%), but adult dispersal was greater than that for yearlings in the year of early cherry blossoming. There were no significant differences in dispersal rates between the sexes. Both age classes may disperse further north in years of early phenology when food resources are available further north than usual during the spring migration period (Rushing et al. 2015).

Limiting Factors

Eggs have been reported in Ontario nests from late May to late July, with most present during the last 3 weeks of June (Peck and James 1987). In Algonquin Park, nests are under construction from late May to late June, eggs are present from late May to mid-July, nestlings are present from mid-June to late July, and dependent fledglings have been observed from late June to mid-August (Tozer 2012).

Females arrive at night and usually select a male and territory the following morning. Females visit very few males before selecting one as a mate and, if a female remains in a male's territory for more than an hour, she does not leave. The female spends 12-60 hours exploring the territory, with early arriving females taking more time. She finally restricts her activities to a few locations and searches them for suitable nest sites. This may take from a few hours to 1.5 days. As soon as the female selects a nest site, she begins to build the nest. Nests typically take 2.5-4 days to complete, but some take as long as 7-10 days. Nests built later in the season may be completed within a day, particularly if material is taken from an old nest. Egg laying started the day after the nest was completed in 2 of 3 Ohio nests and 1 day later in the third nest. Eggs are laid at the rate of 1 a day. Incubation begins in earnest with laying of the last egg, although some time may be spent incubating after the penultimate egg is laid. The incubation period of 17 Ontario clutches was 10-13 days; most clutches hatched in about 11 days. Similar incubation periods have been reported throughout the redstart's range, although 1 Yukon clutch took 14 days to hatch. Young hatch over a 24-hour period. The young typically fledge when they are approximately 9 days old, but may fledge when they are only 7 or 8 days old if they are disturbed. At nests with a single adult, young may not fledge until they are 10-13 days old (Baker 1944; M.S. Ficken 1962b, 1963, 1964; Gross in Bent 1953; Kendeigh 1945; Peck and James 1987, 1998a; Secunda and Sherry 1991; Sherry et al. 2020; Sinclair et al. 2003; Sturm 1945).

The redstart raises a single brood in a breeding season. Second broods are expected in the southern portion of its range where the season is longer, but this has not been confirmed. It is a persistent renester that routinely lays as many as 4 clutches in an attempt to raise a brood; 6 nests per season have been reported. Over an 11-year period near Kingston, fewer than 25% of pairs were successful in fledging any young on their first nesting attempt. Replacement nests are usually in the same territory but occasionally pairs move and establish another territory. Clutches of 2-5 eggs have been reported in Ontario (average 3.69 eggs). The most frequent clutch size was 4 eggs, with 67.7% of nests containing 4 eggs. Throughout its range, clutches of 1-5 eggs have been documented. One-

and 2-egg clutches are uncommon and tend to occur toward the end of the breeding season. Five-egg clutches (5.5% of Ontario nests) are also uncommon and occur at the beginning of the breeding season and at more northerly latitudes. In Alberta, 43% of clutches contained 5 eggs. Most clutches contain 4 eggs. Replacement clutches typically have 3 eggs or occasionally only 2. In New Hampshire, females mated to yearling males had an average clutch size of 3.63 eggs compared with 3.86 eggs for females mated to older males. The difference was due to yearlings initiating nesting later (Campbell et al. 2001; Chapman 1907; Ficken 1962a; Graber et al. 1983; Gross in Bent 1953; McKellar et al. 2013; Peck and James 1987; Sherry et al. 2020; Sodhi et al. 1995; Sturm 1945).

Both sexes are capable of breeding when they are 1 year old. All females of all age classes breed each year, but many males do not breed until they are 2 years old. This is because yearling males arrive later than adult males. There is a surplus of males in the population, so females may all be mated by the time yearling males arrive. In addition, yearling males may be relegated to suboptimal habitat where females are less likely to settle on a territory. In some populations, 100% of adult males are mated, but this percentage may be as low as 70% in some areas. In New Brunswick, 71.9% of adult and 57.4% of yearling males were mated. Another New Brunswick study reported 85.1% of adult and 48.3% of yearling males mated. In New York, 100% of adult and 43% of yearling males were mated. In New Hampshire, less than 50% of yearling males were mated. Some unmated males may hold territories for about 2 weeks and then move considerable distances to repeat the process. Other unmated males are floaters that wander through the habitat. Occasionally a female arrives late and mates with one of the later-arriving yearling males. Yearling males that are mated tend to have smaller clutches because of the lateness of the season, but have similarly sized territories and fledging success rates as older males. Near Kingston, adult males that had successfully mated were temporarily removed from their territories. Those that lost their territory to another male and re-established another territory nested on approximately the same schedule as yearlings. They also had a similar reproductive output as yearlings, indicating that the delay in nesting was the main factor in reducing the number of young fledged. Pairs typically remain mated for the entire breeding season but divorce rarely occurs. Remating of the same birds in subsequent years is rare. In New Brunswick, the probability of both members of a pair reuniting was 8%. Two of 8 previous pairs remated and this involved the same birds twice (Ficken 1962a; Ficken and Ficken 1967; Hickey 1940; Hunt 1996; Kendeigh 1945; Lemon et al. 1996; Lozano et al. 1996; McKellar et al. 2013; Morris and Lemon 1988a; Omland and Sherry 1994; Sherry and Holmes 1982; Sherry et al. 2020).

The American Redstart is typically monogamous, but may be polygynous when ecological and social circumstances allow it. For polygyny to occur, territory density must be low so that a polygynous male can defend an extra-large territory or have multiple territories. In New Brunswick, 0-4% of males were polygynous. In New Hampshire, 6 cases of polygyny were confirmed and others were suspected. Males defended as many as 3 territories and 1 male was successful in attracting a mate to each of his territories. Polygyny appears to be practised mainly by older males (Secunda and Sherry 1991; Sherry et al. 2020). Extra-pair fertilizations may be an important component of the redstart's breeding strategy. In New Brunswick, 55.3% of nestlings were related to the adults caring for them and all nestlings were related to their attending female. Of 32 broods, 41.1% were sired by their putative father, 41.1% were partially sired by their putative father, and 18.8% were sired entirely by extra-pair fertilizations. A total of 41.7% of nestlings were not attended by their biological father.

Subadult males attended a greater proportion of extra-pair young (68%) than adult males (37%). Nine of 10 extra-pair fathers were from neighbouring territories; the other territory was 200 m away. Nestlings in 2 broods were sired by undetermined males that either had distant territories or were floaters. Two of 7 broods were sired by 2 extra-pair males. The number of broods fathered by a single male was greater than expected, suggesting that females were selecting for good genes (Ficken 1962a; Perreault et al. 1997). In Pennsylvania, 44.4% of young were from extra-pair fertilizations and 30% of the extra-pair males were not mated (Kappes et al. 2009). In an Ontario study, 40% of 100 nests contained extra-pair young and 23% of 313 nestlings were extra-pair (Sherry et al. 2020). Near Kingston, females appeared to be mating with extra-pair males that were more genetically similar to themselves than their social mates (Hajdasz et al. 2019).

Numerous studies summarized the foraging strategies of the American Redstart. It is the only warbler that is a true aerial forager. It is intermediate in its foraging techniques between warblers and flycatchers and is significantly different from both. Unlike flycatchers that hunt stationarily from a perch and often return to the same perch after attacking prey, the redstart is constantly in motion. It flashes its wings and spreads its tail, causing soft-winged bugs to drop to the ground, and it flutters downward to capture them. Aerial foraging and gleaning are its primary tactics for obtaining food. It may rarely forage briefly on the ground and as high as the top of the canopy, but most foraging occurs in the mid- to lower portion of the canopy and in the subcanopy. It is highly adaptable in its foraging heights and use of different foraging techniques. Foraging height depends upon the structure of the woodlot, time of day, and sex of the bird. Individuals of the same sex occurring on different territories within the same woodlot use significantly different methods at the same time of day. Birds select areas within their territory and the forest that have more open vegetation that facilitates aerial foraging. Redstarts forage at lower levels at midday than in the morning. There may be an increase in foraging height again later in the afternoon, but there are no consistent patterns to this. Between early morning and midday, the frequency of hawking increases and the amount of hovering declines, and there is a general downward shift in foraging heights. This is related to insect abundance and behaviour. Flying insects increase from a low early in the morning to a peak at midday and are most abundant in the lower strata of the forest, with another concentration near the top of the canopy. The overall abundance of insects differs significantly depending upon time of day and height, and the redstart adjusts its foraging techniques to access the most abundant prey. In New Hampshire, it foraged at heights of 0-24 m, mostly at 5-14 m, except in late afternoon when it foraged at heights of 0-4 m. The only difference in foraging techniques between the sexes in 1 study was that females gleaned more often at midday than males. In most pairs, the sexes foraged at the same heights during the same period. In the 39% of pairs where foraging height differed between sexes, the male foraged higher than the female in all but 1 case. Females may forage lower because they are associated with the nest. The primary foraging techniques are gleaning, hovering, and mid-air captures. Another New Hampshire study found significant differences between the sexes, with males hovering at leaves less and hawking more than females. Males foraged more on yellow birch and less on sugar maple than females. In all tree species in New Hampshire, it attacked prey more on lower leaf surfaces in relation to caterpillar abundance than expected, and less on upper leaf surfaces, petioles, and twigs. More caterpillars were present in beech than sugar maple or yellow birch. The redstart attacked prey in proportion to their availability

only in beech. Caterpillars on beech were mostly leaf miners and leafrollers. Those on the other 2 tree species were mostly free-living and more available. Most of these occurred on leaf blades and undersides of leaves. It may temporarily concentrate on taking adult moths and other prey from tree trunks when such prey is abundant. While moulting, it forages using more inactive behaviours such as hopping with infrequent sallies and few aerial flights. At this time, it tends to stay in dense vegetation, sometimes high in the canopy. In yellow birch in New Hampshire, the redstart fanned its tail more frequently both in the canopy and subcanopy than in ash, maple, or beech. It encountered prey most frequently in yellow birch and also used the flush-chase manoeuvre most often in this tree species. In Parry Sound District, it used a variety of tree species in early successional woods for foraging, but white birch was favoured in spring and autumn. During the breeding season, it foraged 3.9-12 m from the ground compared with 3.8-10 m in autumn (Chapman 1907; Ficken 1962b; Greenberg et al. 1999; Gross in Bent 1953; Holmes 1986; Holmes and Schultz 1988; Holmes and Sturges 1975; Holmes et al. 1978; Keast et al. 1995; Lent and Capen 1995; Mills 2007; Morse 1989; Parnell 1969; Robinson and Holmes 1982, 1984; Sabo 1980; Seidel and Whitmore 1982; Sherry et al. 2020; Williamson 1971).

Morse (1973) compared the foraging strategies of the American Redstart to the Yellow Warbler and spruce-woods warblers on small islands in Maine. In most cases, redstarts used dead limbs more frequently and deciduous foliage less frequently than the Yellow Warbler. Redstarts used manoeuvres other than gleaning, particularly flycatching, more frequently than the Yellow Warbler. Both species preferred to forage on deciduous foliage, using it more than its availability. Most foraging by the redstart occurred on small limbs of deciduous species. There was little overlap in the foraging of the redstart and Yellow Warbler with the spruce-woods warblers due to the heavy usage of deciduous vegetation by the former 2 species. There was no relationship between abundance of defoliating insects and redstart abundance, possibly due to the small size of the islands which prevented establishment of large numbers of territories. In Louisiana, the diet of the redstart overlapped considerably (74-89%) with other insectivorous birds, including the White-eyed Vireo, Hooded Warbler, Carolina Wren, Acadian Flycatcher, Prothonotary Warbler, and other warblers that do not breed in Ontario. Despite high dietary overlap, the species exhibited modest resource specialization in their foraging techniques and substrates with some differences among species in all communities. These small distinctive differences appear to be critical to species coexistence (Kent et al. 2022).

In New Hampshire, the diet of nestlings consisted mostly of 2 orders of insects: lepidopterans (caterpillars and adult moths) and flies (predominantly crane flies). Young are also often fed spiders and mayflies. During a mayfly hatch, 90% of insects brought to young at nests near Lake Michigan were burrowing mayflies. House flies and rosy maple moth caterpillars were fed to young, and gnats have been reported as part of nestlings' diets (Baker 1944; Chapman 1907; Kappes et al. 2009; Omland and Sherry 1994; Secunda and Sherry 1991).

Adults prey predominantly on small winged insects 2-5 mm long. These are mostly flies and hymenopterans, beetles, soft-winged bugs (especially leafhoppers and planthoppers), and moths (both adults and caterpillars). Other prey include aphids, small wasps, stoneflies, spiders and harvestmen, mayflies, caddisflies, ichneumonid wasps, midges, mosquitoes, black flies, dance flies,

cankerworms, spittle bugs, scale insects, and plant lice. Beetles it consumes include weevils, flea beetles, and long-horned beetles. The redstart rarely eats berries and seeds, including those of barberry, juneberry, and magnolia. Near Manitouwadge, it increased in numbers in young and intermediate-aged stands in response to increasing numbers of spruce budworms. In New Brunswick and other locations, no response to budworm numbers was observed. In an aviary study, it preferred cabbage looper moths, followed by mealworms, and gypsy moth larvae. The latter were largely avoided and it would be less likely to eat gypsy moth caterpillars when alternate prey was available. In New Hampshire, redstart populations increased then declined in concert with saddled prominent caterpillar populations. North of Lake Nipigon, stomachs of 5 redstarts contained 41.9% flies (including dance flies), 23.2% lepidopterans, 12.4% beetles (including weevils), 7.3% hymenopterans (including ichneumonid wasps), 6.8% soft-winged bugs (including leafhoppers and aphids), 3.8% spiders, 3.0% mayflies, and 1.5% caddisflies. Stomach samples from New Hampshire contained 34.7% soft-winged bugs (mostly leafhoppers and planthoppers), 30.2% flies, 13.1% beetles, 11.9% hymenopterans, 4.5% caterpillars, 1.1% adult lepidopterans, 1.1% spiders, and 3.4% unidentified. The diet at the same location based on visual observations consisted of 67.3% caterpillars, 25.5% adult lepidopterans, 1.8% beetles, 1.8% flies, 1.8% hymenopterans, and 1.8% spiders. A later analysis of 41 stomachs from the same location determined that the diet consisted of 35.3% flies, 34.5% bugs, 9.7% caterpillars and moths in equal proportions, 6.3% ants and parasitic wasps (including sawflies), 6.3% beetles, 4.1% spiders, 2.6% stoneflies, and less than 1% each of mayflies, bark lice, lacewings, caddisflies, and scorpionflies. In some forests, food availability may be an important factor with birds depleting caterpillar resources during parts of the breeding season (Graber et al. 1983; Gross in Bent 1953; Holmes and Sturges 1975; Holmes et al. 1978; Kendeigh 1947; Morris et al. 1958; Robinson and Holmes 1982; Sherry and Holmes 1992; Sherry et al. 2020; Sturm 1945; Venier et al. 2009; Whelan et al. 1989).

The redstart is a common host of the Brown-headed Cowbird. The redstart usually accepts cowbird eggs, but occasionally abandons the nest or builds another layer over the foreign egg. In Wisconsin, Minnesota, and Iowa, 1.87 fledglings were produced in unparasitized nests compared with 1.48 in parasitized nests. In Ontario, 61 of 364 nests (16.8%) were parasitized; 0 of 47 nests on the more heavily forested Bruce Peninsula were parasitized. Parasitism rates vary considerably geographically and with the amount of forest cover in the landscape. Parasitism rates from elsewhere are: 15.8% of 145 nests in Quebec; 6.2% in the Prairie Provinces; 18% in Alberta; 9% of 131 nests in British Columbia; 17% in Wisconsin, Minnesota, and Iowa; 30.6%, 68%, 74%, and 6% in New York; 5.6% and 32% in Ohio; and 0% in Pennsylvania. In Illinois, 7.4% of 27 nests were parasitized prior to 1900 compared with 36.6% of 41 nests after 1900 (Campbell et al. 2001; Cyr and Darveau in Gauthier and Aubry 1996; Ficken 1962a; Graber et al. 1983; Gross in Bent 1953; Hahn and Hatfield 1995; Hobson and Villard 1998; Peck and James 1998a; Powell and Knutson 2006; Sherry et al. 2020; Sodhi 1995; Sodhi et al. 1999; Sturm 1945).

The species of tree that is selected for the nest site can affect nest success. In New Brunswick, nests in white cedar had a 100% fledging success compared with 37% in the other 4 main nest-tree species. In New Hampshire, nests in yellow birch were significantly less likely to be depredated due to better concealment (Morris and Lemon 1988a; Sherry et al. 2020).

A population near Kingston experienced a 50% rate of nest loss, and this is fairly typical for the redstart. In New Hampshire, nest success was increased from 50% to 77% by placing baffles around tree trunks beneath active nests, thereby reducing access by red squirrels and chipmunks. Weather can also affect nest success. Wind frequently destroys nests or damages them sufficiently that they are abandoned. Rain may also remove material from nests, resulting in abandonment. Heavy rainfall during the nestling period may result in starvation due to depressed insect availability, reduced foraging time, or both. In New Hampshire, daily nest survival increased with increasing May temperatures. June rainfall also had a positive effect on survival. The adverse effects of these factors are often mitigated by renesting, and later nests are less likely to be parasitized (McKellar et al. 2013; Sherry and Holmes 1992; Sherry et al. 2020; Sturm 1945).

Habitat loss and degradation do not appear to be significant issues for the redstart. Nonetheless, some habitat is being lost south of the Canadian Shield due to urban development and clearing for agriculture. Forests that mature and lose their woody understorey growth eventually become unsuitable.

Activities that reduce the amount of woody vegetation in the understorey are detrimental, such as clearing brush on cottage lots. Along the Michigan shoreline of Lake Superior, the redstart was detected more frequently on the forested inland side of cottage roads than on the cottage side of the road (Ford and Flaspohler 2010; Stauffer and Best 1980).

The effects of timber harvesting on the American Redstart vary depending upon the harvest methods. Certain studies concluded that the redstart benefits from forest management; others concluded the opposite. Management that converts deciduous stands to conifers is universally detrimental. Clear-cutting in occupied stands initially results in a short-term loss of the redstart until sapling growth becomes established. Clear-cutting or strip-cutting in coniferous stands can provide short-term habitat where none previously existed. In the Boreal Forest Region of Ontario, it had a negative response to partial timber harvesting. It declined by 25% when 45% of trees were removed, by 50% when 50% of trees were removed, and by 75% when 65% of trees were removed. In the Great Lakes–St. Lawrence Forest Region of Ontario, partial timber harvesting either has no effect or a positive effect. Near Sault Ste. Marie in northern hardwood communities, it responded positively to harvest, with postharvest numbers inversely related to the amount of residual BA. Three studies on group-selection and shelterwood cutting in Algonquin Park found that it was unaffected by harvesting. In the Carolinian Forest Region of Ontario, it was more abundant in diameter-limit cuts that removed all large trees than in forests that experienced single-tree selection or had not been cut for at least 24 years. It was most abundant in recent cuts indicating that it temporarily benefits from opening the canopy. Trends in response to timber harvesting are similar in other portions of its range. In the Boreal Forest Region, it tends to decline as a result of partial harvest, or occasionally there is no effect or a temporary small increase. In northern hardwoods, it may increase with increasing levels of harvest, but in some areas no change was documented. In Pennsylvania, clear-cutting of 75% of aspen and 50% of oak stands resulted in a decline. In Maryland, forest management that opened the canopy was detrimental, but selective cutting and thinning of competing understorey trees was beneficial (Bushman and Therres 1988; Haché et al. 2013; Hanowski et al. 2005; Harrison et al. 2005; Holmes et al. 2004; Jobes et al. 2004; Kingsley and Nol 1999; Sherry et al. 2020;

Tittler et al. 2001; Tozer et al. 2010; Vanderwel et al. 2007, 2009; Webb et al. 1977; Yahner 1993). In the Canadian Shield of Ontario, there was no difference in its abundance in burned and clear-cut forests in early successional stands, but it was significantly more abundant in harvested than burned mid-successional stands. It was significantly less abundant in early successional and mid-successional than mature stands (Zimmerling et al. 2017).

Hunter and Witham (1985) examined the effects of carbyl spraying in Maine. The first year, spraying was spotty, and only 30% of the area was sprayed, but spraying was complete the following year. The spray reduced numbers of caterpillars, particularly in the upper portions of trees. In the first year, there was a sharp drop in warbler numbers after spraying followed by a gradual recovery a week later, but numbers of redstarts did not decline significantly. The average foraging height of all warblers decreased after spraying, but returned to prespray levels during the recovery period, although foraging heights in the control areas increased even further. Use of conifers by foraging warblers decreased from 53% to 24% after spraying but stayed constant at 62-63% in the control area. Because spraying was spotty, birds were able to travel to unsprayed areas to forage. When spraying was complete the following year, there were no changes in numbers, foraging height, or tree selection. The overall impact of the spraying appeared to be negligible.

Presence of the Least Flycatcher can affect habitat selection and use by the American Redstart. The 2 species share similar habitat preferences and have similar foraging tactics and substrates, with an overlap of 49.8%. Their diets are dominated by flies, hymenopterans, and beetles, constituting 79% of the redstart's diet and 92% of the flycatcher's diet. The redstart has a broader diet, also eating substantial numbers of caterpillars and soft-winged bugs. There is considerable aggression between the 2 species, with the flycatcher usually being the aggressor and winning conflicts. During the nestling period, redstarts may be attacked several times a day, and attacks continue throughout the breeding season. Where the territories of the 2 species overlap, they may use different horizontal strata without interspecific territoriality. Because of its broader foraging niche, the redstart may use gaps and margins of niche space left vacant by the Least Flycatcher. In a New Hampshire study area, Least Flycatchers occupied 1 area of a woodlot and adult redstarts occupied much of the remainder of the area. Due to aggression from older males, yearling redstarts occupied the portion of the woodlot that was occupied by the flycatchers. Flycatchers subsequently disappeared from the area and adult redstarts settled throughout, but most frequently in the area formerly occupied by the flycatchers and they clearly preferred this habitat. At the same time, yearling redstarts declined where the flycatchers resided. The flycatchers later recolonized the same area, and the redstart distribution returned to what it was originally. These patterns strongly suggested that the Least Flycatcher directly kept the American Redstart from settling in otherwise preferred habitat and that behaviourally subordinate yearling redstarts settled where adult male redstarts were absent (Sherry 1979; Sherry and Holmes 1988).

In Pennsylvania and New Jersey, hemlock declined from 56% of the total basal area to 46% because of the hemlock woolly adelgid; this resulted in an increase in deciduous understorey. The American Redstart population increased as a result, probably in response to the increased coverage by deciduous undergrowth (Toenies et al. 2018).

In Alberta, there was no difference in abundance of the redstart at noisy compressor stations and quiet well pads. It did not appear to be affected by chronic noise (Bayne et al. 2008).

In Alberta, there was no difference in the abundance of the redstart at seismic lines, pipelines, or well pads than in forest interior adjacent to these features (Bayne et al. 2016). In West Virginia, it was significantly more abundant near well pads than in areas distant from them. It exhibited no response to pipelines and access roads (Farwell et al. 2019).

Factors on the wintering ground may be more significant in limiting redstart populations than those on the breeding grounds. Loss of wintering habitat is the most important concern (Morse 1989).

Status

McIlwraith (1894) concluded that the redstart was generally distributed throughout Ontario. Fleming (1907) considered it common in the Toronto area. Baillie and Harrington (1937) stated that it bred from the southern border of the province north to James Bay and west to the southern Manitoba boundary. In 1891 in Elgin County, it was a very common summer resident; by 1954, it was observed less frequently in the summer. In 2000, it was an uncommon breeder that continued to decline (Lancaster et al. 2004). During the first atlas, its range included the entire area south of the Canadian Shield, where it was spottily distributed in areas of intensive agriculture and urbanization. Its range included all the Great Lakes–St. Lawrence Forest Region in the Shield and most of the Boreal Forest Region, although it was absent or scarce in the western portion of that area. Breeding in the Hudson Bay Lowland was confirmed to the southern portion of the James Bay shoreline and a bit westward. Highest numbers were in the Great Lakes–St. Lawrence Forest Region (Cartwright in Cadman et al. 1987). James (1991) considered the redstart a common breeder across the province north to Sandy Lake and Attawapiskat.

The second atlas demonstrated that there had been no change in the distribution of the redstart since the first atlas. It was seen in a few more locations in the northwestern portion of its range, but it is unlikely that this represented a range expansion. There was no significant difference in its probability of observation province-wide, although the trend was positive. Significant increases were documented in the Boreal Forest Region and in the Great Lakes–St. Lawrence Forest Region south of the Shield. It was most abundant in the Great Lakes–St. Lawrence Forest Region on the Bruce Peninsula, on Manitoulin Island, the northeastern shore of Georgian Bay east to the Quebec border, and around the northern shore of Lake Superior. It was also abundant along the Quebec border northward to the southern extent of the Hudson Bay Lowland (McLaren in Cadman et al. 2007).

Breeding Bird Survey (BBS) results indicated that the redstart declined continentally in the latter half of the 20th century, but not significantly. This decline was attributed to forest maturation, forest fragmentation that resulted in an increase in predation rates, increases in cowbird populations, and habitat loss in the wintering grounds (Sherry and Holmes 1992; Sherry et al. 2020). BBS results indicate that it increased at an annual rate of 0.015% in Canada and decreased at an annual rate of 0.134% in Ontario 1970-2021. Trends 2011-21 were annual increases of 1.02% in Canada and 0.713% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Once the young fledge, the brood is divided with each adult caring for half the brood. The adults provide fledglings with most of their food for the first week after fledging and continue to feed them for as long as 2-3 weeks after this (Sherry et al. 2020).

During the postfledging period, adults and juveniles occur in deciduous forests and shrubby areas such as regenerating clear-cuts and utility rights-of-way through forested habitat. In Michigan, Akresh et al. (2009) compared redstart usage of upland and riparian forests during the postfledging period. The upland forests were mature trembling aspen–large-toothed aspen stands. Riparian stands had a mixture of alder, honeysuckle, and trembling aspen, and a greater diversity of vegetative cover in the understorey. Captures per 100 net-hours were 4.2 in upland and 15.7 in riparian forests; 89% of juveniles were captured in riparian forests. There was no apparent trend in adult usage of habitat by time; 5 moved from upland to riparian habitat and 5 did the opposite.

Two Pennsylvania studies compared redstart usage of forests and early successional areas during the postfledging period. Stoleson (2013) captured 53 adults and 15 juveniles in 3-6-year-old regenerating clear-cuts and 1 adult and 0 juvenile in adjacent mature forest. There was no difference in shrub and sapling coverage in the 2 habitats. In August over a 2-year period, Yahner et al. (2002) observed 124 redstarts on a shrubby hydro right-of-way and 7 in the adjacent forest. No family groups were observed in the forest but the average number seen per day on the right-of-way was 0.67. In Quebec, Major and Desrochers (2012) netted in small clear-cuts among mature forests. All redstarts were caught in nets set parallel to forest edge, suggesting that they were moving through the clear-cut from 1 mature forest to another.

Both adults and juveniles commonly occur in clear-cuts during the postfledging period. Use of clear-cuts has been confirmed in West Virginia, Virginia, Ohio, Minnesota, Pennsylvania, Missouri, and Quebec. It is likely that this habitat is used wherever it is available. Although the redstart may breed in clear-cuts, there appears to be active movement to these areas during the postfledging period. In Minnesota, 11 were netted during a single breeding season; 315 (184 adults and 131 juveniles) were captured during the postfledging period over 4 years. Adults were captured at a consistent rate but very few juveniles were captured prior to August (Marshall et al. 2003; McDermott and Wood 2010; Porneluzi et al. 2014; Streby et al. 2011a, 2011b; Vitz and Rodewald 2006, 2007).

Porneluzi et al. (2014) netted in a Missouri oak-pine-hickory forest during the postfledging period for 2-15 years after it was clear-cut. The numbers of redstarts gradually increased with time after cutting, but the increase was not significant.

Two studies examined redstart usage of habitat within clear-cuts. Both found that presence of adults was correlated with the abundance of arthropods. One study determined that adults were associated with the vertical complexity of vegetation and negatively correlated with understorey stem density. The other study found that canopy height was a significant predictor of adult abundance, but vegetation density was unrelated to captures of adults. In both studies, availability of invertebrates was the most important predictor of juvenile abundance, although at 1 site juveniles were positively correlated with the biomass of caterpillars and negatively correlated with total arthropod biomass. At 1 site, canopy height was a significant predictor of juvenile abundance. At the other site, juveniles were positively correlated with vertical complexity of the vegetation,

density of understorey stems, and residual BA. For both age classes, food availability was the most important predictor of abundance (McDermott and Wood 2010; Streby et al. 2011a).

MIGRATION

The American Redstart is a nocturnal migrant. During migration, it may join mixed flocks of chickadees, nuthatches, and other warblers, particularly in autumn, but also during inclement weather in spring. There is seldom more than a single redstart in these mixed flocks (Brewer et al. 2018; Graber et al. 1983; Morris et al. 1994; Norris et al. 2006; Sherry et al. 2020; Tozer 2012). Gesicki et al. (2016) monitored nocturnal calls of the redstart during spring migration at 2 sites on the Ohio shoreline of Lake Erie and at 2 offshore sites. The number of calls decreased from the coast into the lake in both the western and central basins. It appeared to partially avoid crossing the lake in both basins.

Adult males are first to arrive in spring, followed by adult females a few days to a week later, then by yearling males and finally by yearling females. At Long Point, mean capture dates were 17.0 May for adult males, 22.1 May for yearling males, and 17.6 May for males of undetermined age. Average arrival for males was 3.0-3.6 days earlier than for females. The difference in arrival dates between the sexes was greatest in years when males arrived earlier. The midpoint of migration for all redstarts at Long Point was 21 May. At Prince Edward Point, mean arrival times were 22.7 May for males and 25.7 May for females. Mean arrival date for adult males was 20.7 May compared with 25.1 May for yearling males. In New York and Maine, 2 weeks may elapse between the arrival of adult and yearling males. In New Hampshire 1 year, females arrived 9 days after adult males and yearling males followed females 3 days later. During spring migration at 3 stopover sites in Texas, Louisiana, and Florida, males migrated 5 days earlier than females and older birds migrated 3-4 days earlier than yearling males. In some years and locations, there may be overlaps in the arrival of adult females and yearlings of both sexes. During spring, birds stop at staging areas 1-11 days, but most frequently only a single day with mean stopover times of 2.0-2.6 days. Recapture rates and stopover times are lower in spring than autumn. Spring migration is concentrated with few stopover areas. Autumn migration is extended with more frequent stopovers. On 2 islands separated by less than 1 km in the Gulf of Maine, 1 redstart was caught on both islands in spring and 2 were caught on both islands in autumn indicating daytime movements (Campbell et al. 2001; Cohen et al. 2019; Ficken 1962a; Ficken and Ficken 1967; Flockhart 2010; Francis and Cooke 1986; Gross in Bent 1953; Lozano et al. 1996; McKellar et al. 2013; Mills 2005a, 2005b; Morris and Glasgow 2001; Morris et al. 1994; Procter-Gray 1991; Smith et al. 2009; Stewart et al. 2002; Suomala et al. 2012).

Spring arrival dates may be affected by precipitation and the quality of habitat that an individual used during winter, by increasing temperatures in the breeding grounds, and by local weather conditions. Higher precipitation rates in the wintering grounds are associated with greater food availability, improved body condition, and earlier departure date from the nonbreeding areas. Ontario arrival and egg-laying dates were earlier when rainfall in Jamaica was greater. Egg-laying dates in Alberta were earlier when rainfall in Mexico was greater. Birds occupying wetter winter habitats, such as mangrove swamps, were more likely to arrive earlier in New Hampshire. Arrival time was a significant predictor of nest success with successful males arriving an average of 3.5 days earlier than unsuccessful males. For every day that a male arrived after the first male, he was 11%

less likely to fledge young. Yearling males wintering in mangrove swamps have significantly more black breast plumage than those wintering in scrub habitat. Near Kingston, early arriving yearling males had more extensively black breasts than late arrivals. These earlier arriving yearlings are more likely to attract a mate (Germain et al. 2010; McKellar 2012; Tonro et al. 2011). At Delta Marsh in Manitoba, Murphy-Klassen et al. (2005) compared first observation dates over a period of 63 years. The redstart arrived 0.67 days earlier for every 1°C increase in temperature. Over a 25-year period at Long Point, there was no significant difference in spring arrival times or autumn departure times. Similar results were reported in Massachusetts over 32 years, and there was no change in the relative timing of arrival of the sexes. Males arrived significantly earlier in warmer years, but females followed the same trends. It is possible that the warming in Canada, which would promote earlier migration, is offset by drying in the wintering areas (Bauböck et al. 2012; Mills 2005a). Strode (2003) examined migration dates in relation to climate change in Illinois and North Dakota. Over 100 years in Illinois, there was no significant change in spring temperature or timing of redstart arrival. This resulted in migrants having 20 fewer days to travel between southern Illinois and northern Minnesota, where springs are arriving earlier. In North Dakota, spring advanced by an average of 8.6 days since 1961, but the redstart did not arrive earlier. In Michigan, arrival date was correlated with aspen leaf development and the relationship between arrival date and temperature approached significance. All age and sex classes arrived earlier during warm, food-abundant springs and later during cold, food-poor springs. Migration rate may be adjusted in response to temperature and food availability once it approaches its breeding area (Smith et al. 2009).

In southern and central Ontario, the peak of migration extends from mid-May to the first week of June, with the earliest migrants arriving in early May (Black and Roy 2010; Curry 2006; Keast 1980; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). Kendeigh (1947) first observed the redstart north of Lake Nipigon on 28 May.

It is uncertain if there is differential timing of the sexes and age classes in autumn. Some studies state that there are differences in timing; others have concluded that there is not. It is possible that timing of migration of the sexes and age classes varies geographically. Sherry et al. (2020) reported that the 2 year classes arrived synchronously in Ontario, Pennsylvania, and West Virginia banding stations, but yearlings arrived earlier than adults in 1 of 3 years in coastal Alabama. In Illinois, Graber et al. (1983) reported that females and juveniles preceded adult males southward. In Alberta, females initiated autumn migration 2 days before males (Flockhart 2010). In Mississippi, juveniles are the first to appear in autumn, followed by females and adult males (Gross in Bent 1953). In Maine, there was no significant difference in timing of migration between the sexes and age classes. When the sexes were analyzed separately, there was no difference in the autumn arrival dates of adult and juvenile males, but adult females arrived 6 days later than juvenile females (Morris and Glasgow 2001). In Virginia and West Virginia, adults and juveniles started their migration in the same 5-day period (Stewart 1986). The length of autumn stopovers tends to be longer than those in spring, but not significantly. Most birds stay over a single day, but some stay as long as 6 days. Juveniles have longer stopover periods than adults (Morris and Glasgow 2001; Morris et al. 1994).

Wilson and McRae (1993) observed a migrant at Longridge on 7 September. In the southern Shield, most redstarts leave by the end of September, with some remaining into early October (Mills

1981; Tozer 2012). Autumn migrants move through most of southern Ontario from mid-August to mid-October, with late birds remaining until late November or mid-December (Black and Roy 2010; Curry 2006; Keast 1980; LaForest 1993; Lancaster et al. 2004; Weir 2008). The midpoint of autumn migration at Long Point is 6 September (Mills 2005a, 2005b).

During migration, the redstart may occur in a variety of habitats such as forests, shrubby areas, and miscellaneous areas such as orchards, residential yards, university campuses, city parks, cemeteries, and windbreaks. In woodlots, it is more likely to select tree-fall gaps and edges than forest interior, and it may prefer bottomland and riparian forests to upland forests. In Illinois, highest numbers occurred in bottomland forests, forest edges, and shrubby areas. Where forested habitat was scarce, upland forests were heavily used. Relative abundance by habitat during spring migration in North Carolina was 1.73 in floodplain forests, 1.63 in beech forests, 0.77 in pine-hardwood forests, 0.66 in oak-hickory forests, 0.56 in wet thickets, 0.14 in pine forests, and 0 in dry thickets. During spring migration in Wisconsin and Minnesota, it was more common in floodplain than upland forests, but not significantly. In British Columbia coniferous forests, it was more common in riparian areas in both spring and autumn. During spring migration in Ohio, the redstart was significantly more abundant in mature upland forest than mature riparian forests. The two forest types were similar except that upland sites had a higher density of shrubs. A study of autumn habitat usage in Pennsylvania found no significant differences among habitats in 1 year. When the study was repeated, it was most abundant in forest-agricultural edges and shrub-sapling-stage forests, followed by suburban forests. It was not observed in forest interior or pole-stage forests. These latter 2 habitats were used least in the earlier study indicating that they are not preferred habitat. During migration, the redstart shows a decided preference for shrubby areas over forest cover. During spring migration in Pennsylvania, detections per 100 m were 0.007 in forest and 0.060 in shrubs; captures per 1,000 net-hours were 0.1 in forest and 3.6 in shrubs. In many other areas, it actively selects shrubby areas, particularly along edges of watercourses, ponds, lakes, and wetlands. It selects shrubby areas within forest cover, explaining why it is more common in forest edges and tree-fall gaps. Two studies tested to determine if the redstart is area sensitive during migration. During spring migration in Pennsylvania, it was significantly more likely to be observed in larger patches within fragmented landscapes, but it did not exhibit area sensitivity in autumn. A South Carolina study found the opposite. There was no significant difference in its abundance in differently sized oak hammocks within coastal marshes in spring, but it was detected significantly more often in large hammocks in autumn. Hammocks smaller than 0.5 ha may not have provided sufficient habitat (Campbell et al. 2001; Graber et al. 1983; Keller and Yahner 2007; Kirsch et al. 2013; Leighton et al. 2002; Parnell 1969; Rodewald and Brittingham 2002, 2004; Rodewald and Matthews 2005; Sherry et al. 2020; Sinclair et al. 2003; Smith and Hatch 2008; Somershoe and Chandler 2004; Suomala et al. 2010; Wiebe and Martin 1998).

Just prior to autumn migration, males demonstrate a slight increase in aggression and agonistic encounters may occur between males, although there is no evidence of territorial defence at this time. Older birds are dominant to juveniles, who may be relegated to suboptimal habitat. The increase in aggression prior to and during autumn migration may be a precursor to behaviour on the wintering grounds where birds defend territories. Aggression during spring migration does not appear to have been documented (Ficken 1962a; Sherry et al. 2020).

During migration, the American Redstart forages using similar techniques to those used during the breeding season, predominantly aerial attacks and gleaning. There are no differences in foraging strategies or heights used by the sexes or age classes during migration. During autumn migration, it fed at heights of 1.5-17 m at Prince Edward Point, with a peak around 10 m. Foraging was characterized by aerial pursuits of flying insects and was directed 22% to the air, 11% to outer leaves, 5% to twigs and inner leaves, 17% to outer branches, 17% to inner branches, 0% to trunks, 19% to sapling foliage, 11% to sapling branches, and 0% to low shrubs and the ground. During spring migration in North Carolina, 37.2% of redstart foraging occurred in the canopy, 58.1% in low trees, 4.6% in shrubs, and 0% on the ground. In the canopy, 3.8% of foraging occurred at the top of the crown, 14.6% in the inner crown, 18.8% in the lower crown, and 0% on the bole. In low trees, 5.4% of foraging occurred at the top of trees, 23.0% in the inner crown, 29.7% in the lower crown, and 0% on the bole. In shrubs, 0.4% of foraging occurred at the top of the crown, 1.7% in the inner crown, 1.3% in dense thicket, 0.8% in brush piles, and 0% in grass. It readily adapts its foraging strategy in response to prey availability. There are 2 records of it foraging at night in areas lit by artificial lights. In an area illuminated by stadium lights, it used aerial sallying manoeuvres to capture insects on foliage or in the air. In another area, it was attracted at 0300 hours to a window lit by lights in the room. It alternately hovered and perched on the window screen, selecting the larger insects that were predominantly mayflies, moths, and caddisflies. During spring migration in Michigan, midges are abundant within 0.4 km of the shoreline of Lake Huron. Spiders are also more abundant near the shoreline because they prey upon the midges. There was no difference in the total biomass of arthropods inland and near the shore, but midges were essentially absent inland and spiders were less common. Both sexes of redstarts gleaned more at the shoreline than inland and more sallying occurred inland. Near the shore, redstarts foraged heavily on resting midges and spiders. They foraged predominantly on flying insects inland. White cedar was used for foraging according to its availability near the shore but was used significantly less than expected inland. Near the shore, midges rested on white cedar but few insects used it inland. Foraging rates were much higher near the shoreline. Foraging was most intense in the early morning when temperatures were below 10°C. These temperatures inhibited midge swarming until later in the day and made them readily abundant on vegetation. Midges may be important prey for the redstart during spring migration in areas near the Great Lakes. Spiders may also be important in the diet on shorelines (Bakkan and Bakkan 1977; Keast 1980; Lebbin et al. 2007; Parnell 1969; R.J. Smith et al. 2004, 2007).

The diet during migration consists mainly of insects and spiders. Migrants collected in Texas and Louisiana had eaten 40.1% flies (including 13.5% midges), 17.2% leafhoppers and planthoppers, 11.6% wasps and ants, 10.6% beetles, 8.9% bark lice, 2.9% spiders, 2.7% caterpillars and moths, 1.4% mayflies, 1.3% lacewings, and less than 1% each of odonates, orthopterans, and mites. During cold periods in autumn, the redstart may resort to eating vegetable matter. In Ohio, it was observed inspecting yew and honeysuckle fruit but was not seen eating the berries. Two were observed plucking foxtail and crabgrass seeds from their stalks and 10 others foraged within 2 m of the ground on the trunks of large trees. There were essentially no insects available at that time (Sherry et al. 2020; Tramer and Tramer 1977).

The redstart is commonly killed at television towers and other tall structures during migration, predominantly in autumn, but a few kills occur during spring. From 1972 to 1982, 625 were killed at

the Lennox generating station chimneys near Kingston. At 2 towers in Florida, 908 and 728 were killed over the course of 4 years. Between 2 September and 12 October, 537 were killed at Illinois towers (Graber et al. 1983; Leighton et al. 2002; Sherry et al. 2020; Weir 2008).

James (1991) considered the redstart a common migrant. Daily maxima are in the order of 40-60 birds, but more than 600 have been reported during spring at Presqu'ile (Curry 2006; LaForest 1993; Weir 2008).

At Long Point, the redstart declined significantly during migration at an annual rate of 2.2% 1961-88. Trends during other periods were: 1961-70, −6.7%; 1970-79, +4.8%; and 1979-88, −3.3% (Hussell et al. 1992). More recent data indicate that the redstart population at Long Point increased significantly during both spring and autumn migration 1961-2004 (McLaren in Cadman et al. 2007).

Kirtland's Warbler

Setophaga kirtlandii

BREEDING SEASON

Habitat Requirements

The Kirtland's Warbler has nested in Ontario only at Garrison Petawawa and near Sudbury. Nesting habitat at Petawawa consists of young stands of mixed jack pine and red pine or pure jack pine stands in sandy soils. It inhabited stands less than 20 years old that were mostly 1.5-4 m tall, but as tall as 6 m. Occupied stands had openings vegetated with lowbush blueberry, velvetleaf blueberry, sweet fern, bluestem, sedges, mosses, and lichens. One nest was in a 820-m^2 clearing dominated by these plant species, but there were 4 jack pines in the centre of the clearing (Richard 2008, 2013). A comparison of vegetation in occupied and unoccupied sites revealed that occupied habitats were associated with greater percent ground cover of lowbush blueberry, star-tipped lichen, reindeer lichen, and waxyleaf moss. Blueberries are important ground cover because they conceal nests from predators, provide protection from the elements, and supply berries for food. Unoccupied areas were associated with greater percent cover of bare ground, sheep laurel, red maple saplings, common strawberry, bluestem grasses, juneberry, wintergreen, blackberry, red raspberry, and

whorled loosestrife. There was no significant difference in the percent composition of poplar, red maple, jack pine, white pine, and red pine in occupied and unoccupied sites. There was a significant difference in ages of stands, with occupied stands averaging 14.8 years compared with 32.4 years for unoccupied sites. These sites had as much as 70.9% red pine in the canopy, suggesting that Kirtland's Warbler will occupy stands with a lower percentage of jack pine, higher percentage of red pine, and less oak than typical habitats in Michigan (Richard 2014).

The Kirtland's Warbler has highly specialized habitat requirements that significantly curtail its breeding distribution. It nests only in flat or gently rolling areas with well-drained, nutrient-poor sandy soils. Within this restricted physiographic type, it nests almost exclusively in jack pine stands created by wildfires or in jack pine plantations managed specifically for it. Occasionally it uses red pine stands. To be suitable, pine stands must be dense, young, and even aged but they must also include openings. In addition, it is area sensitive, requiring large tracts of suitable habitat.

The Kirtland's Warbler appears to avoid hilly areas and nests predominantly in flat areas or where the topography is gently rolling. It nests on the ground in porous well-drained sandy soils so that the nest does not become flooded during heavy rains. The sandy soils that it selects for nesting are acidic and nutrient-poor. This allows establishment of the preferred ground cover which may include lowbush blueberry, velvetleaf blueberry, bearberry, little bluestem, big bluestem, poverty grass, Pennsylvania sedge, wintergreen, trailing arbutus, sweet fern, bracken fern, sand cherry, juneberry, reindeer moss, flowering spurge, frostweed, sheep sorrel, and starry false solomon's-seal. More fertile sandy soils are unsuitable because these promote growth of deciduous tree species rather than jack pines. Fertile sands also support denser and taller ground-cover species, such as goldenrods and asters that are not preferred by the Kirtland's Warbler. Only a small area within eastern North America has soil types that are potentially suitable. This includes the Lower and Upper peninsulas of Michigan and a band across central Ontario through Sault Ste. Marie, Thessalon, and Chapleau to Petawawa (Anich et al. 2011; Bocetti et al. 2020; Bowman and Chamberlain 1980; Chamberlain 1978; Kashian and Barnes 2000; Kirk and Pearce 2008; Marshall et al. 1998; Mayfield 1960, 1962; Probst 1985; Van Tyne in Bent 1953; Walkinshaw 1983).

Historically, the Kirtland's Warbler nested in jack pine forests that resulted from wildfires. Jack pine cones open only when exposed to heat and this conifer typically needs fire to propagate. If the fire is too intense, jack pine seeds fail to germinate and they also fail to germinate if the fire is

followed by a period of drought. To be suitable, jack pine stands need to be even-aged but patchy in distribution, with areas of dense tree coverage interspersed with openings. If the stand lacks openings, it usually is not used. Optimum habitat structure consists of a minimum of 3,500 jack pine stems per ha, 35-65% canopy cover, and small openings. Areas with less than 20% tree canopy cover are rarely used. The Kirtland's Warbler may initially occupy a stand when there are more than 2,000 stems per ha and peak occupancy occurs at 5,000 stems per ha. Only young jack pine stands are inhabited because it typically nests on the ground under the lower living branches of pines. The lowest live branches of pines should be less than 1 m from the ground. Once pines become more mature and the lower branches die, the habitat becomes unsuitable. Initial colonization of stands occurs when pines are 3-5 years old and trees are 0.3-1.8 m tall. Populations increase rapidly when stands are 8-11 years old, remain constant when stands are 12-17 years old, decline at stand age of 18-21 years and then disappear. In Michigan, it has been detected in stands 3-24 years old. During years of highest occupancy, stands support trees 2.4-3.8 m tall with as high as 60% tree coverage. The number of years that a site is occupied varies depending upon the growth rate of the pines, but the pattern is consistent with rapid colonization and population growth, a short peak, and then a decline until the site is abandoned. Stands tend to be occupied for 14-18 years, with high populations for only 7-8 years. During the years of decline, average tree height is 4.0-4.5 m in natural stands and 4.5-5.6 m in plantations, and live foliage is absent below about 1.2 m in height. In Michigan where almost all the Kirtland's Warbler population breeds, jack pine stands may contain almost equal numbers of Hill's oak and lesser numbers of red maple and trembling aspen. It has been estimated that less than 10% of natural jack pine stands are suitable habitat due to the exacting requirements of the Kirtland's Warbler. Due to fire suppression, natural jack pine stands are becoming scarce. Jack pine plantations are being planted and managed specifically for this species in Michigan. Pines are planted 1.2 m apart in rows 1.8 m apart; 10 rows are planted, then 15 rows are skipped to provide openings 27.4 m wide and a tree density of about 4,500 trees per ha. In Michigan, more than 90% of the Kirtland's Warbler populations nest in jack pine plantations managed specifically for it. On rare occasions, it nests in red pine plantations (Anonymous 1988; Bickerton et al. 2006; Bocetti et al. 2020; Bowman and Chamberlain 1980; Chamberlain 1978; Eliason 1989; Kashian and Barnes 2000; Kirk and Pearce 2008; Marshall et al. 1998; Mayfield 1953, 1960, 1962, 1963; Morse 1989; Probst 1986, 1988; Probst and Weinrich 1993; Walkinshaw 1983).

Zou et al. (1992) described 11 ecosystems within a large burn in Michigan, and the Kirtland's Warbler colonized 5 of these ecosystems. Habitats used by warblers were characterized by a physiography of level or rolling terrain; well-sorted sandy or sandy loam to silt loam soils; uplands with relatively warm temperatures during the breeding season; vegetation dominated by lowbush blueberry, bearberry, wintergreen, Hill's oak, bluestem grasses, and haircap moss; and a canopy of tall, dense, and patchy jack pine and oak.

Natural red pine stands are unsuitable breeding habitat for the Kirtland's Warbler because these pines seldom, if ever, grow closely enough together to create thickets. Red pine plantations may provide suitable habitat, and it has nested in this habitat in Wisconsin and in red pine plantations specifically planted for it in Michigan. Occupied red pine plantations in Wisconsin were 11-13 years old. They had a tree density of 1,876 per ha of which 66.9% were red pine, 20.6% were Hill's oak, and 12.5% were jack pine; mean tree height was 3.2 m. The lowest live branch of red pine was an average

of 8 cm from the ground compared with 35 cm for jack pine in Michigan and Wisconsin. Canopy closure in occupied red pine plantations was 46%, dominated by red pine but with 9% coverage by oak and 6% by jack pine. Although red pine is not a common breeding habitat for the Kirtland's Warbler, persistent occupancy, annual return rates similar to birds in jack pine, and good nesting success indicate that red pine stands can provide suitable habitat. Nonetheless, most red pine plantations are not suitable. Extensive die-offs of red pine occurred in the occupied plantations in Wisconsin and substantial regeneration by jack pine created the necessary mosaic of openings and thickets (Anich et al. 2011; Mayfield 1953). Olah et al. (2022) determined that nest sites in red pine plantations had greater dead herbaceous vegetation depth, vegetation-height density at 0.25 and 1.0 m, and tree cover than random sites in the territory. Average density of trees within territories (1,577 per ha) was greater than outside territories (1,094 trees per ha). Occupied patches consisted of 70% red pine, 28% jack pine, and 2% oak. The average tree height of both species of pines was 4.1 m.

The Kirtland's Warbler seldom nests in woodlands smaller than 32 ha and jack pine stands larger than 80 ha support 90% of nests that fledge young. It appears to be most successful in stands that are larger than 200 ha. Occupied red pine plantations in Wisconsin ranged in size from 36 to 70 ha. In Michigan, it occasionally uses smaller tracts. In some cases, 2 or 3 males will settle in a stand of 20-25 ha; in a 24-ha stand, there were 4-5 males and nesting occurred. Males have been found in jack pine stands as small as 3 and 4.9 ha but it is uncertain whether they were mated. All occupied stands smaller than 32 ha have been surrounded by taller stands of jack pine (Anich et al. 2011; Bickerton et al. 2006; Bocetti et al. 2020; Mayfield 1960, 1962, 1993; Walkinshaw 1983).

Only 1 nest has been described for Ontario. It was on the ground under a 3.5-m-tall jack pine at the end of a row, 81 cm beneath a lower branch of the tree and 2.1 m from its base. The nest was on the side of a small hummock and well concealed by blueberries and grasses (Richard 2008).

More than 300 nests have been described from Michigan and all were on the ground well concealed in vegetation 8-20 cm tall. Nests are never on steep slopes and are in flat areas or gently rolling topography. Vegetation in a 4-m^2 area centred on the nest was comprised of 40% lowbush blueberry, 20% wintergreen, and 12% sweet fern, and the ground was typically littered with pine needles and oak leaves. Blueberries and/or grasses comprised the major ground cover at 84.8% of nests. Vegetation in the vicinity of the nest is usually 30 cm or less tall. Nests may be completely arched over by vegetation with a single entrance. Nests were 0-305 cm from the base of the nearest live tree. Near large trees, nests tend to be further from the trunk where the branches droop near the ground. Of 146 nests, 139 (95.2%) had jack pine as the nearest tree, 2 (1.4%) had trembling aspen, and 5 (3.4%) had a small Hill's oak. When a nest was closer to a tree species other than jack pine, there were always jack pines present nearby. Nests are often at the edge or near the edge of a dense group of jack pines. Of 126 nests in natural burns, 22 were exactly on the edge of an opening and 40 were within the pine growth. Sixty-four nests were an average of 60 cm (range 1-366 cm) from the edge of trees in an opening. In plantations with 10-row strips, nests tended to be on or near edges. Of 79 nests, 40 (50.6%) were between or very close to the first and second outside rows, 10 (12.7%) were located away from edge in the open, and 33 (41.8%) were deeper in the plantation, but often near an area where several trees had died, creating a small opening. One atypical nest was

under a fallen dead jack pine where the live pines were only 5 cm tall. Nearly all nests have a specific entrance with directional orientation. In Michigan, 134 nests faced south, 134 faced east, 103 faced west, and 102 faced north. Nest sites are not known to be reused, but 1 nest was only 35 cm from a previous year's nest (Bocetti et al. 2020; Chapman 1907; Mayfield 1960; Van Tyne in Bent 1953; Walkinshaw 1983).

The male establishes a territory immediately upon arrival on the breeding ground. Territories are defended well into the summer during the incubation and nestling stages. Both sexes may challenge other species well away from the nest, including Black-capped Chickadees, Nashville Warblers, Chipping Sparrows, and Vesper Sparrows. A single pair may be the only occupants in an area as large as 12-16 ha, but much of this area is unused. The extreme boundaries of the territory are seldom visited once they are established. Grassy clearings within the territory are avoided and infrequently flown over. Territories in natural habitat are approximately circular in shape. Those in plantations are rectangular, conforming to the row pattern of the trees. Territories are clustered into groups with solitary pairs being rare and usually representative of a declining population. Large areas of suitable habitat remain unoccupied with territories grouped together in what may be a small proportion of the available habitat. Although all suitable habitat is not occupied, marginal habitat is occasionally used. Despite being clumped, the territories are rarely contiguous. Territories may be loosely distributed over the habitat in a manner similar to a bunch of grapes, not always touching each other and not filling in the intervening spaces. The Kirtland's Warbler has a large territory for a warbler. Territory size may be affected by tree density and tends to be larger in areas of lower tree density. At Petawawa, males defended territories of 0.47-12.1 ha. One bird defended 3 small territories close to each other and these were 1.4, 2.0, and 3.0 ha within an overall area of 39 ha. Another male had a territory of 7 ha. During the nestling period, 1 pair confined their activities to 1.27 ha. In Michigan, territory sizes of 0.4 ha to more than 12 ha have been reported. In different locations and years in Michigan, average territory sizes ranged from 3.4 to 8.4 ha. Territories were larger where the tree growth was more open and smaller if they were bordered closely by neighbouring territories (Anonymous 1988; Berger and Radabaugh 1968; Bocetti et al. 2020; Richard 2008, 2013; Mayfield 1953, 1960, 1962, 1983; Walkinshaw 1983). Nonbreeders exhibit territorialism at multiple successive locations 200-1,000 m apart rather than at a single location. After 11-58 days (mean 33 days), some nonbreeders moved 5-77 km to other breeding areas (Cooper and Marra 2020).

The Kirtland's Warbler exhibits low natal philopatry, but return rates for it are higher than for many species. From 1931 to 1965, 296 nestlings and fledglings were banded in Michigan, and 8 (2.7%) were seen again. Five returned to their natal colony and the other 3 were in other colonies 6.4-8.0 km distant. These represent minimum return rates because fieldwork was sporadic in the early years. Returning birds could have been missed simply because no one looked for them. Of 57 nestlings banded in 1977, none were seen again, probably due to limited time spent looking for them. Of 446 nestlings banded prior to 1978, 40 (9.0%) returned, including 24 males and 16 females. The rate of return was 12.3% for males and 8.2% for females, which are more difficult to find. At another Michigan site, 25 of 298 nestlings (8.4%) returned. Return rates were 10.6% of young from first nests and 1.4% for second broods. Of 27 returning males banded as nestlings the previous year, 12 (44.4%) were found within 1.6 km of the natal nest and 13 (48.1%) were found an average distance

of 20.4 km from the natal site. The other 2 males were found considerable distances away: 1 at Petawawa 676 km from where he fledged and the other 579 km away in Wisconsin. Five of 9 male nestlings returned to their natal plantation an average of 728 m from the natal site (range 395-1,208 m). Three of these bred in 2 different areas during their lifetime, as far as 14.5 km from each other. A male nestling banded in Michigan in 1974 was found in Quebec in 1978. Of 25 banded nestlings returning to Michigan the following year, 24 returned in 2 or more seasons. Twenty bred in the same vicinity each year and 4 bred in 2 different locations 13.8, 19.7, 21.0, and 36.2 km away. Returning young tend to nest in younger stands than where they were hatched, settling first in very young pine stands. This may be to avoid competition from older males. Returning young tend to avoid settling near territories occupied by adult males (Berger and Radabaugh 1968; Mayfield 1983; Probst 1986; Walkinshaw 1983). Settling into young pine stands may be beneficial for returning young for another reason. Once an individual breeds, it may continue to do so in the same location for several years. Because habitat remains suitable for only a few years, it is advantageous to settle in younger habitat that will not become unsuitable during the individual's lifespan.

Once a bird nests at an area, its site fidelity is very high and most continue to nest in the same area as long as they are alive. Sixty percent of birds observed 1 year are typically seen the next year. Given that some returning birds may be missed, it has been assumed that the annual return rate is about 65%. At a Wisconsin site, 71.4% of males returned the following year. In Michigan, 18 of 23 control males (56.3%) and 28 of 60 males (46.7%) with geolocators returned. The return rates were not significantly different. At Petawawa, most males returned in at least 1 subsequent year. An adult male banded in 2006 returned in 6 consecutive years, but was not observed in 2013. In 2010, 1 male moved to a second territory 100 m away midway through the breeding season, possibly because he failed to attract a mate on the first territory. In Michigan, some females are not seen in 1 year and then return the next, but no males skipped a year and were found later. One Michigan female returned in 7 consecutive years and 1 male returned in 8 consecutive years. Of 28 returning males, 18 (64.3%) returned to the same breeding territory. Fourteen returned exclusively to the same territory but 4 also returned in other seasons to a different territory within the same colony. Nine of the 28 returning males (32.1%) returned to different territories in the same colony. Five remained exclusively on the same territory; 4 switched territories in subsequent years. One of the 18 returning males returned to a different colony and his 2 nests were 6.1 km apart. The average distance between nests of males returning to different territories in the same colony was 437 m (range 229-800 m), and the overall average distance between subsequent nests of returning males was 358 m. Of 41 returning females, 12 (29.2%) returned to the same territory, 23 (56.1%) returned to different territories within the same colony, and 5 (12.2%) returned to distant colonies. Average distances between subsequent nests for the first 2 groups were 115 m (range 3.7-192 m) and 668 m (range 229-1710 m), with an overall average of 475 m if birds moving to other colonies are excluded. Another study in Michigan determined that the average distance between nests in subsequent years was 215 m for males that returned to the same colony. The average for females was 263 m (range 15.9-3,031 m). Four females moved to other colonies 1.7, 2.0, 15.3, and 25.8 km away. Both sexes return at a similar rate and most return to the same colony, but females are more prone to change locations than males. Males that failed to obtain a mate also tend to return to the same territory. As a pine stand ages, the percentage of birds that return increases because older stands

fail to attract new recruits (Anich et al. 2011; Berger and Radabaugh 1968; Bocetti et al. 2020; Cooper et al. 2017; Mayfield 1977b, 1983; Richard 2008, 2013, 2014; Walkinshaw 1983).

Limiting Factors

Upon arrival, the female inspects the territory for suitable nest sites. This may take only a few hours, but more typically 4 or more days for first nests and 1-2 days for replacement or second nests. First nests in Michigan took 2-3 days to build (average 2.8 days). Subsequent nests also took 2-3 days (average 2.25 days). Also in Michigan, first nests were reported to take 6-8 days to build; 4 days were required for replacement nests. Nest building is suspended during cold, wet weather. For first nests, an average of 2.7 days (range 1-4 days, but occasionally as long as 8 days during inclement weather) elapses between completion of the nest and laying of the first egg. The average is 1.6 days (range 1-3 days) for second nests. In Michigan, females laid eggs in the last week of May through to 10 June, except for yearling females which may not initiate nesting until late June. One egg is laid per day and incubation begins the afternoon before the last egg is laid or with the laying of the penultimate egg. The incubation period is 13-16 days (average 14.2 days). Larger clutches and those containing cowbird eggs tend to have a longer incubation period because individual eggs get less heat from the incubating female. Hatching usually occurs within a 24-hour period, and averages 12.6 hours (range 2-25 hours). In Michigan, the first eggs hatch 9-26 June. If disturbed, the young may leave the nest when they are 8 days old, but typically remain in the nest another 1-2 days, with young fledging at an average age of 9.4 days (Anonymous 1988; Bocetti et al. 2020; Mayfield 1960; Richard 2008; Sykes et al. 1989, 1993; Van Tyne in Bent 1953; Walkinshaw 1983).

Early publications stated that the Kirtland's Warbler raised only a single brood per season and it was not until 1954 that double brooding was confirmed. It is now considered a fully double-brooded species, with all pairs that nest successfully early enough attempting to rear a second brood. The latest date for the first brood fledging and a second nesting attempt was 28 June in Michigan. Four to 15 days may elapse between fledging of the first brood and laying of the first egg in the second clutch (average 7 days). The average distance between nests when the first one was successful was 72.4 m (range 16-137.5 m). Renesting typically occurs if the first nest fails. The time between loss of the first nest and laying of the first egg in a replacement nest is 6 days (range 4-14 days). The average distance between failed and replacement nests was 115 m (range 31.1-323 m). The single Ontario nest contained 2 eggs and 2 nestlings, indicating a probable clutch size of 4 eggs. Five eggs are usually laid in the first nest and 4 eggs in second and replacement nests. Clutches may range in size from 3 to 6 eggs, with 3- and 6-egg clutches rare. Yearling females had an average clutch size of 4.82 eggs, which was not significantly different from clutch sizes of older females. In Michigan, mean clutch size of first nests was 4.87 eggs compared with 4.00 eggs for replacement clutches (Anonymous 1988; Berger and Radabaugh 1968; Bocetti et al. 2020; Mayfield 1960; Probst 1986; Richard 2008; Van Tyne in Bent 1953; Walkinshaw 1983).

Both sexes are capable of breeding in their first year. It is probable that all females in every age class breed annually, but the proportion of young males that breed is unknown. Of 63 adults in Michigan, 32% did not breed. In young or poorly stocked areas, only 25-67% of males obtain mates compared with 95% pairing success in more suitable habitat. It is unknown what proportion of unmated males are yearling birds. The mating system is predominantly monogamous, but as many

as 15% of males may be polygynous and some are polyterritorial. One male at Petawawa defended 3 discrete territories, suggesting that it may have had more than 1 mate. Females may be more selective in their choice of habitat, resulting in an excess of females in prime habitat and a scarcity in marginal habitat. Some males in good habitat have more than 1 mate; some males in marginal habitat remain unmated. Clustering of territories may facilitate finding mates. It may also be important if extra-pair copulations are part of the breeding strategy, but this has not been investigated. There is a floating population of males that are either exploring from nearby territories, relocating from remote areas, or both. Most pairs remain mated throughout the breeding season, but some males may mate with 2 females successively within a breeding season. Fourteen of 18 pairs (77.8%) that could remate in a subsequent year did so and 1 pair remated in 3 consecutive years. Of the 4 pairs that did not remate, the males had nests the second year 137, 165, 209, and 217 m from the previous year's nest. All 4 of the females nested on territories adjoining the one occupied by their former mate. None of these pairs remated once they had separated (Anonymous 1988; Berger and Radabaugh 1968; Bocetti et al. 2020; Cooper and Marra 2020; Ford 1996; Probst 1986; Probst and Weinrich 1993; Walkinshaw 1983).

During the breeding season, most foraging occurs within 120 m of the nest, and a large proportion of prey is obtained within 9-12 m of the nest. Foraging occurs mostly in small jack pines and oaks at mid-level, usually 0.9-2.4 m from the ground. The Kirtland's Warbler also feeds in the ground cover and occasionally on the ground, especially in dense pine thickets where the ground is nearly bare. It may also occur at the top of jack pines 15 m from the ground, but these are typically singing males that may not be foraging. It obtains prey mostly by gleaning among pine needles, deciduous leaves, and ground vegetation. It sometimes hovers to snatch insects and capture prey in terminal clusters of pine branches. It often flies out from a tree to capture an insect on the wing (Bocetti et al. 2020; Van Tyne in Bent 1953).

The Kirtland's Warbler appears to eat whatever is most abundant at the time and shows no particular prey preferences. Young are fed caterpillars, moths, flies, cicadas, sawfly adults and larvae, grasshopper nymphs, ant-lions, and other small crawling and flying insects. Young in second and replacement nests may be fed blueberries. The adults' diet is similar to that of the young, and may also include spiders, butterflies, mayflies, true bugs, deer and horse flies, cicadas, crickets, centipedes, and springtails. An analysis of fecal material collected on the breeding grounds determined that 61% of samples contained soft-winged bugs (36% frequency by spittlebugs and 21% by aphids), 45% contained ants and wasps, 42% contained blueberries, 25% contained beetles, and 22% contained moth caterpillars. Miscellaneous food items included spiders (20% occurrence), flies (18%), true bugs (6%), and traces of springtails and neuropterans. In August, both juveniles and adults consume large quantities of blueberries (Bocetti et al. 2020; Deloria-Sheffield et al. 2001; Mayfield 1960; Van Tyne in Bent 1953; Walkinshaw 1983).

Brown-headed Cowbird parasitism is currently not a limiting factor for the Kirtland's Warbler in Ontario. At Petawawa, the cowbird was not observed during 2 years of study. The cowbird is rare in this area, and also infrequent in the Thessalon area where the warbler has been previously documented during the breeding season. If the Kirtland's Warbler becomes established in the Sudbury, Barrie, and Orillia areas where it has previously occurred, parasitism is potentially more of

a threat (Falk in Cadman et al. 2007; Richard 2008), and it has since nested in the Sudbury area. In the core breeding grounds in Michigan, cowbird parasitism is considered a major and significant limiting factor to the Kirtland's Warbler. It appears to be a preferential host for the cowbird because it suffers very high rates of parasitism, in excess of 70% of nests in some years. In contrast, examination of several hundred nests of other suitable hosts in the same area revealed only 7 parasitized nests. The cowbird was formerly absent within the Michigan breeding grounds of the Kirtland's Warbler. As forests were cleared for agriculture, the range of the cowbird moved northward in Michigan to overlap with this warbler's range. The cowbird first reached that area in the 1870s and continued to increase for the next century. From 1903 to 1948, 48% of nests were parasitized compared with 67% from 1963 to 1971; parasitism rates reached 75% some years. The female cowbird typically removes 1 or more warbler eggs for every egg that she lays, but occasionally no warbler eggs are removed. Warbler clutch size in first nests declined from 5 to 3.73 eggs. Nests with 2 cowbird eggs fledge no warblers and the probability that a warbler will fledge from a parasitized nest is only 7%. Warblers typically accept cowbird eggs, but occasionally abandon the nest or rarely build another nest layer over the cowbird egg. At the rate of parasitism that was being experienced, it was projected that the Kirtland's Warbler would become extinct by 1980. Cowbird control began in Michigan in portions of the breeding area in 1972 and the program was expanded the next year to include the entire breeding range. The program was highly successful, with parasitism rates averaging 3.4% from 1972 to 1981. The number of fledglings produced per nest increased from 0.81 to 2.76 during this period. Taking replacement nests and second broods into account, each pair fledges an average of slightly more than 3 young per year. In order to maintain Kirtland's Warbler populations, it was suggested that the cowbird removal program in Michigan, and now also Wisconsin, would have to be continued indefinitely (Anonymous 1988; Bocetti et al. 2020; Kelly and DeCapita 1982; Mayfield 1960, 1961, 1972, 1977b; Probst 1986; Walkinshaw 1983). Although those studying the Kirtland's Warbler are of the opinion that cowbird control is essential to its continued survival, those studying the cowbird disagree. They point out that the warbler population did not increase as a result of cowbird control and that the Kirtland's Warbler only increased once the amount of habitat increased. Most warbler nest losses were due to predation and parasitism accounted for only 16.8% of the losses (Chace et al. 2005; Ortega et al. 2005; Rothstein and Peer 2005).

Another major limiting habitat is the scarcity of suitable breeding habitat. Cowbird control successfully increased reproductive output, but this served only to stabilize the population and the predicted increase did not transpire. Young jack pine stands on nutrient-poor, well-drained soils are rare. With increasing fire suppression, natural stands regenerated by wildfires are becoming increasingly scarce. Fires that do occur are much smaller than they were historically. In Michigan, serious efforts to control fires began in 1927. Prior to that the average size of fires was more than 125 ha, but this decreased to less than 6 ha in the 1940s. Consequently, the amount of habitat created by fire dwindled and many of the resulting pine stands were too small to support a warbler population. From 1961 to 1971, the amount of suitable habitat declined by 40% in Michigan. Once it was realized that habitat availability was a major limiting factor, jack pine stands in Michigan were managed specifically for the Kirtland's Warbler. This involves commercial logging, prescribed burns, and planting of plantations with habitat managed on a 50-year rotation. Approximately 76,000 ha

of habitat are managed for the Kirtland's Warbler in Michigan, with a goal of providing a minimum of 15,200 ha of suitable habitat at any given time. Military exercises at Petawawa create a mosaic of pine stands of differing ages. A lightning strike in 2012 caused a fire that consumed 200 ha, so this should provide suitable future habitat. Habitat may become unsuitable or lost due to stand fragmentation and conversion of jack pine stands to other more desirable species from a forestry perspective. Planting pines at unsuitable densities may make plantations uninhabitable (Bickerton et al. 2006; Marshall et al. 1998; Mayfield 1962, 1983, 1993; Probst 1986; Richard 2013; Walkinshaw 1983).

Habitat quality affects male pairing success. Probst and Hayes (1987) determined pairing success in suitable habitat, young marginal habitat, and open marginal habitat. Young marginal habitats were those that were adequately stocked but that had been used by Kirtland's Warblers for less than 3 years. Open marginal sites were unburned, poorly stocked areas. At 1 burn, 83.3% of males were mated where the trees were dense compared with 41.7% where the trees were more sparse. Male pairing success averaged 96.7% in suitable habitat and 59.1% in marginal habitat, with an overall average of 85%. Earlier slow recovery of the population may have been due in part to low pairing success. Males may not pair successfully in new colonies, old colonies, marginal habitat, and peripheral habitat. It is unknown to what extent polygyny in good habitat offsets low pairing rates in marginal habitat (Probst 1985, 1986; Probst and Hayes 1987). During earlier census years for this species, it was assumed that the sex ratio was equal and that all males were paired. This may have led to an overestimate of the population.

The rarity of suitable breeding habitat and the dispersal behaviour of juveniles continue to create an additional limiting factor. Returning juveniles often disperse to areas other than their natal site, thus decreasing the probability that they will find suitable habitat. Juvenile males that colonize new sites may not be successful in acquiring a mate. The reproductive potential of many juveniles is probably lost (Mayfield 1983; Morse 1989; Probst 1985, 1986).

Nests may rarely be flooded. This typically occurs only when there is extremely heavy rain and nests are in a depression where water accumulates. These nests are not used further even if they are undamaged (Mayfield 1960).

Predation is another significant limiting factor. As many as a third or more of nests are lost to predators. In Michigan, the Blue Jay may be a significant predator of nestlings. Nesting success tends to be higher where there are no hills or snags that offer vantage points for cowbirds and predators searching for nests. Nest success increased significantly where large trees and snags were present after cowbirds were removed. It has been recommended that new habitat be established in extensive flat regions free of large trees and snags. At 1 site, presence of a valley resulted in differential growth rates of pines on the tableland and in the valley. This extended the occupancy of the site by 4-6 years (Kashian and Barnes 2000; Probst 1986; Walkinshaw 1983).

If a nest site is examined by a human shortly after the female selects it, she may abandon it. Otherwise, the Kirtland's Warbler is very tolerant of moderate levels of disturbance. Some individuals will allow themselves to be picked off a branch or the nest, and they may land on humans (Berger and Radabaugh 1968; Bocetti et al. 2020; Van Tyne in Bent 1953; Walkinshaw 1983).

Habitat loss and degradation on the wintering grounds in the Bahamas does not appear to be an issue for the Kirtland's Warbler. Climate change in the wintering area has the potential to affect the size of the breeding population and reproductive success. Many climate models predict significant drying trends in the Caribbean. Numbers of breeding males in Michigan are strongly correlated with the amount of rainfall received in the Bahamas from November until April. Drought on the wintering grounds results in a scarcity of food and poorer physical condition of warblers, except for older males that may be able to defend territories that contain water. All males fledged significantly more young following Marches with more rainfall, with an average increase of 0.23 fledgling for every 1 cm increase in March rainfall. Adult male arrival on the breeding grounds was not related to March rainfall, but arrival of yearlings was delayed by 1.4 days for every centimetre reduction in March rainfall. A 10-day delay in arrival was associated with 0.74 fewer fledgling raised. Although adult males were in better condition than juvenile males and their arrival date was unaffected by winter precipitation, they also experienced reduced reproductive output following dry winters. This is likely because females arrived later and in poorer condition. They frequent the same winter habitats as juveniles (Mayfield 1983; Rockwell et al. 2012). As a result of projected climate changes in North America, Botkin et al. (1991) concluded that jack pine forests in central Michigan will soon be growing at a significantly slower rate than they have in the recent past. Consequently, these forests may become unsuitable for the Kirtland's Warbler within 30-60 years, suggesting that it may be subject to a greatly increased risk of extinction.

Status

The Kirtland's Warbler is one of the most critically endangered bird species in North America. Without active human intervention in the form of habitat management, it is likely that it would become extinct within a short period. Prior to European settlement, it was probably much more abundant and its range may have included Wisconsin and Ontario on the sandy outwash plains following the Wisconsin glaciations. Peak populations may have occurred about 500 years ago. Originally wildfires burned unchecked and there were no cowbirds within the breeding range. Within recorded history, peak populations occurred in the 1880 and 1890s. Around that time, 3 events occurred that greatly affected populations. In the 1870s, a fire burned 500,000 ha in the core of the breeding range, thereby creating extensive suitable habitat. Logging of virgin pine forests also occurred near the end of the 19th century. Both these events were beneficial but short term. The third event was that forest clearing created habitat for the Brown-headed Cowbird, and this was a permanent negative effect. During the late 19th and early 20th centuries, there were numerous reports of migrants and wintering birds in the Bahamas at a time when there were few observers using inferior optical equipment. By the mid-20th century when there were more observers with better equipment, it was rarely observed during migration and winter. The Kirtland's Warbler was first described in 1851 when a migrant was collected in Ohio, but the breeding grounds in Michigan were not found until 1903. The first breeding survey, which was more of a census since it is probable that most males were detected, was completed in Michigan in 1951. During this census, 432 males were discovered and in the next census, in 1961, there were 502 males present. The entire population was confined to 6 counties in a single watershed in the northern part of Michigan's Lower Peninsula. The 1971 census revealed that the population had dropped to 201 singing males with the entire global population within a circle 56 km in diameter. Cowbird control was initiated

the following year but populations remained stable for the first decade of control, with an average of 207 males per year (range 167-243). The first modest increase occurred in 1991 with 347 males recorded. The habitat management program was successful with 804 males in 1998. In 2007, nesting outside Michigan was finally confirmed in Wisconsin and Ontario. Populations continue to increase, with 1,828 singing males in 2011 and 2,014 in 2013 (Anich et al. 2011; Anonymous 1988, 2009a; Bickerton et al. 2006; Bocetti et al. 2020; Graber et al. 1983; Harlon 1995; James 1999d; Kelly and DeCapita 1982; Kirk and Pearce 2008; Marshall et al. 1998; Mayfield 1953, 1962, 1972, 1973, 1977b, 1993; Probst 1986; Richard 2013; Tozer 2012; Weinrich 1989).

There is a band of suitable breeding habitat across central Ontario bounded by Thessalon, Sault Ste. Marie, Chapleau, North Bay, and Petawawa. The Kirtland's Warbler may have nested historically in this area, but this was never confirmed. In 1919, it was fairly common over a large area in jack pines at Petawawa. Nesting was not confirmed at this time and no estimates of numbers were made. At the same site in 1939, only single birds were noted on 2 occasions. The first reported breeding record was from the Barrie area when adults were found feeding a juvenile during August. Although the identification of the adults was accepted by the Ontario Bird Records Committee, the identity of the juvenile was uncertain. It was noted that the bill was quite stout for that of a warbler's and it may have been a cowbird. The Natural Heritage Information Centre did not accept this breeding record, considering it ambiguous and unverified. Until breeding was finally confirmed at Petawawa, the Kirtland's Warbler was officially considered a hypothetical breeder in the province. As of 1999, there were only 8 other subsequent records for it during the breeding season: the Bruce Peninsula in 1958 and 1990, Point au Basil in 1961, Barrie in 1964, Petawawa in 1977 and 1978, Orillia in 1985, and near Thessalon in 1997. Later targeted surveys were completed near Thessalon, Sault Ste. Marie, and Chapleau and these were all negative. After finding the singing male near Orillia, suitable habitat was searched near Orillia, the Chapleau-Cartier area, the Bruce Peninsula, and Manitoulin Island and these surveys were also negative. Searches at Petawawa were negative in 2002 and 2004, but 2 singing males were found there in 2007. The first Ontario nest was found at Petawawa on 28 June 2007. The population at Petawawa appears to be stable, with 2 or 3 males documented each year from 2006 to 2013, except in 2012 when 4 males were present. At least 27 fledglings had been produced by the end of the 2013 breeding season, but some may have been overlooked (Austen et al. 1994; Bickerton et al. 2006; Bowman and Chamberlain 1980; Chamberlain 1978; James 1999d; Kirk and Pearce 2008; Natural Heritage Information Centre 2008; Richard 2008, 2013; Speirs 1984). In 2012, Holmes et al. (2015) deployed song meters at 38 locations in central Ontario in potentially suitable habitat. In 1,631 hours of recording, they documented 66 Kirtland's Warbler songs on a single day at 1 site in eastern Algoma District. It was in a 20.4-ha stand that was 6 years old with 80% jack pine and 20% red pine coverage. Because it was detected on only 1 of 28 dates of surveying at this site, the authors suggested that either the recording location was outside the core range of a territorial bird or that it was prospecting for a mate, but was unsuccessful and moved to another location. The latter explanation seems more likely.

The Kirtland's Warbler was designated endangered in Ontario in 1971 and in Canada in 1979. Recovery of the species in Ontario is considered feasible, but this is dependent upon dispersal from Michigan. If the Michigan population continues to grow, the Ontario population may either remain stable or increase slightly, provided that suitable habitat is maintained. If the Michigan population

declines, the Ontario population may not be able to sustain itself (Bickerton et al. 2006; Chamberlain 1978; James 1999d).

The prognosis for the Kirtland's Warbler currently looks promising. It was delisted from the United States Endangered Species Act in 2019. The goal of the United States conservation plan was to eventually reach 1,000 nesting pairs per year. That goal has been surpassed with approximately 2,000 pairs present in 2020. The population has expanded from the Lower Peninsula of Michigan to the Upper Peninsula, Wisconsin, and Ontario (Anonymous 2019). In Ontario, a 42-ha site in Simcoe County is being established as a pine-oak forest specifically to create and manage habitat for the Kirtland's Warbler. In 2018, more than 100 km^2 of jack pine rock barrens was burned by Parry Sound Fire 33 and this area has high potential to provide suitable habitat for the Kirtland's Warbler (Burke 2020). In 2022, males were documented in Simcoe County, but no females were present. Tuininga and Burke (2023) concluded that the Ontario population had likely been approximately 20 pairs for the last decade. Several birds and a nest were found in the Sudbury area in 2024.

POSTFLEDGING PERIOD

Young fledged from an Ontario nest on 2 July. Fledglings may be fed by adults until they are 26-44 days old, but start obtaining their own food when they are 23 days old. At this time, they are almost as proficient at flight as adults. Adults have been seen feeding young as late as mid-August, but these may be second broods (Bocetti et al. 2020; Richard 2008).

As soon as young fledge, they immediately flutter to concealment in ground cover. At first, they can fly only 2-3 m but can fly 10-20 m within a week. During this time, fledglings sit for long periods of time under ground cover or on a low twig in a pine thicket. By the second day, fledglings may have moved 100-200 m from the nest but remain in undergrowth and low branches for about 2 weeks. During this period, they remain in an area not much larger than the original territory, but not identical with it. Brood division occurs, with each adult caring exclusively for half the brood. The 2 sub-broods move about separately but remain in close association with each other. If a second brood is started, the female may initiate the second nest while feeding the first brood. Once incubation of the second clutch begins, the male takes charge of the entire first brood. In late summer, family groups tend to concentrate in a few areas, leaving the remainder of the breeding habitat devoid of warblers. Fledglings chose perches close to one another for sleeping until they are about 9 months old then chose isolated perches (Anich et al. 2011; Anonymous 1988; Bocetti et al. 2020; Mayfield 1960; Walkinshaw 1983).

Most observations of fledglings have been in breeding habitat and young may remain in the natal area until autumn migration (Anich et al. 2011; Bocetti et al. 2020). Bocetti (1993) reported an exception after finding a juvenile in Michigan 4.8 km from the nearest occupied breeding area. It was in a second-growth mixed forest surrounded by mature coniferous forest. The canopy was dominated by black cherry, trembling aspen, Hill's oak, and jack pine. Canopy closure was 70% with openings patchily distributed; average tree height was 4.5 m (range 2-6 m). The ground was completely covered with vegetation, predominantly by little bluestem and sweet fern, with some areas of lowbush blueberry, snowberry, and Pennsylvania sedge. In Wisconsin, fledglings used areas with lower foliage-height diversity and bare ground and greater herbaceous vegetation height than unoccupied areas. The probability of fledgling use increased from 24% to 75% when vegetation

height increased from 0 to 52 cm. Probability of use decreased from 74% to 0.5% as foliage-height diversity increased from 0 to 3.24. All fledgling locations had bare ground coverage of 50% or greater. The probability of fledgling use increased from 37% to 49% when bare ground coverage changed from 0 to 1-50% cover (Olah et al. 2023).

Sixty percent of nonbreeders and 11% of breeders made long-distance movements after the nestling and fledgling periods. Both breeders and nonbreeders made an average of 3 movements (1-7 for breeders and 1-13 for nonbreeders). Mean distances moved were 59 km for breeders (range 10-183 km) and 65 km for nonbreeders (range 5-166 km). The mean distance moved by all birds was 63 km (Cooper and Marra 2020).

Fledgling survival rates in Wisconsin red pine plantations were much lower than for fledglings in young jack pine forests in Michigan. Populations breeding in red pine plantations with low pine densities may be sinks. These plantations may be suitable for breeding but have low fledgling survival rates (Olah et al. 2023).

MIGRATION

Migration is presumably nocturnal and birds move solitarily or occasionally in the company of other warblers. Cooper et al. (2017) used geolocators to determine the wintering areas, migration routes, and stopover locations of Kirtland's Warblers breeding in Michigan. Almost all tracked males wintered in the Caribbean, mostly in the central Bahamas but also in eastern and western Bahamas. One male wintered in Cuba. After leaving the breeding grounds in an easterly direction, 25 of 27 males (92.6%) stopped over in southern Ontario or the northwestern mid-Atlantic states. Most stopped again on the coastline of either North or South Carolina prior to initiating over-water migration. During spring migration, males spent an average of 58% of their time at 1-5 stopover sites. Most used 3 main stopovers. Most (74%) made a stopover of an average of 4.8 days shortly after making landfall in Florida. The remaining birds travelled further north before their first stopover. Ninety-six percent of males spent 1.5-14.5 days (mean 4.7 days) in northern Florida, southeastern Georgia, or southwestern South Carolina before crossing the Appalachians. Southwestern Ontario and the region directly to the south also appeared to be important, with 33% of males spending 1-3.5 days (mean 2.2 days) there before reaching Michigan. Cooper et al. (2018) banded 220 Kirtland's Warblers at a site in the central Bahamas. They resighted 56 of these (25.5%) on the breeding grounds: 87.5% in the Lower Peninsula of Michigan, 7.1% in the Upper Peninsula of Michigan, 3.6% in Wisconsin, and 1.8% in Ontario. Loss of wintering habitat at a single location could have a diffuse effect across the entire breeding population.

Adult males arrive at the breeding grounds before juvenile males and females. The earliest record at Petawawa is 9 May. In Michigan, males arrive from 2 May to 5 June (mean 14.6 May). First arrivals of males usually occur 2-7 May. Females do not arrive until after 18 May. Some males arrive at new locations as late as 23 June. These birds may have abandoned territories established earlier elsewhere, or they may be late-arriving yearlings (Anonymous 1988; Berger and Radabaugh 1968; Bocetti et al. 2020; Ewert et al. 2012; Probst 1985; Richard 2013; Rockwell et al. 2012; Walkinshaw 1983).

By August, the first Kirtland's Warblers have returned to the wintering grounds. On the Michigan breeding grounds, there is a significant decline in both age classes from late August to late

September, with significantly greater declines for juveniles than adults. Juveniles comprised 49% of all birds captured during the postbreeding period. They represented 60% of birds netted 16-31 August, 42% 1-15 September, and 0% 16-30 September. A substantial portion of the population remained on the breeding grounds at least through September, but a few birds remain during the first half of October. Juveniles leave earlier than adults. They complete their moult by the end of August but the moult for adults extends through September (Sykes et al. 1989). The latest observation at Petawawa was 4 August (Richard 2014).

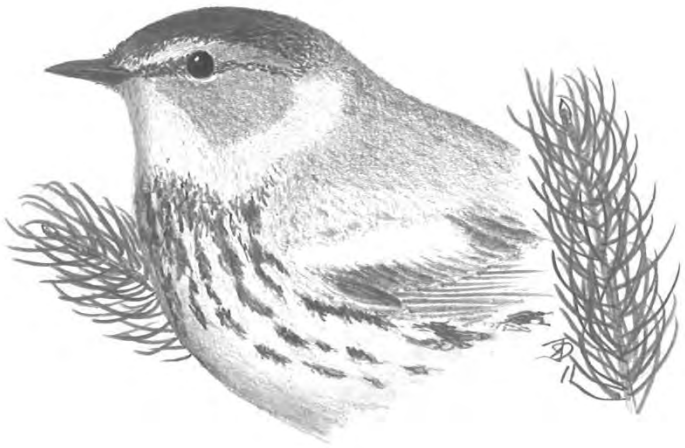
In Pennsylvania, an autumn migrant was captured in an old field with dense coverage by hawthorn and crabapple. It was recaptured twice in the same year in the same 45-m stretch of net despite being released 250 m and 850 m from this area. It appeared to prefer this habitat type over willow thickets bordering a pond, old fields in varying stages of succession, and second-growth forest. This bird remained at the same location for a minimum of 11 days. In 2 other years, single Kirtland's Warblers were observed at this site foraging in birches on abandoned strip-mine spoil. Migration habitat is dissimilar to breeding habitat and consists of low deciduous scrub in open situations (Bocetti et al. 2020; Clench 1973).

During migration, the Kirtland's Warbler has collided with windows and lighthouses (Walkinshaw 1983).

The Kirtland's Warbler is a rare migrant in Ontario. The first Ontario record was from Toronto in May 1900. With the population increase in Michigan, there has been an increase in the number of migrants observed in Ontario since 1990. There is now an average of just over 1 sighting per year, predominantly in May. From 1900 to 2005, there were a total of 47 spring and 7 autumn records (Austen et al. 1994; James 1999d; Kirk and Pearce 2008; Richard 2013).

Cape May Warbler

Setophaga tigrina



BREEDING SEASON

Habitat Requirements

Ontario Cape May Warbler nests were found in white spruce forests and second-growth mixed forests of birch and spruce (Peck and James 1987). In Ontario, it prefers mature coniferous and mixed forests. Although it occasionally inhabits dense woods, it prefers open forests and forest edges and openings. Conifers at least 10 m tall are an important habitat component. It is typically associated with white spruce and/or balsam fir and with black spruce to a lesser extent. It is one of the spruce budworm specialists, typically increasing as budworm populations increase. When budworms are absent or scarce, large tracts of suitable habitat are unoccupied, but it uses marginal habitat when budworms are abundant. At Manitouwadge, it was not observed in young (1-21 years) or intermediate-aged (24-36 years) stands when budworms were scarce and was restricted to stands 60-223 years old. When budworms became abundant, it occupied all age classes of forest. Near Quetico Park, it was found only in stands 112-176 years old. Near Hearst, it occurred in uncut upland mixed and lowland coniferous stands, and in clear-cuts in these forest types 17-24 years old. In Algonquin Park white pine stands, it was absent to rare in clear-cuts 10-16 years old and was absent

in younger cuts. North of Lake Nipigon, it preferred white or black spruce stands with trees as tall as 30 or more metres, with balsam fir in the canopy and grey alder, Labrador tea, and raspberries in the shrub layer. In the Clay Belt, it was most common, in decreasing order of abundance, in stands dominated by trembling aspen, trembling aspen mixed with conifers, trembling aspen–balsam poplar, white spruce–balsam fir, black spruce–trembling aspen, black spruce, and jack pine. It occurred in both wet and dry stands and those that were moderate to rich in nutrients. It appears to nest only in spruce and balsam fir, so it is associated with these species even in stands dominated by deciduous trees. Along the James Bay coast in 1978, the Cape May Warbler occurred exclusively in mature coniferous stands (Apfelbaum and Haney 1999; James 1984b; Kendeigh 1947; Kingsley and Nol 1999; Tozer 2012; Vanderwel et al. 2009; Venier et al. 2008; Welsh in Cadman et al. 1987; Welsh and Fillman 1980; Welsh and Lougheed 1996).

The Cape May Warbler is one of only 14 passerines whose breeding range is confined or nearly restricted to boreal conifer forests, although its Ontario range includes the northern portion of the Great Lakes–St. Lawrence Forest Region. It is regular in spruce forests only in the presence of spruce budworms, and also occurs in mature spruce–balsam fir stands. The stands it uses may include a mix of intolerant hardwood species such as trembling aspen, balsam poplar, white birch, and yellow birch. In most cases, it is restricted to intermediate-aged, mature, and old-growth stands dominated by spruce and balsam fir, but may use younger stands when budworms are abundant. It prefers spruce stands where trees are a minimum of 10 m tall with well-developed crowns and some supercanopy trees that provide song perches. Sites it uses tend to have an open understorey comprised of low shrubs. It prefers large isolated white spruce for nesting, but it is also attracted to open stands. In dense stands, it is associated with edges or small openings. The Cape May Warbler tends to occur more frequently on drier sites. Wet sites are dominated by black spruce which is seldom attacked by the spruce budworm. In addition to spruce and spruce–balsam fir stands, it has nested in black spruce bogs, 50-year-old white spruce plantations with sparse understorey and 2.4 m between trees, in mature balsam fir–white cedar stands, and occasionally in recent clear-cuts. In spruce–balsam fir stands in Maine, it occurred only in mature forests and clear-cuts 1-2 years old dominated by dense slash coverage and considerable bare ground. In Quebec, it was equally abundant in riparian and nonriparian stands of mature balsam fir–white cedar. In the northeast, it was in a guild of species that was most common in mature coniferous lowland forests. In the western Canadian boreal forest, it was in a guild of birds associated predominantly with coniferous

species. In Quebec, its breeding distribution corresponds closely with the distribution of the spruce budworm. In the Boreal Forest Region of Saskatchewan, it was significantly more abundant in white spruce stands within contiguous forest than in fragmented forests. In fragmented landscapes, it was more common than expected by chance in mature white spruce stands that were larger but isolated (Baltz and Latta 2020; Bent 1953; Campbell et al. 2001; Chapman 1907; Crawford and Titterington 1979; Dawson 1979; Erskine 1977; Hobson and Bayne 2000; Kirk et al. 1996; Lamoue and Morrier in Gauthier and Aubry 1996; LaRue et al. 1994; Morse 1978; Niemi and Pfannmuller 1979; Sinclair et al. 2003; Temple et al. 1979; Titterington et al. 1979).

Peck and James (1987) described 5 Ontario nests, although a few more have been found subsequently. All were near the top of either white or black spruce and placed against the trunk or as far as 5 cm from it. Nests were 0.3-0.75 m from the top of nest trees at heights of 7.6-15 m.

Few nests of the Cape May Warbler have been described. Nests are very difficult to find because of their position and the female's behaviour when returning to the nest. Nests are in dense vegetation very close to the top of a conifer and cannot be detected from the ground. One nest was so well hidden that the researcher could not see it even when he was even with it in the tree, and only found it by feeling for it in the dense vegetation with his hand. When the female returns to the nest, she lands low in the tree and hops branch to branch in the interior of the tree to reach the nest. Consequently, she is very difficult to detect. All nests were 0.6-1.8 m from the top of a conifer, usually spruce (white, black, or red) but occasionally balsam fir. Most nest trees are in the open, at least on 1 side. Nests tend to be at the trunk or as far as 23 cm from it. Most nests are affixed to a branch with insect silk but one was simply sitting on a branch. Nests have been found 10.7-18.3 m from the ground (Baltz and Latta 2020; Bent 1953; Philipp and Bowdish 1919).

Kendeigh (1947) mapped Cape May Warbler territories north of Lake Nipigon during a spruce budworm outbreak when warblers were present at a supersaturated level. The average size of 22 territories was 0.4 ha (range 0.16-0.97 ha). These were based on few observations, so territories may have been larger. Most territories were isolated or barely touched each other and some contained considerable amounts of grey alder swamp. There appear to be no other estimates of territory size, but others have noted that territories mostly do not adjoin each other. Territory size may be determined by food availability, with larger territories prevalent when food resources are low (MacArthur 1958; Morse 1978).

No information is available on natal philopatry (Baltz and Latta 2020). In the Gaspé Peninsula of Québec, 1 of 28 adults (3.6%) returned to the site where it was banded (Moisan Perrier et al. 2020).

Limiting Factors

Peck and James (1987) concluded that nests with eggs could occur in Ontario throughout June. In Algonquin Park, dependent fledglings have been seen from late June to mid-July (Tozer 2012). No information is available on how long it takes to build the nest, if time elapses between nest completion and initiation of egg laying, rate of egg laying (although it is probably 1 per day), when incubation is initiated and how long it takes, the nestling period, or how long fledglings are dependent upon the adults (Baltz and Latta 2020; Bent 1953).

It is likely that a single brood is raised in a season, but this has not been confirmed. It is unknown if replacement clutches are laid if the first one is lost. One Ontario nest contained 6 eggs and another held 4 young. The Cape May Warbler, along with the other budworm specialist warblers, lays the largest clutch of the warblers. The clutch size ranges from 4 to 9 eggs. Six eggs is the most frequent clutch size and the average across its breeding range is 5.8 eggs. It has been assumed that clutch size increases during spruce budworm outbreaks resulting in an increase in population, and that smaller clutches are laid when budworms are scarce, resulting in a declining population. These relationships have never been positively confirmed (Baltz and Latta 2020; Bent 1953; MacArthur 1958; McCracken 2004; Peck and James 1987; Philipp and Bowdish 1919).

The mating system is probably monogamous, but this has not been studied. It is likely that both sexes are capable of breeding when they are 1 year old. Removal studies demonstrated that there is a large floating population suggesting that some individuals may delay breeding until they are older (Baltz and Latta 2020; Hensley and Cope 1950).

Kendeigh (1947) observed the Cape May Warbler's foraging strategies north of Lake Nipigon. Feeding was done at the same levels where males sang, typically within 2.1 m of the top of a conifer. The average height of song perches and male feeding areas was 10.7 m (range 2.7-16.8 m). One male sang from the top of a 16.8-m dead tree but all other observations were of birds in live conifers. It occasionally flew out to capture an insect in the manner of flycatchers. In the Boreal Forest Region of Ontario, 95% of foraging occurred in conifers, 79.0% occurred in foliage, 17.6% of attacks were aerial and 3.4% were by hanging; average foraging height was 15.3 m (Greenberg et al. 1999). There are 5 warbler species that coexist in homogeneous mature boreal forests: Cape May, Yellow-rumped, Black-throated Green, Blackburnian, and Bay-breasted warblers. These species are very similar in their ecological preferences, suggesting that they have different microhabitat requirements. The Cape May Warbler forages more consistently near the top of trees than any other species except the Blackburnian Warbler, from which it differs principally in the type of feeding action. The Cape May Warbler not only hawks more than the Blackburnian Warbler but moves vertically rather than radially in trees, causing its feeding zone to be more restricted to the outer shell of the trees. Of observations of feeding Cape May Warblers, 43.8% were in the terminal zone of new needles and buds in the top 3 m of the trees, 21.3% were in the terminal zone in the next lowest 3 m, 13.8% were in the middle zone of old needles in the top 3 m, 11.2% were in the middle zone 3-6 m from the top, and 6.2% were in the middle and terminal zones 6-9 m from the top. No birds foraged in the lower 6 m of trees. During windy, rainy, and cold days, it did not occur at the top of conifers and instead foraged in low willows and among flowers of pin cherries. The Cape May Warbler has a noticeably different bill than the other 4 species, being more slender, especially near the tip. In addition, it has a semitubular tongue that is unique to warblers. It may occasionally forage on the ground and often forages from the undersurface of fir needles. In Maine, approximately 77% of foraging occurred on outer limbs, 12% at tips of branches, 10% on inner limbs, and 9% on dead limbs and in deciduous species. Fifty percent of foraging occurred at heights of 15-18 m, 30% at 18-21 m, 11% at 21-24 m, 5% at 12-15 m, 2% each at 9-12 m and 6-9 m, and 0 below 6 m. Almost all foraging was by gleaning with only 2 observations of hawking. It foraged 71.2% of the time in red spruce, significantly more than the 52.0% of time spent in this species by the Bay-breasted Warbler (Baltz and Latta 2020; Campbell et al. 2001; MacArthur 1958; Morse 1978, 1989).

During a spruce budworm outbreak north of Lake Nipigon, the stomach of 1 male contained 60 spiders, 25 aphids and 15 beetles (Kendeigh 1947). Near Longlac during a budworm outbreak, McMartin et al. (2002) quantified the diet of the Cape May Warbler and compared it with that of the other 2 budworm specialists (Tennessee Warbler, Bay-breasted Warbler). The diet was examined during 2 periods: 7-11 June and 18-24 June. During the early period, only small instars of budworms were available and these are seldom eaten by birds. In the later period, large larvae and pupae of budworms were present. The diet of the Cape May Warbler during the early period consisted of 52.7% adult beetles, 18.9% flies, 17.6% caterpillars, 8.1% other invertebrates, and 2.7% spiders. Other invertebrates included soft-winged bugs, hymenopteran adults and larvae, true bugs, beetle larvae, snails, odonates, caddisflies, and neuropterans. The late-season diet consisted of 79.1% caterpillars, 8.8% adult beetles, 5.5% spiders, 4.4% flies, and 2.2% others. The food-niche breadth of the Cape May Warbler declined by two thirds from the early to the late period. The 3 warblers differed significantly in their consumption of beetles and caterpillars early in the season. At that time, the Bay-breasted Warbler ate more beetles, the Cape May Warbler ate more flies, and the Tennessee Warbler ate more caterpillars than the other species. Later in the season, the only difference in diets was that the Bay-breasted Warbler continued to eat more beetles than the other 2 warblers. All 3 warblers fed on budworms in the later sampling period and these were so abundant that there was no competition for food resources. Twenty-four Cape May Warbler stomachs collected during a moderate budworm outbreak in Maine averaged 48% and 39% budworm larvae and pupae by volume in 2 years (Baltz and Latta 2020; Mitchell 1952). Crawford and Jennings (1989) examined predation on the spruce budworm by the Cape May Warbler in New Hampshire and Maine. Large larvae and pupae of budworms were available to birds from 11 June to 21 July. An average of 5.7 budworms was found in stomachs, second highest to the Purple Finch. The 4 species that ate the most budworms were Blackburnian Warbler, Cape May Warbler, Bay-breasted Warbler, and Magnolia Warbler, but they exhibited only a weak feeding response to increasing numbers of budworms. Although not confirmed, the authors expected that nestling consumption of budworm larvae and pupae would equal or exceed adult consumption. High densities of budworms far exceeded the food requirements of all of the woodland birds that were present. It was estimated that birds consumed only 22% of the budworms.

Food availability appears to be the main limiting factor to Cape May Warbler populations. It depends upon occasional outbreaks of superabundant food, such as the spruce budworm, for its continued existence. It may immigrate to areas experiencing outbreaks and is a good example of a fugitive species. Between outbreaks, it suffers reductions in numbers and may experience local extirpations. North of Lake Nipigon, densities approached 100 pairs per km^2 during a budworm outbreak but it was absent in the same location 2 decades later when budworms were scarce. Near Manitouwadge, numbers of Cape May Warblers increased by 10.4-fold over a 4-year period during a budworm outbreak. It was initially 35th in abundance of the bird species present, but increased to 10th as budworm populations increased. These results confirmed that the Cape May Warbler is a budworm specialist, so that factors that affect budworm populations may have an impact on it. These may include climate change, changing forest species composition due to forestry, forest fire suppression, and use of insecticides such as Bt. Most other studies have found a positive response to budworm populations, but 2 in New Brunswick and Maine did not. This may have been because

warbler populations increased gradually over several years (Baltz and Latta 2020; Crawford and Jennings 1989; Kendeigh 1947; MacArthur 1958; Morris et al. 1958; Sanders 1970; Venier et al. 2009).

The Cape May Warbler is a rare host of the Brown-headed Cowbird. There are few locations where the distribution of the 2 species overlaps. In addition, the warbler nests in habitat that is rarely visited by cowbirds. There are no records of cowbird parasitism in Ontario, but few warbler nests have been found. In British Columbia, there is 1 record of an adult warbler feeding a fledgling cowbird (Baltz and Latta 2020; Campbell et al. 2001; Peck and James 1987).

The effects of spraying for spruce budworms are uncertain. In 1975, 2.7 million ha were sprayed in New Brunswick and 4 million ha were sprayed the following year with similar coverage in Quebec. In 1975, it was estimated that there were several million bird casualties due to spraying, primarily from exposure to phosphamidon. In 1977, aminocarb was used solely and there was no convincing evidence of spray effects on songbird populations. More recently, Bt is used, which attacks only lepidopteran caterpillars. Modifications to spruce budworm spraying programs appear to have reduced mortality, although studies are limited. In some areas, Cape May Warbler populations have stabilized over several decades because budworm control programs keep budworm numbers at low to medium levels over long periods of time (Baltz and Latta 2020; Morse 1989).

Repeated fires and logging may limit the Cape May Warbler by preventing development of the mature forests required both by the warbler and budworms. Effects of partial timber harvesting are uncertain and have not been extensively studied. Based upon the results of several studies in the Boreal Forest Region, with particular emphasis on Ontario, it appeared to increase when 30%, 50%, or 70% of trees were removed from a stand. The reliability of these data was low. In Alberta, no effect was noticed on the Cape May Warbler as a result of partial harvest. In British Columbia, it often inhabits stands where only the largest spruces have been removed. Creating openings in dense stands is probably beneficial but excessive thinning that promotes growth of deciduous trees and shrubs may be detrimental (Baltz and Latta 2020; Campbell et al. 2001; Harrison et al. 2005; Vanderwel et al. 2009). In the Canadian Shield of Ontario, there was no difference in its abundance in early successional and mid-successional clear-cuts compared with burns in the same seral stages. It was equally abundant in early successional, mid-successional, and mature stands (Zimmerling et al. 2017).

In Alberta, there were no significant differences in the abundance of the Cape May Warbler at seismic lines, pipelines, well pads, or in forest interior adjacent to these features (Bayne et al. 2017).

DesGranges and LeBlanc (2012) determined that the Cape May Warbler was found mostly in warmer microclimates in the Boreal Forest Region of central Quebec and Labrador. Warblers in this area may benefit from climate change. This study was conducted near the northern extent of the warbler's range. Studies conducted further south may have differing results.

Status

The Cape May Warbler appears to have been rare in Ontario and throughout its range in the late 19th century. McIlwraith (1894) considered it very rare and had only 6 records of migrants from the Hamilton area. In the Toronto area, there were only 4 records of migrants from 1889 to 1897. An increase began in 1898 and in 1900 they were fairly common in the city during migration (Fleming

1907). Although these early records were only of migrants, they give a general picture of the breeding status of the species. Baillie and Harrington (1937) considered it a very rare summer resident between the Bruce Peninsula and James Bay west to Lac Seul, but noted that it was a fairly common breeder in Sudbury District. Baillie and Hope (1947) reported that the only known nesting locations were Sudbury District, Moosonee, Lac Seul, and Dorcas Bay on the Bruce Peninsula. James (1984b) reported that it probably bred north to Sandy Lake and Moosonee south to the tip of the Bruce Peninsula and Algonquin Park. Tozer (2012) summarized trends in populations in Algonquin Park, and these are probably indicative of province-wide populations. It was first observed in the park in 1921, became common as a breeder and migrant in the 1940s, was uncommon in the 1960s, and common again in the 1970s. Since the 1990s, numbers of migrants and breeders have been low. The first atlas extended the known range slightly northward to Sachigo Lake and a bit north of Moosonee. Its range probably included all the Boreal Forest Region. It was not reported in some northern blocks where it was likely present but overlooked. In the south, it nested on Manitoulin Island, the Bruce Peninsula, throughout Algonquin Park, and a bit south of the park (Welsh in Cadman et al. 1987). James (1991) considered the Cape May Warbler a locally common breeder north to Big Trout Lake and Moosonee, south to the Algonquin Park area. He considered it occasional and rare on Manitoulin Island and the Bruce Peninsula.

The second atlas indicated few changes in the range of the Cape May Warbler. It occurred in a few squares in the Hudson Bay Lowland north to the Sachigo River and Swan River. It continued to be concentrated in the Boreal Forest Region where it was apparently absent in some squares. In the south, it nested to the southern edge of the Canadian Shield, although sparingly. South of the Shield, it was confirmed breeding east of Ottawa, but was not detected on the Bruce Peninsula and it apparently disappeared from many squares on Manitoulin Island. There was no change in its overall probability of observation between the 2 atlases. A significant decline occurred in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield. This was due to its disappearance from many squares in Algonquin Park and in the Sudbury area. Budworms were about twice as common in Algonquin Park during the first atlas compared with the second atlas, and this probably had a direct effect on its local abundance. It was not particularly common anywhere despite its broad distribution. It was most common in the northern Boreal Forest Region. There was little spruce budworm activity in Ontario during the second atlas, so the densities and distribution recorded represent baseline population data. Highest abundance areas for the Cape May Warbler did not correspond to those for the Tennessee, Bay-breasted, or Blackburnian warblers, suggesting that the observed densities were not linked to budworm outbreaks (McLaren in Cadman et al. 2007).

The Cape May Warbler was universally rare in the 19th century, but experienced a marked increase early in the 20th century. In Ontario, the first signs of increase occurred in 1898. It did not become common in New England until 1909, but it was among the most common species in Maine by the late 1940s (Bent 1953; Fleming 1907; MacArthur 1958). McCracken (2004) compared the abundance of migrating Cape May Warblers at Long Point Bird Observatory (LPBO) with the timing of spruce budworm outbreaks in the province. No budworm outbreaks of any consequence occurred during the 1960s, but massive outbreaks began in the 1970s, peaking in 1980. Infestations fell off dramatically after that except for 2 resurgences in the mid-1980s and early 1990s. In 1980, approximately 19,000,000 ha of forests were affected by budworms compared with 131,000 ha in

2002, similar to the 1960s levels. Banding of Cape May Warblers at LPBO closely tracked the extent of insect infestations in boreal Ontario. Peak populations of the 3 primary budworm warblers combined occurred in 1977, with an index value of 4.7. Numbers dropped to an index level of 1.4 in 2002, a level slightly below the prebudworm era of the 1960s. For North America, Breeding Bird Survey (BBS) results indicated an annual increase of 3.1% 1966-91, but a decrease of 9.4% 1982-91 (Baltz and Latta 2020). BBS results indicate that the Cape May Warbler increased at annual rates of 2.39% in Canada and 0.637% in Ontario 1970-2022 and 7.58% in Canada and 3.02% in Ontario 2012-22 (A.C. Smith et al. 2023).

MIGRATION

Judging by kills at tall structures, the Cape May Warbler appears to be a nocturnal migrant (Baltz and Latta 2020).

Males arrive before females in spring, and the duration of spring migration is shorter than in the autumn. At Long Point, mean capture dates for males were 12.7 May for adults, 14.6 May for yearlings, and 13.1 May for males of undetermined age. For females, average arrival dates were 16 May for adults, 17.5 May for yearlings, and 19.3 May for those of undetermined age. Differences in timing between age classes were significant for males but not for females. In southern and central Ontario, migrants begin to arrive in the first week of May or rarely, the last week of April, and almost have passed through by the end of May (Baltz and Latta 2020; Black and Roy 2010; Curry 2006; Fleming 1907; Francis and Cooke 1986; Keast 1980; LaForest 1993; Lancaster et al. 2004; Mills 1981; Stewart et al. 2002; Tozer 2012; Weir 2008). North of Lake Nipigon, it was first observed on 24 May (Kendeigh 1947). A bird observed at Shagamu on 2 June was probably a spring overshoot because this is well north of the known breeding range (Wilson and McRae 1993).

Autumn migration may begin in late July after nesting is complete, but more typically in late August, and most birds have left the breeding grounds by late September. The sexes may travel together and older birds tend to migrate earlier than juveniles, although there were no differences in timing of migration of the age classes in Virginia (Baltz and Latta 2020; Campbell et al. 2001; Stewart 1986). Wilson and McRae (1993) observed an autumn migrant at Moosonee on 2 September. Autumn records in the southern Shield are from early August to late September, with birds rarely remaining into the second week of October. Peak autumn passage is from mid-August until the end of the third week of September (Mills 1981; Tozer 2012). Lawrence (1950) observed one at her feeder at Pimisi Bay on 23 November 1949. Although this was autumn according to the calendar, there were 25 cm of snow on the ground and the low temperature was –23°C. It travelled with a flock of chickadees and appeared to be in excellent health until a Northern Shrike killed it 4 days later. Six years previously, one was seen in Weston on 3 December. In southern Ontario, average arrival is in mid-August and average departure is late September. Birds may arrive as early as mid-July and remain until mid-October, with rare records into early December (Black and Roy 2010; Curry 2006; Keast 1980; Lancaster et al. 2004; Weir 2008).

During migration, the Cape May Warbler frequents coniferous and mixed forests and often forages in nearby shrubs. These habitats become scarce once it travels south of the Canadian Shield. South of the Shield, it may still seek conifers in mixed woods and anthropogenic areas such as residential plantings, university campuses, golf courses, tree nurseries, and plantations. Presence of

conifers is not essential during migration, and they become increasingly rare further south. It may frequent deciduous woodlands, flowering shade and fruit trees, overgrown fencerows, weedy roadsides, orchards, suburban parks and residential areas, riparian vegetation, bottomland forests, and weedy patches in fields and dried lake beds. In Maine, it is common on treeless coastal islands where it forages in the grass. It has been observed along drainage ditches and the high-tide line on the Atlantic coast. In Indiana, it often occurs in drier woodlands such as those dominated by oaks. In spring in Illinois, it was most abundant in mature upland forests, but also occurred in forest edges and shrubs. In autumn, it is most abundant in forest edges and shrubs followed by mature bottomland forests and pastures. During autumn migration in Pennsylvania, there were no differences in its abundance in forest interior, forest edges, forest-agricultural edges, suburban forests, pole-stage forests, or shrub-sapling-stage forests (Baltz and Latta 2020; Bohlen and Oehmke 1993; Campbell et al. 2001; Chapman 1907; Dawn 1957; Graber et al. 1983; Leighton et al. 2002; Morse 1989; Rodewald and Brittingham 2002; Sealy 1988).

The Cape May Warbler frequently forages in mixed-species flocks of warblers during migration (Baltz and Latta 2020; Tozer 2012), but it also forages solitarily in territories that it defends from other Cape May Warblers and other species. It has been observed expelling the Ruby-throated Hummingbird, Yellow-bellied Sapsucker, Least Flycatcher, Philadelphia Vireo, Swainson's Thrush, Northern House Wren, Northern Waterthrush, Tennessee Warbler, Orange-crowned Warbler, Black-and-white Warbler, Yellow Warbler, Yellow-rumped Warbler, Common Yellowthroat, American Redstart, Blackpoll Warbler, Palm Warbler, and Black-throated Blue Warbler. It defends territories only when food resources are scarce, such as during inclement weather or extreme drought conditions. At other times, it forages with other species and other Cape May Warblers without aggression. In peach-leaved willow forest in Manitoba, these warblers were spaced 1.5-2 m apart in tree crowns and individual birds remained in the same territory for about 2 days. In 1 tree, 2 warblers each defended territories of 3 m^2 on opposite sides of the tree. They appeared to be feeding on the nectar of the willows. During a storm in another spring in Manitoba, warblers defended fixed territories about 8 m long along a water-filled ditch. Some held their territories as long as 4 days until the weather improved. Birds walked the shoreline and perched on bent-over and floating branches to access prey on the surface of the water. During autumn migration in Illinois, 1 defended an area 3-7.6 m above ground in the lower branches of a black maple and held this territory for at least 15 days. During spring migration in Florida, a male defended flowers on a plant and chased all birds that approached it, although it ignored birds in a pine a few feet away and the leaves of the same plant. Territorial birds most often defend flowers and other nectar sources, but may also defend unusually abundant prey in an area where food is otherwise scarce, and occasionally unusual prey is defended. The Illinois territorial birds were defending portions of trees that were heavily infested with aphids. This was during a drought and food was very scarce away from the infested trees. The birds that defended territories along a ditch in Manitoba foraged on springtails, an apparently rare prey item. During the storm when these territories were defended, it is unlikely that traditional insect prey were available (Bohlen and Oehmke 1993; Kale 1967; Sealy 1988, 1989).

During migration, foraging typically occurs in the upper, outer canopy of trees. In spring in North Carolina, 71.4% of foraging was in the canopy and the Cape May Warbler foraged higher than any other warbler species; 28.6% of foraging occurred in low trees and none occurred in shrubs or on

the ground. In the canopy, 14.3% of foraging occurred at the top of the crown and 57.1% was in the inner crown. In low trees, 14.3% of foraging was at the top of the crown and 14.3% was in the inner crown. No foraging occurred in the lower crown or on the bole in either the canopy or low trees. During cold spells, it may forage lower in the vegetation, on tree trunks, and on the ground. During such weather during spring at Point Pelee, limited aerial foraging occurred. Of other substrates, 50% were bare twigs, 40% were branches, and 10% were sapling trunks. No birds foraged more than 17 m from the ground, 40% foraged at 13 m, 30% foraged at 10 m, 20% foraged at 7 m, and 10% foraged at 3 m. Foraging was not observed at heights of 5, 0.6-1.8, and 0 m from the ground. It searched for most food on bare trunks and branches. Of 231 prey captures in Manitoba, 67.1% were arthropods gleaned from vegetation and the remainder were aerially hawked. There are several records of it feeding at hummingbird feeders and sapsucker wells (Baltz and Latta 2020; Keast 1980; Kilham 1953; Marvel 1948; Parnell 1969; Sealy 1989).

During migration, the Cape May Warbler eats a mix of insects, nectar, and fruit. Four stomachs examined in autumn near Prince Edward Point each contained about 15 beetles. Ten stomachs collected in autumn in Pennsylvania contained 57.5% hymenopterans (parasitic wasps, ants, and small bees), 16.7% flies, 16.7% small moths, 7.8% beetles, and small numbers of true bugs, spiders, and miscellaneous insects. Other prey items include small crickets, leafhoppers, bark lice, termites, moth larvae, dragonflies, and harvestmen. On the Atlantic shoreline of New York, it ate amphipods approximately 14 mm in length. In spring in Illinois, it is especially attracted to flowers, particularly those of hawthorns. In Manitoba it favours willow catkins. It has fed on orange slices. In autumn, it regularly pierces grapes with its bill and sucks out the juice with its tubular tongue. It may be quite destructive to commercial grape crops (Baltz and Latta 2020; Bent 1953; Dawn 1957; Graber et al. 1983; Keast 1980; Sealy 1989).

The Cape May Warbler frequently strikes communication towers and other tall structures during migration. Although mortality at Illinois television towers is rare, predation and collisions are the primary sources of mortality during migration. Hundreds are killed at towers in the United States but few strikes involve more than 100 birds in a night. At the Lennox generating station chimneys, 231 were killed the night of 5 September 1981 and an additional 176 were killed the following night (Baltz and Latta 2020; Graber et al. 1983; Weir 2008). Loss et al. (2014) analyzed bird collisions with buildings in the United States. The Cape May Warbler was highly vulnerable to striking high-rises and was 16.7 times more likely to strike this type of building than birds on average. It was not on the lists of the 20 most vulnerable species for striking residences 1-3 stories tall or low-rises.

In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season for 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming occurred during the second period. Autumn departure of the Cape May Warbler was significantly later in the second period, but there were no differences in spring arrival dates or length of the breeding season.

James (1991) considered the Cape May Warbler an uncommon to common migrant in Ontario. Numbers in individual locations vary considerably depending upon spruce budworm populations. Its numbers have experienced long-term trends as well as short-term changes and these are all likely related to budworm numbers. It was a very rare migrant in the province prior to 1900: McIlwraith

(1896) had only seen 6; none had been observed in Elgin County by 1891 (Lancaster et al. 2004); and Fleming (1907) considered it one of the rarest warblers prior to 1898. Peak numbers of migrant Cape May Warblers occurred in the 1970s and early 1980s, with a continuing decline since then (Hussell et al. 1992; McCracken 2004). In Niagara Region, Black and Roy (2010) considered the Cape May Warbler a rare spring migrant that had clearly declined since 1970 when it was common during migration. Black (2017) reported that numbers of Cape May Warblers observed during May at the Port Weller pier declined 1993-2017. LPBO data indicate significant declines during spring and autumn migration of 4.4% per year from 1981-86 to 2001-06 (Venier et al. 2009).

Cerulean Warbler

Setophaga cerulea

BREEDING SEASON

Habitat Requirements

Ontario Cerulean Warbler nests were in deciduous second-growth and mature forests, but one was in a mixed woods. The stands that it occupied were usually open, and nests were often at edges or near clearings (Peck and James 1998a). It requires dense and tall second-growth or mature woodlands. It prefers swamps and floodplain forests, but also occurs in moist upland forests. It requires extensive areas of forest and seems to be area sensitive (James 1984b). Austen et al. (1994) summarized its habitat requirements as mature deciduous forests in extensive woodlands, particularly in floodplains or other mesic habitats characterized by large mature trees and closed or semiopen forest canopies. It also occurs in drier, open upland forest. The largest Ontario population of the Cerulean Warbler is in the Canadian Shield north of Kingston. The landscape in this area consists of extensive forest with embedded beaver meadows, abandoned farm fields, and dry rocky ridges. The forest cover is 80-90 years old and dominated by sugar maple, bitternut hickory, and white ash, with occasional oaks, elms, basswoods, and birches. The mid- and understorey is dominated by sugar maple and hophornbeam saplings. Two study areas north of Kingston that

supported large populations experienced different land-use strategies. The Lake Opinicon site was mature sugar maple–beech-oak forest that has remained undisturbed since the early 1900s. The Canoe Lake site experienced extensive grazing by cattle in the late 1950s and has also experienced selective thinning of large oaks and poplars. The eastern Ontario population breeds in a broad range of habitats from deciduous forests to sumac-juniper thickets, although it is typically associated with forests (Barg et al. 2005; Jones and Robertson 1997, 2001; Oliarnyk 1995; Oliarnyk and Robertson 1996a). In Durham Region, it nested in a mature sugar maple–oak forest arising from the floodplain of the St. John River. Tree growth was sparse on rocky ridges, but most of the plot had an upper canopy (Speirs and Orenstein 1975). In southwestern Ontario, predominantly in the Carolinian Forest Region, it preferred tall canopies in late-successional wet to mesic deciduous woodlands. McCracken (1993) stated that canopy height and structure were probably critical habitat features. He also noted that it required large forests in excess of 100 ha, and concluded that it was a forest-interior species. It occurs in Vanessa Swamp, a 700-ha tract in the Carolinian Forest Region, predominantly in areas dominated by oaks and, to a lesser extent, maples. It also occurs in the extensively forested floodplains of the Grand River from Paris to Cambridge and in large woods adjacent to them. These forests are dominated by sugar maple, but contain a mixture of oaks, hickories, and other deciduous species as well as white pine. The forest cover in both these areas is mature second growth (personal observation).

A good proportion of what is known about the Cerulean Warbler's habitat requirements and breeding biology is a result of intensive studies in eastern Ontario in the Kingston region. From this and other research, it is apparent that it has distinct habitat preferences at several scales: the landscape, the structure and composition of the forest, the territory, the core of the territory, the singing perches, and the nest site.

The Cerulean Warbler nests both in extensively forested habitat north of Kingston and in agricultural landscapes in most of its remaining range in Ontario. Landscape type affects the suitability of individual forest patches for the species and its degree of area sensitivity. In the Kingston area, it breeds successfully in woodlots as small as 10 ha. It may require woodlands larger than 100 ha in the agricultural areas of southwestern Ontario. In these agricultural areas, the spatial distribution of forest patches and especially the distance between suitable patches undoubtedly play an important role in settlement patterns and area sensitivity, but this requires more study. Even in eastern Ontario, the minimum patch size used is considerably larger than a single territory,

suggesting that area sensitivity is occurring to some degree even within extensively forested landscapes. This may be due to its habit of clumping territories, requiring stands to be large enough to accommodate multiple territories (Barg et al. 2003; Jones 2000; McCracken 1993). The Cerulean Warbler is area sensitive throughout its United States range but, similar to Ontario, the size of tract that is required varies geographically. In Wisconsin and Minnesota, it occurs only in stands larger than 16 ha. In Ohio, it prefers tracts that are at least 20-30 ha and avoids tracts smaller than 8-10 ha. These tract sizes may be similar to what is used in New York. In the mid-Atlantic states, maximum probability of occurrence occurred in woodlots larger than 3,000 ha, probability was reduced to 50% at 700 ha, and the 3 smallest woodlands it was detected in were 1,500, 637, and 138 ha. In Connecticut, the average size of patches where it was observed was 1,634 ha; the minimum-sized forest it occurred in was 647 ha. In Tennessee in the Mississippi River valley it appear to require 1,600 ha and forests as large as 8,000 ha may be required to support a viable population. Despite these numbers, it was documented breeding in a grove of trees at a church in 1925, but no information is available on the landscape context. In Arkansas, it occurred in a 3-ha 100-year-old forest. In Illinois, it nested in a 7-ha woodlot (Askins et al. 1987; Buehler et al. 2020; Hamel 2000; Robbins et al. 1989; Thogmartin et al. 2004). Thompson et al. (2012) related Cerulean Warbler abundance to landscape levels of forest cover in Missouri and Arkansas. They surveyed along rivers in landscapes containing 30.7-97.3% forest cover within 10 km. Its abundance increased 390.7 times over the observed range of forest cover within 10 km, 8.7 times over the range of riparian forest within 250 m, and 4.1 times over the range of upland forest within 250 m. Their results were consistent with the theory that habitat selection is hierarchical and that landscape conditions provide important cues to breeding warblers. In other areas, suitable riparian forest surrounded by agricultural land is often unoccupied (Hamel 2000). In West Virginia, fewer territories than expected by availability occurred in forest fragments and more than expected occurred in intact forests. Seventy-three percent of territories occurred in intact forests although only 28% of the area surveyed was in intact forest (Weakland and Wood 2005). There is strong evidence that habitat selection at the landscape level and area sensitivity are linked to precipitation and moisture regimes. Thogmartin et al. (2004) modelled its abundance in the Prairie-Hardwood Transition Area that includes all or portions of Minnesota, Wisconsin, Michigan, Iowa, Illinois, and Indiana. Its greatest abundance occurred where precipitation rates and forest patch size were coincidentally higher. It was abundant in small deciduous patches if the mean precipitation was high. Small, dry deciduous patches contained few Cerulean Warblers. It increased as the percentage of the landscape in forested wetland increased, but chose forested uplands within this matrix of moist bottomland forest. In Wisconsin upland forests, Bond (1957) recorded it in woodlots ranging in size from 6.1 ha to more than 200 ha. Its frequency of occurrence was 4.0% in woodlots 6.1-14.2 ha, 17.4% in woodlots 16.2-32.4 ha, and 23.6% in woodlots larger than 32.4 ha. There was a close relationship between the effects of forest size and the seral stage. It was most common in the most mesic forests regardless of the size class. It appeared in xeric stands only if they were large or in smaller stands only if they were mesic. It was responding simultaneously to patch size and moisture regime. Small woodlots appeared to present more pioneer conditions to birds than larger woods of a similar seral stage. Insect density on foliage may have been greater in the moister stands because the main foliage gleaners were more common in these stands.

At the forest patch scale, the Cerulean Warbler is selective in the forest types that it inhabits. In Ontario, the primary habitat components are that the woodland must be deciduous, although it tolerates scattered white pine and hemlock are tolerated. The forest must be dominated by late-successional tree species such as sugar maple and oaks; and it must contain large, tall trees such as sugar maple, oak, and elm. Old-growth forest is not essential, but mature woods that are more than 80 years old are required for successful breeding. It may breed in riparian forests that range from wet to dry, in swamps dominated by maples or oaks, and in upland forests dominated by either maples or oaks or a mixture of these. Large forest patches dominated by early successional tree species or those that do not contain large trees are usually unoccupied (Austen et al. 1994; Oliarnyk 1995; Savignac 2010b).

In the core of its range, the Cerulean Warbler prefers mature deciduous bottomland forests. These forests are dominated by species such as hackberry, sycamore, black walnut, green ash, bur oak, silver maple, tulip tree, elms, and Manitoba maple. It has been suggested that its occurrence in floodplain forests may be an artifact because many of the potentially suitable upland forests have been destroyed. In North Carolina and Kentucky, it selected floodplain forests and avoided upland forests. In many areas, it nests in upland forests dominated by oak-hickory, sugar maple–beech, and occasionally black locust–black cherry. It highly prefers ridgetops in mountainous areas and slopes facing north or east. To be suitable, woodlands must be a minimum of 21 m tall and support some taller, large-diameter trees. Along rivers in Missouri, presence of tall sycamores was a significant predictor of presence of the Cerulean Warbler. Floodplain forests in North Carolina that are even-aged and support no old-growth trees support few, if any, breeding pairs. Habitat requirements at the forest level include a closed canopy (usually greater than 85% but as low as 65%), but often with gaps; presence of scattered, very tall (24-30 m) old-growth canopy trees; and varied vegetation strata with a distinct zonation of canopy, subcanopy, shrub, and ground-cover layers. Woodlands that it occupies tend to have large, well-spaced trees, a moderately complex canopy structure, small canopy gaps, an open understorey with few saplings or shrubs, and almost complete coverage by ground flora. There are some exceptions: it has nested in black locusts in regenerating old fields; in an old field overgrown with sumac, blackberry, and black gum; areas with a large proportion of pines in the canopy; and in 15-18-year-old clear-cuts that were 10-12 m tall with a closed canopy (Bannon and Robert in Gauthier and Aubry 1996; Bent 1953; Bond 1957; Boves et al. 2013; Buehler et al. 2020; Carpenter et al. 2011; Chapman 1907; Graber et al. 1983; Hamel 2000; Hamel et al. 2004; Hands et al. 1989d; Hartman et al. 2009; Linehan 1973; Mossman 1988; Mossman and Hoffman 1989; Noon et al. 1979; Register and Islam 2008; Robbins et al. 1992, 1998; Rogers 2006; Samson 1979; Savignac 2010b; Schukman 1996; Temple et al. 1979; Wood et al. 2005, 2006).

Habitat within territories is often different from that of the occupied woodland. Several studies on this level of habitat selection have been conducted in eastern Ontario. Territories are usually characterized by well-spaced large trees with high canopies and dense foliage cover in the upper mid-canopy and canopy. The Cerulean Warbler tends to avoid areas of dense understorey. Territories had significantly higher mean basal area (BA) (0.23 m^2 compared with 0.17 m^2), higher BA per stem (0.02 m^2 compared with 0.01 m^2), and higher foliage cover at 12-18 m from the ground (4.4-4.5 compared with 3.0) than unoccupied sites within the same forest. There was a tendency for territories to have higher maximum tree heights (15.7-17.3 m compared with 13.3 m) and fewer

saplings (38.9-42.5 compared with 50.2; Barg et al. 2003; Jones and Robertson 2001). The detailed work on territory selection in Ontario is very important because other authors have observed that data collected in 1 area may not be representative of conditions throughout the Cerulean Warbler's range. A single range-wide management strategy for this species may not be effective in stabilizing or enhancing populations. In most cases, territories are characterized by larger diameter trees than are present in unoccupied areas of the same woodland, but in at least 1 case the opposite was true. Canopy height is typically taller in territories, but not always. Basal area of deciduous trees is usually higher in territories than in unoccupied areas. Results from Alabama are typical for the species. Compared with unused habitats, territories had significantly fewer trees 3 cm or smaller diameter at breast height (DBH) (840.4 compared with 1,305.3 per ha); higher ratio of BA to the number of stems (0.04 compared with 0.03); greater percent BA by deciduous trees (100.0 compared with 96.2%); taller lower, middle, and upper canopy heights (5.8 m compared with 5.2 m, 17.0 m compared with 15.5 m, and 29.4 m compared with 26.2 m, respectively); greater canopy cover (90.0% compared with 82.5%); larger diameter trees (22.0 cm compared with 13.5 cm), and larger canopy gaps (31-40 m^2 compared with 10-20 m^2). Much of the variability in territorial habitat occurs in the Appalachians. This variability suggests that habitat selection by the male may be quite plastic and may be affected by landscape characteristics. In the least-forested landscapes (74-75% forested), males selected areas with greater BA and greater canopy cover, features normally associated with closed-canopy, undisturbed mature forests. Where the surrounding forest cover was greater, it selected territories with lower BA, greater understorey cover, and closer proximity to canopy gaps. Presence of canopy gaps appears to be an important habitat component, particularly in extensively forested landscapes. They may be of lesser importance in forest fragments. Some analyses determined that presence of small snags is important, possibly because these create gaps in the canopy. In the Appalachians, it strongly selected ridges for territories and presence of slopes was also important. Territories tended to be on slopes facing north and east; these support the most productive forests. In the Appalachians, territories supported more sugar maple and the red oak group of species. It avoided red maple, chestnut oak, and ash (Boves et al. 2013; Buehler et al. 2020; Carpenter et al. 2011; Robbins et al. 1992; Roth and Islam 2008; Weakland and Wood 2005; Wood et al. 2006). In the Cumberland Mountains of Tennessee, males selected locations with less average solar exposure (based on elevation), greater distance to streams, higher elevations, and sites that occurred more on ridge tops, upper slopes, and on steeper slopes than what was available on average. More than 90% of territories were in mature deciduous forests, but this habitat represented only 50.7% of the study area. No selection was made for terrain moisture (Buehler et al. 2006). In Arkansas, it preferred forests with larger trees averaging 40 cm DBH. These trees were significantly larger than those in males' territories (35 cm DBH) and at random sites (32 cm DBH). Males preferred areas closer to canopy gaps characterized by greater BA and understorey cover (Wessels and Boves 2021).

In eastern Ontario, males have distinct areas of high use in territories called the core. These are vegetatively and structurally different from the rest of the territory, and are used predominantly for singing. Compared with the remainder of the territory, core areas were characterized by lower stem densities and higher average canopy heights. Territories of all males examined were dominated by sugar maple (38-63% coverage), but core areas of 6 of 7 males were dominated by species other than sugar maple: 4 by bitternut hickory, 1 by white ash, and 1 by hophornbeam. At the territory

scale, the Cerulean Warbler used canopy trees in proportion to their availability, but core areas contained more bitternut hickory and oak than the remainder of the territory. The 5 most commonly used trees for singing posts were: sugar maple, 36.5%; bitternut hickory, 30.0%; white oak, 12.1%; oaks, 8.1%; and white elm, 5.7%. Song post densities were 9 times greater in core than noncore areas (303.9 compared with 34.0 song posts per ha). In noncore areas, males predominantly used sugar maple (34.4% of observations); bitternut hickory was used most often in core areas (36.8% of observations). Distance between the core area centre to the nearest canopy gap averaged 12.2 m compared with 13.6 m for random sites within the territory. Only 3 of 14 core areas encompassed a gap. Bitternut hickory was highly selected, representing 45% of all song posts but only 9% of available trees. This tree's distribution was not clustered so this was not the reason for territory clustering. Males appeared to select tree species for song posts that have delayed leaf-out in spring. Bitternut hickory and white ash (the second-most used species) were late to leaf out and had less leaf cover than the other species. Males with less densely foliaged song perches will both send and receive clearer song messages. When a male failed to return the subsequent year, the new male tended to use the same song perches. It selected tree species at random for nesting, but highly selected hickories for singing perches. Bitternut hickories support significantly more arthropods in their canopies than other species. No core areas contained a nest, but they were located significantly closer to the within-territory nest than to neighbour's nests. Because core areas are close to the nest, they may be advantageous to nest defence (Barg et al. 2003, 2006a).

Studies in other areas confirmed significant differences between core areas and entire territories, and the preferences for hickories or other species or features that maximize song projection. In West Virginia, gap densities were 3 times higher in core areas than in entire territories. Seventy percent of all observations occurred in the lower and mid-canopy strata; males were rarely detected in the understorey. The upper canopy was used more frequently than expected for singing and less than expected for foraging, perching, and preening. The lower canopy was used more frequently than expected for perching and the mid-canopy was used more than expected for preening. Singing occurred more in the upper canopy than expected in core areas and less than expected outside core areas. Midstorey singing occurred more than expected outside core areas and less than expected in core areas. Singing locations in the upper canopy were associated with canopy gaps more than expected. Foraging occurred more frequently than expected in the midcanopy in core areas and less than expected in noncore areas. Males were associated with canopy gaps for 34% and 19% of observations at 2 sites. At 1 site, black cherry was used more in core than noncore areas; hickory was used more in core areas at the other site. Males foraged more than expected outside core areas and these areas were used predominantly for singing and opportunistic foraging in the midcanopy. The high use of canopy gaps may be due to higher insect prey in the openings but is more likely related to superior transmission of song in areas unimpeded by leaf cover (Wood and Perkins 2012). In Kentucky, potential indicators of singing posts, presumably within core areas, were large diameter trees, an east-facing aspect, and understorey density. Song perches averaged 54 cm DBH compared with 40 cm DBH for random trees. This supports the hypothesis that the size of song-perch trees relative to other trees in the stand is important. More than 85% of Cerulean Warblers and 95% of song perches were on east-facing slopes that coincided with more mesic and protected sites that allowed birds to take advantage of the morning sun while avoiding midday heat stress

(Hartman et al. 2009). In Illinois, the Cerulean Warbler had definite preferences for tree species. Species used more than expected given their availability, from greatest to least preferred, included shellbark hickory, bitternut hickory, silver maple, green ash, overcup oak, sweet gum, black gum, and sycamore. Species used less than expected included silver maple, blue beech, pumpkin ash, Shumard oak, swamp chestnut oak, bald cypress, cherrybark oak, pin oak, and white elm. The 2 hickories were strongly preferred, as in Ontario, but were only 11th and 19th in tree species abundance (Gabbe et al. 2002). In Missouri, 1 study observed it 70% of the time in pecan (a type of hickory), and 15% of the time in sycamore. Other studies have found it strongly associated with sycamore (Ball 1948; Robbins et al. 1998; Schukman 1996). Sycamores are typically tall supercanopy trees that would offer ideal perches for broadcasting songs. Throughout the Cerulean Warbler's range, hickories and oaks in the white oak group appear to be preferred for foraging and song posts. It avoids red maple and oaks in the red oak group (Buehler et al. 2020).

Studies in eastern Ontario demonstrated that habitat at Cerulean Warbler nest patches and nest sites differed from each other and from other areas within the territory. Nest patches consisted of 5 5-m radius circles with 1 at the nest and 4 11.4 m away in cardinal directions. There were 2 significant differences between nest patches and random sites, with nest patches having fewer trees and a higher BA per stem. There were 3 significant differences between nest sites and other locations within the territory. Nest sites had more foliage cover 12-18 m from ground, more foliage cover above 18 m, and taller and fewer trees. There were 5 significant differences between nest sites and random sites. Nest sites had a higher BA, higher BA to stem ratio, more foliage cover at 12-18 m, less foliage cover above 18 m, and taller trees. There were no significant differences between nest sites and nest patches, but there were 3 suggestive differences. Nest patches tended to have fewer trees, more foliage cover above 18 m, and taller trees than nest sites. The small differences between nest sites and other areas within the territory suggested that important nest-patch and nest-site decisions were made by the male when selecting the territory, thereby maximizing the probability that a female would settle on the territory (Jones and Robertson 2001). Females may choose nest sites outside but close to the male's core area allowing the male to be vigilant over the nest while advertising (Barg et al. 2006a). Boves et al. (2013) examined habitat within nest patches within the Appalachians. Nest patches had taller canopies than other areas within the territory at 2 sites and lower canopies at another 2 sites. Females consistently selected nest sites characterized by fewer but larger-diameter trees with a high amount of understorey cover and low amount of midstorey cover. Overall habitat characteristics at all sites for nest sites compared with territories included: lower average DBH in nest patches, lower BA at nest patches, higher percent understorey cover in nest patches, lower midstorey canopy cover, and greater distance to a canopy gap in nest patches. At the nest-patch level, sugar maple was avoided at 1 site, tulip tree was preferred at 2 sites, and white oak was preferred at 1 site. At the nest-site level, preferred species were cucumber tree at 1 site, sugar maple at 1 site, tulip tree at 1 site, and white oak at 4 sites. Black cherry was avoided at 1 site, hickory at 1 site, and the red oak group at 3 sites. Across all study areas, females consistently selected nest patches with large, well-spaced trees, increased understorey cover, decreased midstorey cover, a high proportion of white oak, and a low proportion of sugar maple. These areas were usually within or near edges of small-scale canopy disruptions in mature forest. Sugar maple was avoided at the nest-patch scale but preferred at the territory and nest-tree scales. Differences in

preferences for the different species of maple and oak may be related to differences in bark or foliage structure that may influence insect availability or suitability for nest attachment or concealment. Nest-patch selection by females was more consistent than territory selection by the male.

In West Virginia, Wood et al. (2006) examined the effects of edge on the Cerulean Warbler. The study area consisted of large patches of second-growth oak-hickory forests surrounded by extensive grasslands. The remaining forests had also been subjected to periodic disturbances such as natural canopy gaps, old timber harvests, jeep and all-terrain vehicle trails, and utility rights-of-way. There was an abrupt change from mature forest to reclaimed grassland and edge shape was convoluted, resulting in a high edge-to-area ratio. Occurrence of the Cerulean Warbler did not vary with distance from edge suggesting a degree of tolerance to edge. Territory density and abundance increased significantly from edge leading the authors to speculate that habitat near the edge was less suitable for breeding. They were not able to test this hypothesis. Effects on abundance of the Cerulean Warbler extended 340 m from edge. In the same area, Weakland and Wood (2005) found that territory placement in relation to the closest edge type differed from the expected distribution. Fewer territories than expected were adjacent to streams and valleys filled with mine waste and more than expected were adjacent to roads with open or semi-open canopies. The proportion of territories adjacent to natural gaps did not vary from availability with 63% of territories crossing either a road or trail. Distance to mine edge had no relation to territory density when all distances were plotted. When plots further than 400 m from edge were excluded from the analysis, density increased beyond 100 m of mine edge suggesting that edge effects extended about 100 m into the forest. Internal edges were not avoided and territorial placement was closer than expected to these. In both West Virginia studies, the Cerulean Warbler did not avoid hard edges but had lower densities near edge suggesting that edge habitat may be inferior. In another West Virginia study, Perkins and Wood (2014) examined selection of forest canopy gaps by males. One study area supported only gaps created by fallen trees. The other also had gaps created by a trail and 3 wildlife openings 0.17-0.32 ha. Gap densities were greater within core areas than in territories or random plots. The size of gaps that intersected territories ranged from 12 to 3,163 m^2, but 86% of gaps were less than 500 m^2. Small gaps in the 50-100 m^2 range occurred more frequently within territories and less frequently on the periphery of territories. The largest gap-size class (larger than 300 m^2) occurred more frequently than expected on peripheries and less frequently in territories. The most common type of gap within territories was created by tree falls, representing 68% of gaps within territories. Trail and wildlife gaps occurred only on the periphery of territories. Tree-fall gaps occurred more than expected within territories and less than expected in the periphery of territories. Trail gaps were often used as territorial boundaries. A 4-year study at Vanessa Swamp determined that the Cerulean Warbler was most abundant on plots 120 and 180 m from edge, although a few were recorded on edges and 60 m from edge. A county road bisects this swamp and it was common along the road in the centre of the swamp but not at its edges. The centre of the swamp was characterized by very tall trees with canopies that overhung the road, with only about a 5-m gap between the treetops on each side. The main area inhabited by this warbler consisted of tall, well-spaced sugar maples and oaks. Single-tree selection occurred during the study, and this had no effect on the number of Cerulean Warblers present. Habitat around the agricultural edges of the forest consisted of shorter trees with greater coverage by shrubs and saplings (personal observation). It appears as though the

Cerulean Warbler does not actively avoid edges but that habitat conditions are often superior distant from edges.

Ontario nests were in medium to large deciduous trees, including maples, oaks, elms, basswood, American chestnut, and bitternut hickory. In 1 eastern Ontario study, 66.7% of nests were in maples, 11.1% were in bur oak, 7.4% were in white oak, and 3.7% were in each of red oak, hophornbeam, bitternut hickory, and elm. Another study in the same area determined that 56.3% of nests were in maples, 16.9% were in elms, and 18.3% were in bitternut hickory. Nests near and west of London were mostly in basswood and elms. There appeared to be no selection for nest-tree species, although the high number in bitternut hickory reported by 1 study suggests that this may be a preferred nest tree. In eastern Ontario, 70% of nests were within 10 m of a territorial boundary and 59% were within 30 m of a canopy gap compared with 23% of random sites. Most nests were in contiguous forest and only 1 nest occurred near a gap between differing adjacent habitats. At this site, the most commonly used nest trees (maples and oaks) were those with the greatest overall BA. In eastern Ontario, the average DBH of nest trees was 40.2 cm (range 11.2-49.8 cm). Average nest height was 11.8 m (range 7.0-18.6 cm), and overall heights in the province range from 4.6 to 19.8 m, with most 8.8-13.1 m from the ground. Seventy-one percent of nests were in the lower canopy of trees, 59% had no other vegetation between the nest and ground, and 77% were on the outer edge of a lateral branch. Distance of nests from the trunk averaged 3.62 m (range 0-4.69 m), but some Ontario nests were as far as 6 m from the tree trunk. The nest resembles a knot and is saddled on a horizontal branch 1.3-5 cm in diameter. The nest is a very shallow cup attached to the limb by nest fibres; often the nest is simply saddled on the branch but it may also be supported by a small twig. Materials from the first nest are used to build replacement nests. Cerulean Warblers may also take nesting materials from neighbours' nests and from other species' nests. In eastern Ontario, Cerulean Warblers stole nesting materials from nests of the Red-winged Vireo and Blue-gray Gnatcatcher (Jones and Robertson 2001; K.C. Jones et al. 2007; Oliarnyk and Robertson 1996a; Peck and James 1987, 1998a; Saunders 1900; Savignac 2010b).

Throughout its range, the Cerulean Warbler nests in the canopy of tall deciduous trees. In addition to the nest-tree species used in Ontario, it has nested in sycamore, cottonwood, shagbark hickory, Osage orange, white ash, cucumber tree, black walnut, black cherry, tulip tree, black locust, black oak, red oak, and white pine. It appears to select the largest available trees for nesting. In some areas, there appear to be no preferences for nest-tree species, but sycamore, white elm, cucumber tree, white oak, and sugar maple have been selected in some areas. Sugar maple may be preferred for nesting because of its early leaf-out and thick foliage, and areas dominated by this species tend to have suppressed midstorey vegetation. In certain areas, it tends to avoid trees in the red oak group, red maple, and tulip tree as nest trees. Many nests are near a stream, a small artificial gap created by internal roads or selective harvest, or natural openings such as tree falls, snags, or small wetlands. One Delaware nest was only 5.2 m from the ground and overhung a busy road and parking lot. Nests have been reported at heights of 4.5-30 m, but mostly higher than 10 m. Average nest height in Indiana was 18 m. Similar to Ontario, nests are on a horizontal branch in the mid- to upper canopy concealed from above by leaves or Virginia creeper vines. One Michigan nest was completely encircled by Virginia creeper. Nests are characteristically over an open space that may be as small as 1 m between the nest branch and a lower branch of the same tree. More frequently,

the open space is 5-20 m from the nest to tops of trees below the nest branch, to shrubs below the tree, or to the herbaceous layer or bare ground. When leaving the nest, the female drops vertically before flying away horizontally, so the open space below the nest accommodates this behaviour (Bent 1953; Boves et al. 2013; Buehler et al. 2020; Chapman 1907; Graber et al. 1983; Hamel 2000; Hands et al. 1989d; Harrison 1984; Linehan 1973; Nemes et al. 2005; Rogers 2006; Roth and Islam 2008; Wagner and Islam 2014; Weakland and Wood 2005).

The Cerulean Warbler is aggressively territorial. Males may attack each other at heights of 20 m or more and flutter to the ground while grappling with each other. Females are equally aggressive. Male territorial boundaries shift considerably prior to the arrival of females. Territorial boundaries broke down in eastern Ontario in mid- to late July. If a pair has a successful first nest, the maximum time that a territory is held is 22 days. Despite the aggressiveness of the birds, territories appear to be clumped and areas of apparently suitable habitat are unoccupied. In eastern Ontario, territories may either be aggregated or cover most of an area with boundaries of several territories abutting each other. In Missouri and Arkansas, territories are arranged linearly where riparian forests are narrow but are more densely packed in broader floodplain forests. In Indiana, territories were clustered on 3 plots, regularly spaced on 1 plot, and randomly located in another plot. Territories were clustered in areas with significantly more vertical stratification and a greater number of smaller trees. Clusters of territories in West Virginia were also associated with numbers of small trees. It is possible that the Cerulean Warbler clusters territories in areas of forest with large amounts of foliage where there would be greater food availability. Territories also tended to be near streams and ravines in areas with more slope. Habitat selection therefore plays a role in aggregation of territories but clustering occurred even in areas of uniform high quality habitat. This suggests that social factors may also be involved in territorial clustering, such as settling where a neighbour could be heard. Presence of other singing birds may signal high reproductive success potential because birds that fail to raise young in 1 year seldom return the subsequent year. Another potential reason for clustering is to facilitate extra-pair copulations (Barg et al. 2003, 2005; Buehler et al. 2020; Hamel 2000; McCracken 1993; Oliarnyk and Robertson 1996a; Robbins et al. 2009; Roth and Islam 2007; Weakland and Wood 2005).

Several estimates of territory size are available from eastern Ontario. Oliarnyk and Robertson (1996a) reported that territories averaged 1.04 ha (range 0.38-2.4 ha). Jones et al. (2001) reported average territory sizes of 0.74 ha in 1996 and 0.63 ha in 1997, 2 years prior to a severe ice storm, 0.57 ha in 1998 during the first breeding season after the ice storm, and 1.17 ha in 1999. There were no significant correlations between territory size and the amount of storm damage in either poststorm year. Territory size does not appear to be directly related to pair density. Using minimum convex polygon estimates, eastern Ontario territories averaged 0.96 ha (range 0.23-2.21 ha). The kernel (or core) territory size averaged 0.70 ha (range 0.12-2.35 ha). Overall, territory sizes of 0.1-2.4 ha have been documented in eastern Ontario. Males occasionally made long direct flights without song or other territorial behaviour. These were probably extra-territorial forays, possibly to seek extra-pair copulations (Barg et al. 2003, 2005). Average territory sizes reported elsewhere include 0.9 ha in Missouri, 0.21 ha in Indiana, 0.31 ha in West Virginia, 1.14 ha in Arkansas, and 0.45 ha in Tennessee. In another West Virginia study, territory size averaged 0.30-0.42 ha and core areas averaged 345-680 m^2 (Buehler et al. 2020; Perkins and Wood 2014; Robbins et al. 2009; Wessels and Boves 2021).

Limited information is available on natal philopatry. Three of 20 (15%) nestlings banded at Lake Opinicon returned in subsequent years. Long-distance dispersal of juveniles may occur in eastern North America. Three of 32 nestlings (9.4%) subsequently bred in a Bird Conservation Region other than their natal area. Some breeding birds in eastern Ontario hatched in Illinois and Arkansas (Girvan et al. 2007; Savignac 2010b).

Earlier workers assumed that adult site fidelity was high and this led to the conclusion that mortality rates were higher than they actually are, suggesting that most populations were not replacing themselves with their annual recruitment rate. The misinterpretation resulted from the fact that certain birds returning to a given area may exhibit high site tenacity, with certain individuals nesting in the same territory for as many as 7 breeding seasons. Adult males may disperse widely between breeding seasons, which contributes to underestimates of survivorship. In some areas, breeding success effects return rates with failed breeders seldom returning. In other areas, breeding success appears to have no effect on return rates. At Lake Opinicon, an attempt was made to band all males, but each year 40-70% of the older breeding males were unbanded. These birds may represent local recruitment and only a few of these were long-distance immigrants. In eastern Ontario, only 1 adult male was recorded moving more than 500 m between breeding seasons over a period of 7 years. In the Appalachians, site fidelity was very low, with fewer than 20% of males returning to their former breeding territories. In Arkansas, 26% of adults returned. Four males returned to the same territory; 2 shifted their territories a few hundred metres. One returning female nested 6.64 km from her previous year's nest (Wessels and Boves 2021). In Michigan, 74% of returning males chose territories within 500 m of the previous year's territory. Seven males moved a mean of 1.7 km (range 1.1-2.2 km) between nesting seasons. Long-range movements of adult males also occur as determined by stable hydrogen isotopes, with as many as 28% dispersing long distances between breeding seasons. Populations varied in the number of immigrants they received, from 4% in Ontario to 38% in West Virginia. The eastern Ontario population may be acting as a source to United States populations (Barg et al. 2005; Boves et al. 2013; Buehler et al. 2020; Girvan et al. 2007; Jones and Islam 2023; Jones et al. 2004, 2008; Rogers 2013; Roth and Islam 2007). In Pennsylvania, Arkansas, and Missouri, return rates of birds fitted with geolocators were 16% compared with 35% for birds without geolocators (Raybuck et al. 2017).

Limiting Factors

Egg dates for nests reported to the Ontario Nest Records Scheme (ONRS) ranged from the last week of May until the end of June, with most eggs present in the first half of June (Peck and James 1998a). In eastern Ontario, initiation of nest construction for first nests was 18-24 May; replacement nests were initiated from 31 May to 4 June. The extreme dates for incubation were 30 May to 23 June and fledging typically occurs in the first week of July (Oliarnyk and Robertson 1996a; Savignac 2010b).

Pair formation commences shortly after females arrive and nest-site selection and initiation of nest construction occurs 1-2 days after the females arrive. Nests may take 3 to more than 8 days to build, with first nests typically taking 4-6 days to complete. Nest building may be expedited if the female gathers material from an old nest or steals material from another species' nest. Nest building may be prolonged if other species rob material from the nest while it is being built. No information is available on whether there is a gap between nest completion and initiation of egg laying.

Presumably, eggs are laid at the rate of 1 a day. Incubation takes 10-13 days in Ontario, most frequently 11-12 days (mean 11.4 days). The nestling period is typically 10-11 days, but young may leave the nest at age 7-9 days if they are disturbed (Barg et al. 2005, 2006b; Buehler et al. 2020; Graber et al. 1983; Hamel 2000; Hands et al. 1989d; Jones et al. 2007; Oliarnyk and Robertson 1996a; Peck and James 1998a; Wagner and Islam 2014).

One brood is typically raised per breeding season. The only record of a second brood is from eastern Ontario and it occurred under unusual circumstances. The female was the secondary female of a bigamous male who provided very little care to her brood. She moved her fledglings 800 m (4 territory widths) and remated with a different male. This male adopted her fledglings, the only known case of brood adoption by this species, while she laid a second clutch. The Cerulean Warbler readily renests if a clutch is lost and may make as many as 3 attempts to fledge young. Nests reported to the ONRS had clutches of 3-5 eggs (mostly 3 or 4 eggs, average 3.69). In eastern Ontario clutches contained 2-5 eggs with most clutches containing 5 eggs (average 3.8 eggs). Throughout its range, the clutch size is 3-5 eggs with 4 eggs most frequent. Mean clutch sizes reported elsewhere include 5.00 in Illinois, 4.33 in Michigan, 3.58 in New York, 3.82 in Pennsylvania, and 3.78 range-wide (Barg et al. 2003, 2006b; Bent 1953; Buehler et al. 2020; Graber et al. 1983; Hamel 2000; Oliarnyk and Robertson 1996a; Peck and James 1998a; Savignac 2010b).

The mating system is typically monogamous, but 10% of Ontario males and 7% of Tennessee males were bigamous. The pair bond is maintained for the duration of the breeding season, even when renesting occurs. Both sexes are capable of breeding at age 1 year. Some populations contain unmated males that are presumably yearlings. Unpaired males comprised 20.5% of a Missouri population, 38.7% of an Indiana population, and 35% in another Indiana population. These numbers probably represent maxima as some females may not have been detected in these studies. Once a bird breeds, it typically does so for the remainder of its life. Northern populations may be dominated by adult males. Only 15% of Ontario breeding males were yearlings and 10-20% of Michigan birds were yearlings. Extra-pair copulations may be common, but this has not been studied extensively. In eastern Ontario, extra-pair copulations were observed and blood samples from 2 families revealed that 4 of 7 young were sired by a male other than the social male (Barg et al. 2005, 2006b; Buehler et al. 2020; McKillip and Islam 2009; Robbins et al. 2009; Rogers 2006).

Foraging occurs in the canopy of tall trees. In eastern Ontario, males foraged significantly lower than where they sang (12.8 m compared with 15.0 m). Singing and foraging both occurred within the canopy at 83.9% and 71.9% of the tree height. In Arkansas and Tennessee, average perching and foraging height was 15 m in trees averaging 22 m (68.2% of tree height). In Ohio, males foraged at an average height of 16.9 m (76% of tree height); females foraged at 14.4 m (72% of tree height). The Cerulean Warbler has been documented foraging at heights of 2 m to more than 45 m, but mostly in the lower to midcanopy, particularly in dense foliage. Males forage in larger trees in higher canopy positions than females. In Indiana, males foraged at an average height of 19.2 m compared with 16.9 m for females. Females in the Mississippi River valley often foraged extensively in poison ivy vines that encircled the bole of canopy trees, working in a spiral around the tree trunk. In Illinois, it preferred hickories, silver maple, green ash, black gum, and sycamore for foraging. It used red maple, blue beech, pumpkin ash, white elm, and oaks in the red oak group significantly less than

their availability. In Ohio, males foraged in hickories 27% more than expected, but were not observed foraging in black oak. White oak and tulip tree were used in proportion to their availability. Hickory trees supported twice the number of greenish-coloured caterpillars as oaks. Most foraging occurs by hopping along twigs peering at the upper and lower surfaces of leaves, petioles, and twigs and gleaning insects from these surfaces. It may infrequently capture prey by hovering or sallying. In West Virginia, males leaf-picked 73.3% of the time, wood-picked 19.3% of the time, sally-gleaned 6.8% of the time, and aerially hawked less than 1% of the time (Barg et al. 2006a; Buehler et al. 2020; Gabbe et al. 2002; Hands et al. 1989d; Newell et al. 2014).

In eastern Ontario, 35% of males fed incubating females, mostly caterpillars. Nestlings are fed mostly caterpillars, but also adult lepidopterans, crane flies, smaller flies, beetle larvae, and spiders. In Ohio, adults fed nestlings predominantly greenish caterpillars, accounting for 69% of prey items. Other food provided to young included 12% caterpillars with darkish colouration, and 19% winged insects. Adults brought large prey that extended beyond the bill on 56% of deliveries. In Indiana, young were fed predominantly green-coloured caterpillars. These constituted 53% of nestling food items; caterpillars represented only 14% of potentially available prey. The nestling diet was comprised of 83% caterpillars in the early part of the season during the peak nestling period. The proportion of caterpillars in the nestling diet decreased with the season, and was 80% less for the last nest of the season compared with the first nest. Caterpillars of prominent and owlet moths dominated the diet. Nestlings were also fed flies, adult lepidopterans, harvestmen, spiders, true bugs, hymenopterans, beetles, and walkingsticks. Most flies fed to young were crane flies. The mean length of prey provided to nestlings (14.7 mm) was significantly longer than the mean length of prey on branches (6.1 mm). Adults are predominantly insectivorous during the breeding season, but also eat some spiders. Four Alabama stomachs contained 42% hymenopterans by frequency, 35% lepidopterans, and 23% beetles, including weevils. In West Virginia during a gypsy moth outbreak, 14 adults consumed 52% soft-winged bugs by volume, 37% lepidopterans (mostly caterpillars), 7% beetles, and small amounts of hymenopterans, flies, true bugs, spiders, and other arthropods. Diet was investigated at a site that was treated with diflubenzuron, an insecticide that interferes with moulting of larval insects. Birds in control plots ate 2 times more lepidopterans than soft-winged bugs. Those in treatment plots ate 3 times more soft-winged bugs than lepidopterans. Prior to and a month after treatment, more lepidopterans than bugs were consumed (Auer et al. 2016; Barg et al. 2003, 2006b; Buehler et al. 2020; Hands et al. 1989d; Newell et al. 2014).

Cowbird parasitism rates of the Cerulean Warbler are almost zero in extensively forested landscapes and moderate in agricultural landscapes. Peck and James (1987) reported that 7 of 39 Ontario nests (17.9%) were parasitized, and all these nests were from the agricultural southwest. Peck and James (1998a) reported 8 of 57 nests (14.0%) parasitized, and this sample included a mix of nests from the southwestern and eastern portions of the province. Nest parasitism is rare in the Kingston area. From 1994 to 2006, cowbird eggs were found in only 2 Cerulean Warbler nests; both were abandoned. No cowbirds fledged from eastern Ontario nests out of a few hundred nests (Barg et al. 2003, 2006a; Oliarnyk 1995; Oliarnyk and Robertson 1996a, 1996b). Similar results have been reported from elsewhere. Parasitism rates in Indiana were 0% in extensive forest and 15.4% elsewhere, very low at 1 Michigan site and 25% at another. In the Cumberland Mountains of Tennessee, 1 of 52 nests (1.9%) was parasitized and 9 of 66 nests (13.6%) were parasitized in the

Mississippi Alluvial Valley. In Illinois, no parasitized nests were found (Buehler et al. 2008, 2020; Graber et al. 1983; Hamel 2000; Rogers 2006; Roth and Islam 2008; Savignac 2010b). Some authors stated that cowbird parasitism posed a potential significant threat to the Cerulean Warbler. Parasitism is more prevalent where human activities have fragmented forests. The actual impacts of parasitism on the Cerulean Warbler require additional study. In Michigan, the effects of parasitism were considered low, with few nests parasitized whereas more than 60% of Hooded Warbler nests were parasitized. The Cerulean Warbler appeared to be a poor host for the cowbird in this region (Buehler et al. 2020; McCracken 1993; Robbins et al. 1992; Rogers 2006).

Habitat loss is the greatest threat to the Cerulean Warbler. The extensive deforestation associated with European settlement undoubtedly resulted in the loss of habitat in southwestern Ontario. More recently, the amount of forest cover in the province has increased due to abandonment of former agricultural land. The more recent forest cover may not be suitable habitat because it often occurs in small patches, has inappropriate tree species composition, or is too immature. Most of the gains in forest cover have been due to creation of coniferous plantations which are unsuitable habitat. Most large forest patches that support the Cerulean Warbler are protected from development, but there is no protection from agricultural activities. With the current high value of row crops, there is an increasing tendency to attempt to farm marginal land and this is resulting in some loss of habitat. In the core of its range, a high proportion of upland forests in the Mississippi Alluvial Valley have been eradicated and there has been serious encroachment into floodplain forests. In the Appalachian Mountains, ridgetop mining has resulted in the loss of thousands of hectares of prime habitat. In several states, the Cerulean Warbler was once the most abundant warbler species and it is now rare and declining in many of these states (Barg et al. 2003; Brett 2011; Buehler et al. 2020; Hamel 2000; Hamel et al. 2004; Hands et al. 1989d; McCracken 1993; Robbins et al. 1992; Savignac 2010b; Thogmartin et al. 2004; Weakland and Wood 2005).

Habitat fragmentation is another significant limiting factor to the Cerulean Warbler. Loss of woodlots that do not even support this species can have significant detrimental effects by reducing the amount of overall forest cover in the landscape. This may have the effect of increasing the minimum size threshold for forests. In the core of its range, it appears to be more restricted to large tracts now than it was from 1930 to 1960. The minimum forest size requirement is larger in the western portion of its range where forest coverage is less than in the east. Fragmentation of the landscape creates better habitat conditions for many nest predators and the Brown-headed Cowbird. Woodlands in fragmented habitats may not produce enough young to sustain populations without immigration. In West Virginia, density of the Cerulean Warbler was 6.6 times higher in contiguous forest than in forest fragments of similar habitat quality (Barg et al. 2003; Brett 2011; Buehler et al. 2020; Hamel 2000; Robbins et al. 1992; Savignac 2010b; Weakland and Wood 2005).

Human activities can degrade occupied habitat in a number of manners. Partial removal of a forest may drop it below the minimum threshold size, reduce territorial density, and improve habitat for predators and the cowbird. Drainage of swamps and mesic woods may make them less attractive to the Cerulean Warbler. Acid precipitation has been identified as a threat in some areas. This is unlikely to be an issue in southwestern Ontario where soils neutralize the effects of acid

precipitation, but it is a possible issue on the Frontenac Axis and the southern Canadian Shield. Forest harvesting and other forest management activities may have no apparent effects, possible benefits, or be very destructive to habitat depending upon the type and intensity of management. In eastern Ontario, the Cerulean Warbler population was robust in areas that were managed for sugar maple productivity. This activity appeared to have no effect nor did shelterwood cuts. In extensively forested areas, harvests that create small openings may be beneficial because it is attracted to gaps for nesting. In eastern Ontario, nest success was lower near canopy gaps than distant from them, so this may potentially be a form of ecological trap. Forest management that removes all mature and old-growth timber is detrimental and is considered responsible for the species' eradication in large areas of its core range. Short rotations that do not allow persistence of mature and supercanopy trees essentially render the habitat unsuitable. In southwestern Ontario, single-tree selection may be acceptable in large tracts if portions of the forest remain unharvested during each rotation. Cuts that include an entire tract and diameter-limit cuts have the potential to eradicate the species. For the most part, current forest management practices in southwestern Ontario are not conducive to maintaining Cerulean Warbler populations and there are few mature to old-growth stands remaining. Even in the Appalachians, timber harvest often results in lower daily nest survival rates and numbers of young fledged (Barg et al. 2003, 2006a; Boves et al. 2013; Brett 2011; Buehler et al. 2020; Hamel 2000; Jones and Robertson 2001; McCracken 1993; Robbins et al. 1992; Savignac 2010b; Wood et al. 2005).

Farwell et al. (2019) studied the effects of shale gas infrastructure (well pads, access roads, and pipelines) on the Cerulean Warbler in West Virginia. Initially, it occurred in least-developed areas of the forest but began to occur in greater abundance near pipelines and access roads as the development expanded. It increased closer to linear infrastructure but not well pads. Nonetheless, it still declined across the site by 34%. They considered it a forest-interior gap specialist. In West Virginia, Margeneau et al. (2019) determined that it was more abundant in intact than remnant forests associated with strip mines. Remnant forests were surrounded by strip mines on 3 sides but were not directly affected by them.

Severe weather events may significantly alter habitat and result in declines in the Cerulean Warbler or a decrease in productivity. A severe ice storm in eastern Ontario in 1998 affected approximately 60% of its habitat, reducing the canopy foliage structure; average cover was reduced by as much as 60%. Warblers nested in the same areas and same territories as in the previous year. The nest success rate declined from 75.7% in prestorm years to 8.9% in the breeding season after the storm, and the number of fledglings per nest fell from 2.0 to 0.4. The reason for the decline in productivity appeared to be related to a decline in insect availability. The following year, warblers expanded their territory sizes and shifted their locations and productivity increased. There was another severe ice storm in southern Ontario in December 2013 but it is uncertain what effects it had on Cerulean Warbler habitat and populations. It was observed regularly in the Montreal area in the 1960s and 1970s. A severe ice storm hit this area in the early 1980s and it has been seen only rarely since. A severe ice storm in Arkansas resulted in a significant decline in the population, to the point where it disappeared from the area where it was being studied. A large thunderstorm altered the forest structure in 1 location in Point Pelee National Park, and the Cerulean Warbler has not been

seen at that site since 1977 (Bannon and Robert in Gauthier and Aubry 1996; Barg et al. 2003; Brett 2011; Buehler et al. 2020; Hamel et al. 2004; Jones 2000; Jones et al. 2000a, 2001).

Certain key tree species for nesting and foraging for the Cerulean Warbler may be at risk due to disease or insects. The European oak borer has recently been discovered in Ontario and it may pose a threat given that oaks constitute about 50% of nest trees in certain areas. The potential effects of the emerald ash borer are unknown. Other potential threats in Ontario include the Asian longhorned beetle, gypsy moth, beech bark canker fungus, and forest tent caterpillar. In other areas, oak wilt, sycamore anthracnose, and Dutch elm disease have been identified as potential threats (Brett 2011; Hamel 2000; Robbins et al. 1992; Savignac 2010b).

Microhabitat features may affect reproductive success. In eastern Ontario, nests in areas with larger than average trees and denser foliage 6-12 m and higher than 18 m from ground were more likely to be successful. Nests near small canopy gaps and where there was a dense understorey were less likely to be successful. At 1 site in the Appalachians, white oak was a preferred nest tree species, but daily survival rates were significantly lower in these trees (Barg et al. 2006a; Boves et al. 2013; Hamel 2000; Jones and Robertson 2001; Oliarnyk and Robertson 1996b).

Habitat loss in migration areas in Central America and the wintering area in South America is a concern. The wintering area is increasingly being inhabited by humans and deforested for agriculture (Brett 2011; Hamel 2000; Savignac 2010b).

In Ontario, aggressive interactions between the Cerulean Warbler and the Least Flycatcher, Red-eyed Vireo, and American Redstart are common, and aggression has also been noted between the White-breasted Nuthatch and Cerulean Warbler. Most of these species are dominant to the Cerulean Warbler, but an Ontario study concluded that the frequency of aggression was too low to have detrimental effects. Aggression toward the Cerulean Warbler has been observed elsewhere by all these species except the nuthatch. In addition, aggression has been observed from the Blue-gray Gnatcatcher, Northern Parula, Hooded Warbler, Black-throated Blue Warbler, Black-throated Green Warbler, and Scarlet Tanager. The reasons for the aggressive interactions are unknown. The resource selection of these species may overlap or it may be related to nest-material kleptoparasitism (Barg et al. 2003; Buehler et al. 2020; Carpenter et al. 2011; Hamel 2000; K.C. Jones et al. 2007; Varey and Robertson 1997; Wood and Perkins 2012).

The eastern Ontario population experiences high nesting success and reproductive output, although annual productivity may vary considerably (Barg et al. 2003; Jones 2000; Jones and Robertson 1996; Oliarnyk 1995; Oliarnyk and Jones 1997; Oliarnyk and Robertson 1996a, 1996b). It was initially assumed that eastern Ontario and Tennessee were source populations, contributing birds to other areas within the Cerulean Warbler's range. Jones et al. (2004) conducted a demographic study on the eastern Ontario population and concluded that it may not be self-sustaining because of apparent high mortality rates during migration and winter. The calculated mortality rate was based on the premise that adults exhibited high site fidelity and that return rates were representative of survival rate. This was a reasonable assumption because this is generally the case for most passerines. These authors concluded that the outlook for the species was potentially grim, but acknowledged that they had no estimates of survivorship for females or juveniles. Several other studies were conducted on populations in the United States using the survival rates calculated

in Ontario, and all were deemed to be declining sink populations. Concerns were raised in both Canada and the United States that populations in their jurisdiction would decline due to lack of immigration from the other country. Only 1 Michigan study concluded that site-specific demographic information was required to determine if the local population was a source or a sink (Buehler et al. 2005; Rogers 2006, 2013; Savignac 2010b). Girvan et al. (2007) studied adult male dispersal patterns in Ontario and 4 states using stable hydrogen isotopes. They discovered that 28.2% of males nested in a location geographically distant from their capture site the previous year. This countered the earlier findings by Jones et al. (2004) that the Ontario population was not reproducing at replacement rates and was likely not a source population. Their study demonstrated that Jones et al. (2004) significantly underestimated adult male survival due to breeding dispersal. Consequently, the Ontario population is a source, and other populations in the United States may be as well. Another conclusion of the study by Girvan et al. (2007) was that the size of a given population was not a good indicator of population health or habitat quality.

DNA studies of birds from Ontario and many of the states confirmed that the entire population should be considered a single genetic population. A possible exception is the New England population which has not been studied. No genetic structure was observed in the population even between birds at the extreme northern and southern limits of the range. Lack of structure is related in part to ongoing gene flow with birds throughout having a 4% probability of being immigrants or descendents of immigrants. Most birds that were sampled were males and female dispersal rates tend to be higher than those of males, so dispersal rates may be higher than suggested by these data (Deane et al. 2013; Veit et al. 2005). The genetic study results support the conclusions of Girvan et al. (2007) that there is a high rate of dispersal among populations.

In Pennsylvania, Alabama, and Missouri, Raybuck et al. (2017) determined that fitting Cerulean Warblers with geolocators had no effect on breeding season survival, daily nest survival, or nestling provisioning rates. Birds with geolocators were less likely to return to their breeding grounds in the following year than control birds. Geolocators may cause one or more of the following: displacement from the previous year's territory, potentially due to later arrival on the breeding grounds or decreased aggression toward territorial intruders; reduced site fidelity; and decreased annual survival rates.

Price (2004) concluded that the breeding range of the Cerulean Warbler might expand in southern Ontario if the average summer temperature increased by 2°C.

Status

The historical status of the Cerulean Warbler is uncertain, with most of the uncertainty focused upon whether its original range included eastern Ontario. McIlwraith (1894) considered it a regular but local summer resident in southern Ontario, but provided no details on its range. Saunders (1900) considered it uncommon near London and noted that it was seldom observed in the Toronto area. Macoun and Macoun (1909) concurred, stating that it was common in southwestern Ontario, but not found much north of London. Baillie and Harrington (1937) stated that it bred only in southwestern Ontario in Chatham-Kent, Middlesex, Hamilton, Lambton, and Niagara Region, and that it was rather common in some locations. At that time, it occurred rarely in the Ottawa area and there was an indefinite nesting record for Leeds County. It is probable that the Cerulean Warbler

was more common in at least the Carolinian Forest Region prior to extensive deforestation by European settlers (Austen et al. 1994; McCracken 1993). There are some historical trends within this forest region, suggesting that it continued to decline after the original clearing. In Elgin County, it was a tolerably common summer resident in 1891; in 1954, it was considered a regular but not very common summer resident; and by 2000 only 3 woodlands supported the Cerulean Warbler (Lancaster et al. 2004). Curry (2006) recounted a bicycle trip undertaken by George North in the 1930s along Highway 3 from St. Thomas to Point Pelee when he estimated he heard more than 100 singing Cerulean Warblers. Former major breeding locations in the Hamilton area and their last known years of occupation were: Rock Chapel Woods, 1966; Westdale Ravine, 1969; Glen Morris, 1993; Six Nations, 1995; Caister-Canborough Slough Forests, 2001; and the Halton Region Forest, 1998. In Niagara Region, it was a rare and local breeder in the 1960s but, as of 2010, there had been only 1 confirmed breeding record in the past 24 years (Black and Roy 2010). The population in eastern Ontario increased recently. The first record for the Cerulean Warbler in the Kingston area was in 1928 and the next record was in 1950. It has been seen there annually since 1961 and the first nest was found in 1963 (Austen et al. 1994; Weir 2008). The first atlas documented a significant expansion of its known breeding range. It continued to occur in the Carolinian Forest Region, with notable concentrations in the Long Point area and in the lower Grand River watershed. A second northern band was occupied from the Bruce Peninsula along the southern edge of the Canadian Shield, with a high concentration on the Frontenac Axis north of Kingston, where there were an estimated 130 pairs. During the first atlas, 372-1,580 breeding pairs were estimated to occur in the province (Austen et al. 1994; Eagles in Cadman et al. 1987). James (1991) considered the Cerulean Warbler a rare to locally uncommon summer resident in the south, north to Bruce County and to northern Leeds and Grenville County.

There are 2 plausible explanations for the recent increase in population in eastern Ontario: the Cerulean Warbler was formerly present there, became very rare or extirpated with early deforestation, and returned when second-growth forests matured; or it has recently extended its range to include eastern Ontario. The latter explanation appears more likely despite the 2 records from eastern Ontario prior to the mid-1930s. It was not observed regularly in the Kingston area until 1961, an area with a very active naturalists' club. It is also unlikely that forest clearing by the settlers would have completely eradicated it. It was not eradicated in the Carolinian Forest Region where deforestation was probably more extensive. The entire expansion into the Great Lakes–St. Lawrence Forest Region in southern Ontario appears to be recent. Possibly most convincing is the fact that it has expanded its range northward and eastward over a widespread area. It was first reported in Quebec in 1950 and the population in the province expanded slightly eastward until 1960. There has been no recent change in range or numbers since then. This was considered to be a range extension from Ontario's eastern population rather than recolonization of historical range. In 1929, it was rare or accidental in New England and extremely rare east of the Appalachians. It has increased its range and abundance in Massachusetts, Connecticut, Rhode Island, Pennsylvania, and New York (Bannon and Robert in Gauthier and Aubry 1996; Barg et al. 2003; Buehler et al. 2020; Chapman 1907; McCracken 1993; Oliarnyk and Jones 1997; Oliarnyk and Robertson 1996a; Ouellet 1967; Robbins et al. 1992; Savignac 2010b). Buehler et al. (2020) concluded that the eastern Ontario population represented a range expansion rather than recolonization of an area where it formerly occurred.

The second atlas demonstrated that there had been no change in the distribution of the Cerulean Warbler since the first atlas. There was no evidence of a continued range expansion to the north or east. Its probability of observation decreased significantly in the Carolinian Forest Region and did not change significantly in other regions or province-wide, although all trends were negative. It was observed in 108 squares during the first atlas and 86 during the second. The number of squares it was observed in within the Carolinian Forest Region declined from 46 to 28 between atlases. The largest population continued to be in the Kingston area on the Frontenac Axis followed by the Long Point area. Densities of 5 or more pairs per atlas square were documented in these 2 locations as well as at Skunk's Misery, Pinery Provincial Park, and Awenda Provincial Park (Francis in Cadman et al. 2007).

The atlases suggest that the population in the Frontenac Axis is stable but the Carolinian population is declining. Approximately 20% of the Ontario population resides in the Carolinian Forest Region and a 47% proportional decline occurred in that area. This decline was significant at the 0.10 level and the data suggest a 16% decadal decline that is not significant. It was concluded that there was also a positive bias in the second atlas because participants were asked to look for it at known historical sites and disappearance from a single square would have involved more than 1 pair (Savignac 2010b). A possible negative bias in the atlas results is that only those species found within a square within the first 20 hours of atlassing were considered when comparing abundance between atlases. All squares where the Cerulean Warbler was documented after 20 hours would have been considered devoid of this warbler.

Additional population estimates were made since the attempt during the first atlas to estimate the size of the Ontario Cerulean Warbler population. The estimate provided by McCracken (1993) was 680-2,880 pairs. Population sizes in different areas ranged from a few pairs to 58 in Minesing Swamp near Barrie in 1974. Barg et al. (2003) reported the Canadian population, which includes a few in Quebec, at 500-1,000 pairs. The largest cluster was approximately 250 pairs in the Kingston area where the population has remained constant over the past 20 years. The largest clusters in southwestern Ontario consisted of 20-30 pairs and it was estimated that this entire area supported fewer than 100 pairs. After the second atlas, a targeted survey was completed for the Cerulean Warbler. This resulted in a more refined estimate of 408-493 pairs in Ontario. This included approximately 300 pairs on the Frontenac Axis and 80 pairs combined in Middlesex and Norfolk counties, Georgian Bay National Park, Awenda and Pinery Provincial Parks, and Minesing Swamp. It was estimated that the remainder of Ontario held no more than 50-150 pairs in scattered locations (Brett 2011; Savignac 2010b). Due to the differing survey methods used each time population estimates were made, the various estimates cannot be used to estimate trends. The results reported in 2010 were the most accurate surveys and also represent the most current knowledge.

The Committee on the Status of Endangered Wildlife in Canada has evaluated the Cerulean Warbler 3 times and a federal management plan and recovery strategy were prepared for it. It was initially designated special concern in 1993 and this status was confirmed in 2003. In 2010, its status was upgraded to endangered. In Ontario, it was also originally designated special concern and its status was upgraded to threatened. The objective of the 2010 management plan was to maintain the population at its current rate until 2015 (Barg et al. 2003; Brett 2011; McCracken 1993; Savignac

2010b). The 10-year objective of the recovery strategy was to halt the population decline. The 30-year objectives were to maintain a stable population of at least 1,000 mature individuals and to maintain its range, or where possible, increase its area of occupancy within its current range (Brett 2021).

The Breeding Bird Survey (BBS) determined that the Cerulean Warbler decreased in Ontario at annual rates of 2.22% 1970-2021 and 0.917% 2011-21. The trends were of low reliability (A.C. Smith et al. 2023). BBS data indicate that the Cerulean Warbler has declined rangewide at a rate of about 3% per year since 1966. This is one of the most precipitous declines recorded by this survey, with only 6 other passerines exhibiting a higher rate of decline (Buehler et al. 2008, 2020; Hamel 2000; Hamel et al. 2004; Hands et al. 1989d; Robbins et al. 1992). The BBS has significant limitations and its adequacy to monitor Cerulean Warblers has been seriously questioned. The number of BBS routes recording the species is too low in most areas such that trends can be estimated in only approximately 50% of its range. The fact that the BBS is a volunteer program creates problems in certain areas. It is particularly abundant in eastern Kentucky and West Virginia where there are few volunteers. A BBS survey consists of a roadside survey where 50 point counts are taken at evenly spaced intervals on 1 day in June. The roadside count method may be biased against forest-dwelling species such as the Cerulean Warbler. In West Virginia, it is most common on mountainous ridges, but all roads are in valleys. In Missouri, the average number of Cerulean Warblers recorded is only 0.2 birds per route. Canoe-float surveys along rivers determined that it was one of the most abundant riparian species, and unprecedented numbers were detected. The BBS suggested an annual decline of 3.1% in that state but canoe surveys noted either constant trends or possibly an increase. BBS data analysis involves averaging the number of birds observed on the 50 points of the route, thereby including data from points where there is no suitable habitat. Most routes with birds typically support only 1 or 2 birds and rarely 3 or more. A study in the Appalachians analyzed BBS data using only points where it was recorded and compared the results to the standard BBS results for 2 periods. The number of detections did not change between 1982 and 2001 across 1,375 BBS stops that were analyzed. There was an increase from 14% to 17% of stops where the species was detected and this approached significance. During the same period, the BBS reported declines of 4.1-6.8%. One of the main reasons for the disparity in results was that the study was done in the core of the species' range whereas the BBS results were based on 75 routes that included areas near the periphery of its range. Another limitation of the roadside survey technique is that changes in habitat along roadsides would reduce the detectability of birds in greater proportion than their actual decline. In all cases where detailed studies have been conducted, rates of population declines have been lower than estimated by the BBS. In some areas, populations were stable where the BBS indicated precipitous declines (Buehler et al. 2020; Hamel 2000; Link and Sauer 2002; McElhone et al. 2011; Robbins et al. 2009; Weakland and Wood 2005).

BBS data are also used to estimate the size of the Cerulean Warbler population. Point counts conducted on the BBS are of 3 minutes duration, and it is assumed that all birds present are detected. In Missouri, Robbins et al. (2009) estimated that 52.5% of Cerulean Warblers would be missed on a point count of 5 minutes or less. Even doubling the sample time to 10 minutes resulted in significant proportions of males not being detected. These authors concluded that the assumption that 100% of birds would be detected in a 10-minute point count was seriously flawed and that numbers may

be underestimated by 2-4 times. In addition, unmated males sang at twice the rate of mated males, so there is a lower probability of detecting mated males. Jones et al. (2000b) compared results from 50-m and 100-m fixed radius points and variable circular plots to known densities of Cerulean Warblers in eastern Ontario. They found that results from all 3 methods correlated with actual densities. The 50-m plots consistently overestimated densities; the other 2 plot types underestimated densities. The magnitude of the error increased significantly with actual density in both years for the latter 2 plot types but in only 1 year for the 50-m fixed radius plot. They concluded that it was better to underestimate than overestimate densities and recommended the variable distance plot as being easiest to employ. They noted that detailed information on a population, such as its extent, habitat, and population trend, is required before the appropriate survey technique is selected. They also cautioned that well-trained observers who studied the site year to year were required.

The current population estimates and trends for the Cerulean Warbler are deficient in many areas. It may be necessary to refine data collection techniques or change methods of analyzing existing data to obtain more reliable results. There are now several detailed studies available on discrete populations and it may be necessary to conduct more of these throughout its range to obtain better information on population demographics.

POSTFLEDGING PERIOD

In eastern Ontario, a pair was observed feeding fledglings 19 days after they left the nest. Elsewhere, a male was observed feeding 2 fledglings 30 days after they fledged. In eastern Ontario, fledglings used all parts of the canopy and often hid under leaves. In other areas, adults took fledglings into deep tangles of grape vines. In eastern Ontario, adults fed chicks within the territory for at least 10 days after fledging in half of successful territories. One male was observed feeding a fledgling 100 m outside his territory in the territory of an unpaired male. In the Appalachians, adults and young often dispersed outside their territories (Boves et al. 2013; Buehler et al. 2020; Hamel 2000; Oliarnyk and Robertson 1996a).

In Pennsylvania, fledglings remained within an average of 45 m of the nest for the first 2 days. Brood division occurred 3-6 days after fledging, with adults and fledglings moving as far as 150 m from the nest. By 7-12 days, most had moved as far as 305 m, beyond the male's territory. After 13-20 days, they were as far as 717 m from the nest. By the end of the tracking period (average 28.1 days after fledging), young had moved an average of 2.4 km from the nest. Fledglings were usually in the mid- to upper canopy and selected areas with greater sapling cover, less BA, and areas closer to water bodies than random sites. Until 2 days after fledging, young selected areas with greater sapling cover and less BA, but as they matured, they selected areas further from canopy gaps with greater mid-canopy cover. Compared with habitat selected by their parents, fledglings used areas with smaller and more numerous trees, fewer canopy gaps, and greater mid-storey cover (Raybuck et al. 2020).

In Missouri, Porneluzi et al. (2014) netted during the postfledging period in an oak-pine-hickory forest 2-15 years after it had been clear-cut and captured a total of 4 Cerulean Warblers.

MIGRATION

The Cerulean Warbler is a nocturnal migrant that travels alone or in small groups. During the day, it may occur in flocks with other warblers and resident species (Buehler et al. 2020).

Males arrive in spring about a week in advance of females. In eastern Ontario, males began to arrive in the first week of May and females arrived in the second week of May. Most Cerulean Warblers move through Long Point between 18 April and 25 May. In most of southern Ontario, it arrives in early to mid-May and migrants are present to the end of May; it has been recorded into early June. At Lake Opinicon, there appears to have been a shift toward earlier arrival, with first arrival on 13 May in 1994 and on 2 May in 2001 (Barg et al. 2003; Black and Roy 2010; Buehler et al. 2020; Curry 2006; Hamel 2000; LaForest 1993; Lancaster et al. 2004; Oliarnyk and Robertson 1996a; Weir 2008).

The Cerulean Warbler ceases singing in July and is very difficult to detect after that, hindering migration monitoring. It is an early autumn migrant and most leave the Ontario breeding grounds by the end of August. It is one of the earliest warblers to reach the Mississippi coast. In the Kingston area, the average date of the last sighting is 21 July and the latest record is 7 September. There are no autumn records from Prince Edward Point, suggesting that birds move early during late July and early August. Birds may also have an aversion to the Great Lakes shoreline. It is a rare to uncommon migrant at Long Point despite the presence of a fairly large population a short distance north of there, but it occurs more frequently at Point Pelee. There are only 2 autumn records for Presqu'ile, between 10 and 17 September. Average autumn departure in the Hamilton area is 23 August and the latest record is 27 October. The 3 autumn records from Elgin County are from 11 August to 28 September (Barg et al. 2003; Curry 2006; LaForest 1993; Lancaster et al. 2004; McCracken 1993; Robbins et al. 1992; Weir 2008).

During migration, the Cerulean Warbler occurs in the canopy of deciduous second-growth or mature trees. During spring migration in Illinois, it was most frequent in bottomland forests in the south and in upland forests in the central portion of the state. It has also been observed in orchards and shrubby areas during migration. It usually uses areas of lower vegetation only under adverse weather conditions such as strong winds and rain (Barg et al. 2003; Graber et al. 1983; Hamel 2000).

The Cerulean Warbler remains predominantly insectivorous during migration but also eats small amounts of plant material (Buehler et al. 2020; Hamel 2000).

During migration, the Cerulean Warbler is occasionally killed at communication towers and other tall structures. Numbers killed are relatively modest, but the population is small so it is unknown whether this is a significant impact. At the Lennox generating station chimneys near Kingston, 2 of 22,779 mortalities were Cerulean Warblers. Over 25 years at Florida television towers 141 Cerulean Warbler casualties were documented; over the first 11 years, 93 were killed of a total of 29,451 birds. No spring casualties were documented at Florida television towers. Two were killed at towers in spring in Illinois and there were no autumn casualties (Brett 2011; Buehler et al. 2020; Graber et al. 1983; Hands et al. 1989d; Robbins et al. 1992; Savignac 2010b; Weir 2008).

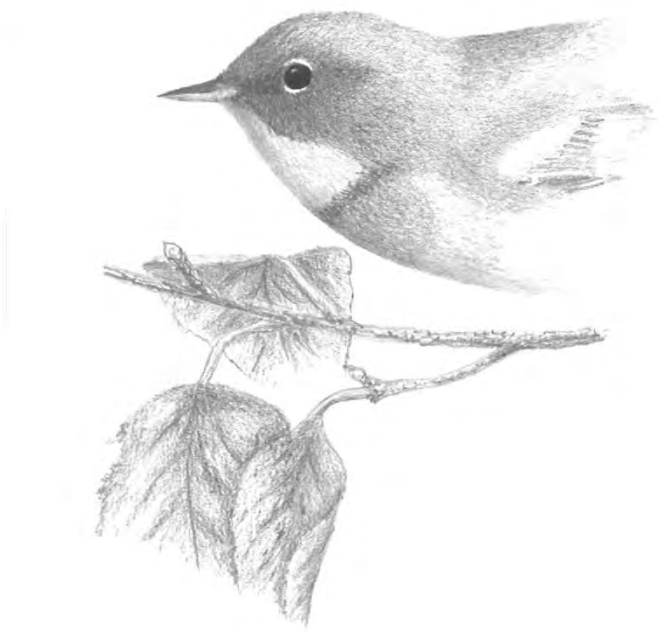
Before it was known that considerable dispersal of adults occurred on the breeding grounds, it was concluded that significant mortality must occur during migration and winter. Migration was

considered the time of maximum mortality because the species travels as far as 4,000 km 1 way and the migration period spans 2 months in spring and 4 months in autumn (Barg et al. 2003; Buehler et al. 2008; Jones et al. 2004). It is now known that annual mortality rates are not excessive. Undoubtedly some mortality occurs during migration, but it may not be a significant limiting factor. There are several other passerines that travel just as far. Although the species may spend extended periods migrating, it is unlikely that individuals do. The length of the Cerulean Warbler's migration period is similar to that of many neotropical migrants.

James (1991) considered the Cerulean Warbler a rare migrant. Only 30 were detected on daily surveys at Long Point Bird Observatory since 1960. The maximum daily count there is 3; the maximum recorded at Point Pelee is 25 (McCracken 1993). In Niagara Region, the high count of 3 was on 11 May; it has not been documented there in autumn (Black and Roy 2010). At Presqu'ile, the high count of 3 was on 19 May and usually only 1-4 birds are reported all spring (LaForest 1993).

Northern Parula

Setophaga americana



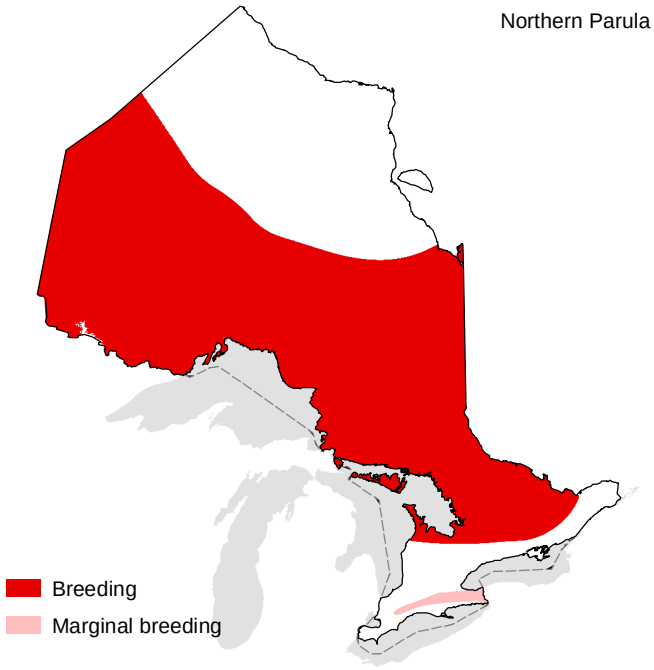
BREEDING SEASON

Habitat Requirements

Limited information is available on the breeding season habitat requirements of the Northern Parula in Ontario. James (1984b) observed that it was characteristic of sugar maple–beech forests but that it also occurred in mixed and deciduous forests. He noted that it required mature and dense upland forests.

In the Boreal Forest Region, the Northern Parula occurred in hemlock stands but was more characteristic of transitional sugar maple–beech forests. It sometimes extended far into the boreal region in deciduous or mixed woods. It is also characteristic of swamps and floodplains dominated by balsam poplar and tree-sized willows and alders (Erskine 1977). In the Clay Belt, Welsh and Lougheed (1996) detected it in only 2 stands. Both were dominated by balsam poplar on moist soils in areas rich in nutrients. Near Quetico Park, it tended to be associated with old-growth forests with scattered old red pines or white pines that formed an overstorey in a somewhat open forest of spruce and balsam fir. It also occurred in some forests 1-23 years old (Apfelbaum and Haney 1985). Near Manitouwadge, Venier et al. (2009) found it only in stands 60-223 years old; it was absent in

stands 1-21 and 24-36 years old. Near Hearst, Welsh and Fillman (1980) reported it breeding in 6-year-old clear-cuts in upland mixed forests.



In Algonquin Park, the Northern Parula is characteristic of hemlock stands. It also nests in spruce swamps and tall, mature coniferous and mixed swamp and bog forests where beard lichen is abundant. In addition, it nests in drier coniferous forests with white spruce and balsam fir where this lichen is often absent (Martin 1960; MacLulich 1938; Tozer 2012). In Ontario and much of its range, its distribution is closely linked to beard lichen or other epiphytes growing on trees. Nests are frequently placed in these and also constructed of them. It is not entirely constrained by lichens and mosses and will nest in areas where they are absent.

In the northern portion of its range, presence of the Northern Parula is often associated with beard lichen. This species is found most frequently in damp habitats where it grows predominantly on branches of conifers, although it also occurs on deciduous trees. The Northern Parula frequently breeds in mixed and coniferous lowland forests and swamps. These are most frequently dominated by white, red, or black spruce or balsam fir, but it also inhabits stands dominated by white cedar, tamarack, and hemlock. It nests not only in coniferous inclusions in deciduous forest stands, but also in pure deciduous forests. In Manitoba, typical habitat is mixed forests of trembling aspen, balsam poplar, white birch, white spruce, and balsam fir with profuse growth of beard lichen. It has also nested in white cedar–tamarack swamps and is locally distributed in dense coniferous and mixed forests containing a high proportion of black spruce, tamarack, white cedar, or balsam fir. In the Maritime Provinces, it is common in northern hardwood communities, including tolerant hardwoods dominated by sugar maple and intolerant hardwoods dominated by trembling aspen and balsam poplar. Densities are higher in deciduous than mixed or coniferous stands. It is less abundant in stands with increasing amounts of beech where it needs larger territories for food resources, but it prefers beech forests in South Carolina. In Maine, it is found mostly in forests dominated by spruce. In Illinois, it was more common in bottomland forests than upland forests. In 1 Illinois study, its abundance was correlated with presence of sycamore which it often used as a singing perch. Another Illinois study examined tree species preferences by the Northern Parula. Preferred species, in order of preference, were shellbark hickory, sycamore, silver maple, cherrybark oak, bitternut hickory, pin oak, and green ash. Avoided species, in decreasing order of avoidance, were overcup oak, sugar hackberry, pumpkin ash, blue beech, bald cypress, red maple, white elm, sweetgum, swamp chestnut oak, black gum, and Manitoba maple. Of the preferred trees, shellbark hickory was 11th in abundance, silver maple was 18th in abundance, and bitternut hickory was 19th

in abundance. Of the avoided trees, pumpkin ash was the second-most abundant tree, sweetgum was third in abundance, overcup oak was fourth in abundance, and blue beech was seventh in abundance. In Massachusetts, the Northern Parula nested in old apple orchards where the trees were covered profusely with beard lichen. As the apple trees died, the beard lichen declined as did the parula. Eventually both the lichen and warbler disappeared entirely. In many areas, it may be widely distributed despite the absence of beard lichen. In the more northern portions of its range, it has nested in stands dominated by oak-chestnut-hickory, oak-pine, white pine, red pine, white birch, balsam fir–white cedar, birch-basswood, white birch–yellow birch–white cedar, hemlock–yellow birch, sugar maple–yellow birch, and elm–Manitoba maple–sycamore in addition to the more traditional habitats (Beals 1960; Bent 1953; Brooks 1940, 1947b; Chapman 1907; Cruickshank 1956; Dawson 1979; Freedman and Johnson 1999; Gabbe et al. 2002; Graber and Graber 1951; Graber et al. 1983; LaRue et al. 1995; Lemieux et al. in Gauthier and Aubry 1996; McNicholl and Taylor 1982; Moldenhauer and Regelski 2020; Morgan and Freedman 1986; Morse 1967; Pagen et al. 2000; Parker et al. 1999; Parnell 1969; Rich et al. 1994; Samson 1979; Temple et al. 1979).

In the southern portion of its range, the Northern Parula nests most frequently in bottomland forests, often along rivers and lakes where Spanish moss grows on the trees. It also occurs in areas where this moss and other epiphytes are absent, and in upland forests. Stand types it has been reported using in the south include those dominated by hackberry, black walnut, sweetgum-oak, beech, oak-hickory, pine, pine-hardwoods, hemlock in moist ravines, hemlock–tulip tree, hemlock-hardwoods, black willow, and bald cypress. In upland habitats, it is associated with the more mesic portions of stands. In Missouri, preferred tree species included sycamore, hackberry, cottonwood, pecan, and green ash (Brittain et al. 2010; Brooks 1947b; Buffington et al. 1997; Bushman and Therres 1988; Chapman 1907; Harrison 1984; Hayden et al. 1985; Moldenhauer and Regelski 2020; Morse 1967; Parnell 1969; Schukman 1996).

The Northern Parula nests most frequently in mature forests with a closed canopy. It occasionally nests in younger or more open stands. Small canopy openings may be attractive to it and it frequently nests around these. Canopy closure of occupied forests ranges from poorly developed to an average of 70%. In northern hardwood stands in New Brunswick, it was one of the 6 most dominant species in stands 20 and more years old. It is also a dominant species in unharvested deciduous forests in Nova Scotia. In New Hampshire and Maine, it was significantly more abundant in the large-sawtimber size-class of forest that was dominated by trees larger than 60 cm diameter at breast height (DBH). It was equally abundant in sapling-sized forests and sawtimber-sized forests and uncommon in poletimber-sized forests. The Northern Parula is not an obligate old-growth forest species. In Pennsylvania, it occurred in 9.1% of old-growth forests compared with 10.1% of forests statewide and 9.9% of forests on the Appalachian Plateau. In South Carolina, it occurred in black willow stands 6, 27, and 60 years and older, but was most frequent in the oldest stand. It exhibited neither a positive or negative affinity for old-growth. In Maine, Minnesota, and New Brunswick, it consistently selected areas where there were highest densities of large trees. In the 2 states, these were coniferous species but they were deciduous species in New Brunswick. In South Carolina, breeding density was 4.5 times higher at edges of gaps 0.13-0.50 ha created by group-selection harvest than in unbroken canopy in the same forests. In Maine spruce forests, it also frequently nests around canopy gaps (Bowen et al. 2007; Buffington et al. 1997; Bushman and

Therres 1988; Collins 1983a; DeGraaf et al. 1998; Freedman et al. 1981; Haney 1999; Morgan and Freedman 1986; Morse 1967; Parker et al. 1999).

Collins (1983a) compared habitat usage by the Northern Parula in Maine and Minnesota. There were 3 habitat variables that were significantly different in the 2 states: number of tree species, number of trees 7.5-15 cm DBH, and number of trees 15.1-23 cm DBH. In Minnesota, it was in a forest–forest edge guild that occurred in habitats with tall canopies, moderate coniferous cover, few small trees, and more larger trees. In Maine, it was in a guild inhabiting areas with high percent canopy cover, variable coniferous cover, and many trees in the smaller size classes. In both states, it consistently selected larger trees and areas of conifers. The author concluded that it may not have different habitat preferences in the 2 areas but may simply be selecting the most optimal available habitat.

Some studies examined microhabitat requirements of the Northern Parula. In Arkansas, its density was correlated with the number of tree species, the number of small trees, and canopy height. In Nova Scotia, its density was correlated with tree density, basal area (BA), percent canopy cover, and canopy height. In the mid-Atlantic states, its abundance was positively correlated with BA and moisture gradient and negatively correlated with slope and percent coverage by conifers. In Maryland, its abundance was correlated with the total number of plant species. Average habitat characteristics in Minnesota were 60.3% ground cover, 50.0% shrub cover, 76.4% canopy cover, canopy height 16.8 m, 49.3% coniferous cover, and 6 tree species within a 0.04-ha circle. Numbers of trees of different size classes in 0.04-ha circles were: 10.0 that were 7.5-15 cm DBH; 11.0 that were 15.1-23 cm DBH; 7.3 that were 23.1-30 cm DBH; 3.6 that were 30.1-38 cm DBH; 2.8 that were 38.1-53 cm DBH; 0.4 that were 53.1-68 cm DBH; and 0.2 larger than 68 cm DBH. Habitat was characterized as mature forest with moderate ground and shrub coverage and greater than 75% canopy closure. Territories consistently contained more than 50% coniferous coverage, mostly in the large tree-size categories. It was associated with moderate amounts of large trees, more canopy cover, and less ground cover. In Georgia, the Northern Parula showed a strong positive association with shrub height and a weaker association with shrub density, canopy cover, and BA. It was negatively correlated with herbaceous cover. In New Hampshire and Maine, its presence was significantly correlated with the number of snags larger than 10 cm DBH and taller than 5 m and the total foliage volume of coniferous trees larger than 10 cm DBH. It was negatively correlated with the total foliage volume of deciduous trees larger than 10 cm DBH (Collins et al. 1982; DeGraaf et al. 1998; Klaus et al. 2010; Lynch 1987; Moldenhauer and Regelski 2020; Robbins et al. 1989).

In Minnesota, Collins (1981) compared the vegetation at Northern Parula nest sites and perch sites. Nests were in forest and forest-edge habitat with variable numbers of large deciduous and coniferous trees and an open canopy. Perches were also variable, but were most often in forest rather than at forest edge. Perch sites had significantly higher ground and shrub coverage and a higher percent coverage by conifers than nest sites.

Some studies reported that the Northern Parula is area sensitive and others have found it nesting in small patches with no indication of area sensitivity. Most reports of area sensitivity are from Maryland and other mid-Atlantic states and Missouri. In Maryland, Lynch (1987) reported that it was area sensitive and Bushman and Therres (1988) concurred. They reported that it was found in

few woodlots smaller than 70 ha. Robbins (1979) concluded that 100 ha were required to support a viable population in Maryland. In the mid-Atlantic states, its probability of detection was at its maximum in forests larger than 3,000 ha. Its probability of detection declined to 50% at 520 ha and the 3 smallest forests it inhabited were 516.0, 415.0, and 10.1 ha. In Missouri, Hayden et al. (1985) estimated that the minimum patch size required to support the Northern Parula was 53.6 ha. James (1984b) reported that it appeared to be area sensitive in Ontario, probably requiring 100 ha or more of continuous forest in order to maintain a viable population. In Maine, the Northern Parula regularly nested on small islands 0.2-1.5 ha. It nested on smaller islands than any other warbler species (Morse 1971b). Beals (1960) studied the avifauna on islands in Wisconsin and found that it was not confined to larger islands. In Georgia, Hodges and Krementz (1996) compared the densities of breeding Northern Parulas in corridors less than 350 m in width and those 400-700 m and wider than 1,000 m. It did not show a positive association with corridor width, with highest density in the medium-sized corridor and least in the widest.

Bushman and Therres (1988) considered the Northern Parula a forest-interior species, but provided no supporting documentation. In many areas, the opposite is true and it is an edge species. Hayden et al. (1985) considered it an edge species in Missouri as did Bowen et al. (2007) in South Carolina. In Maine spruce forests, it was confined to forest edge and rarely ventured into unbroken forest. It occasionally occurred in forest gaps created by blowdown and bedrock outcrops. Avoidance of forest interior appeared to be a response to competition with the Golden-crowned Kinglet. Both species have very similar foraging strategies, foraging on the outer tips of limbs, and the kinglet is socially dominant to the parula. There were few kinglets foraging at the forest edge, so the Northern Parula could forage there without competitive interference. In Louisiana, it was evenly distributed throughout the forest; there were no other species present that foraged in a similar manner (Morse 1967, 1989). In Quebec balsam fir–white cedar stands, it was more than 3 times abundant in riparian than nonriparian stands. In riparian stands, there was an edge effect due to a band of deciduous thicket swamp (LaRue et al. 1995). In northern Michigan, it was most abundant in mature riparian zones where it responded positively to even narrow riparian strips (Moldenhauer and Regelski 2020).

Only 4 empty nests have been described from Ontario and all were in mixed wooded areas. Nest-tree species included yellow birch, white birch, balsam fir, and white spruce. One nest was above the roof of a tourist lodge. One nest was built in hanging beard lichen. Another nest was in a curl of bark attached to the trunk of a white birch at a height of 8 m (Peck and James 1987).

Nests are invariably in trees, typically in forest or at forest edge, and rarely in isolated trees. Nest trees may be either coniferous or deciduous, including spruce, balsam fir, red cedar, birches, white oak, sycamore, and apple. Nests may be in live or dead trees, with dead trees used only if they support beard lichen. Nests have been reported 12.7 cm to 30 m from the ground, with most 3 or more metres up. Seventy-one Maine nests were 1.6-16.5 m from the ground, mostly 3-12 m up. In the north, most nests are built in and of beard lichen but Spanish moss is used in the south. Nests may be free-swinging in trailing lichen or moss or hung from small branches in a pendant or semipensile manner, similar to oriole or vireo nests. Although most northern nests are in beard lichen, there is no relationship between the density of warblers and lichens. The presence of the

lichen is important but lichen abundance is not. One nest in a spruce tree in Minnesota was built entirely of beard lichen, which was not known to occur within 1.6 km of the nest. The female must have travelled a considerable distance to find it. Of 81 nests reported in Maine, all were in beard lichen and constructed of it. Most nests constructed of lichen or moss are at the extreme tips of branches. Pendant nests attached to twigs usually open at the top. Nests in free-hanging lichens or moss have an entrance in the side at the level of the nest bowl. Some nests have 2 holes at this level. One is used as an entrance and the other as an exit. Where beard lichen and Spanish moss are absent, the Northern Parula may nest in clumps of leaves at the tips of oaks, sycamore, hemlock, and spruces. Nests may also be in debris deposited by flood waters in shrubs and trees along watercourses. Other nests have been on the horizontal limb of a spruce, in the crotch of a hackberry tree, in ivy within a tree, in witches'-brooms in hardwood trees, and burlap deposited by flood water on the branch of a Manitoba maple limb. Nests that survive the winter may be used in subsequent years. One Maine nest was used in 4 successive years (Bent 1953; Brooks 1940, 1947b; Chapman 1907; Cruickshank 1956; Graber and Graber 1951; Graber et al. 1983; Harrison 1984; Lemieux et al. in Gauthier and Aubry 1996; Moldenhauer and Regelski 2020; Morse 1967; Mousley 1916a, 1924, 1926, 1928; Parmelee 1973; Peterson 1946).

In Nova Scotia, average territory size was 0.32 ha (range 0.08-0.65 ha). Territory size increased with increasing abundance of beech and stand size, suggesting that it was more common in small stands without beech. In mainland forests in Maine, territories averaged 0.4 ha (range 0.30-0.51 ha). This area supported its main competitors (Golden-crowned Kinglet and Black-throated Green Warbler) as well as other Northern Parulas. On small islands, territories averaged 0.17 ha and were as small as 0.16 ha. The main competitors were absent on these islands and they supported only a single pair of Northern Parulas. There are 2 reports of colonial or semicolonial nesting. A Connecticut swamp was reported to support 75 breeding pairs and as many as 200 were reported nesting in trees surrounding a small lake in Virginia. Details of both of these observations are rather sketchy and the area of the habitat was not provided in either case so that densities could be estimated (Bent 1953; Chapman 1907; Moldenhauer and Regelski 2020; Morse 1967, 1977, 1989).

No information is available on natal philopatry or return rates of adults. One adult male was recaptured in the same area in Maine the following year. Two adult females were recaptured in the same 10-minute block in Maryland 3 years later (Moldenhauer and Regelski 2020).

Limiting Factors

Peck and James (1987) concluded that eggs could be present throughout June until mid-July. In Algonquin Park, nests are under construction from mid-May to early June, eggs are present from early to mid-June, nestlings are present from late June to late July, and dependent fledglings have been observed from late June to mid-August (Tozer 2012).

Nests may take 4-10 days to build. At 1 nest, the first egg was laid the day after the nest was completed, but this was an unusually late nest. One egg is laid per day. At a nest with a single egg, incubation began with laying of the egg but incubation started with laying of the penultimate egg in more traditionally sized clutches. Limited data suggest that the incubation period is 12-14 days. No information is available on the nestling period. One nestling left a nest prematurely when it was

disturbed at age 10 days (Bent 1953; Graber and Graber 1951; Moldenhauer and Regelski 2020; Mousley 1924, 1926, 1928).

Two clutches per season have been confirmed in the Carolinas and egg and nestling dates in Florida, Georgia, Alabama, and Texas suggest double brooding. It is unknown if second broods are raised in Ontario. Renesting after nest loss occurred in Maine. Typical clutches contain 3-5 eggs (range 2-7, mean 3.94). Clutches initiated near mid-July in Illinois contained only 1-3 eggs (Bent 1953; Chapman 1907; Graber and Graber 1951; Moldenhauer and Regelski 2020; Morse 1971b; Mousley 1916a).

Both sexes are capable of breeding at age 1 year. In Maine, individuals occasionally appeared on islands where they did not breed, indicating a floater population. The mating system is monogamous, although there is at least 1 record of polygyny. Extra-pair copulation is considered rare, but this warrants further study (Moldenhauer and Regelski 2020; Morse 1971b).

Considerable information is available on the foraging strategies of the Northern Parula and how they change in the presence of competitors. In South Carolina, it foraged from twigs and small branches 77% of the time and 20% of the time on larger branches (Moldenhauer and Regelski 2020). It typically gleans insects in the upper and mid-canopy, but occasionally forages along tree trunks similar to a nuthatch or searches for insects on the ground (Lemieux et al. in Gauthier and Aubry 1996). It often feeds chickadee-like by hanging upside down (Chapman 1907). During the breeding season in North Carolina, 53.8% of foraging occurred in the canopy and 46.2% in low trees, with no observations of it in shrubs or on the ground. In the canopy, 23.0% of foraging occurred in the inner crown and 30.8% in the lower crown with none in the upper crown or on the bole. In low trees, 7.7% of foraging occurred in the inner crown and 38.5% in the lower crown, with none in the upper crown or on the bole. Singing males were observed at heights of 1.5 to more than 15 m (average 11 m). Nonsinging birds occupied the same range of heights, but averaged 7.6 m from the ground (Parnell 1969). Morse (1967, 1971b, 1989) studied the foraging habits of the Northern Parula in Maine and Louisiana. Its foraging strategies are suggestive both of kinglets and the larger warblers in the genus *Setophaga*, although no other species forages exactly as it does. In Maine, it foraged at moderate heights an average of 10.0 m from the ground (range 1.5-18.3 m). It appeared to minimize overlap in foraging with the other warblers by feeding heavily in the extreme tips of foliage. There was considerable overlap with Ruby-crowned and Golden-crowned kinglets. Potential competition with kinglets was minimized by feeding mainly on disturbed edges; the kinglets concentrated on spruce in undisturbed areas. There were also some differences in the techniques of the Northern Parula and Golden-crowned Kinglet. The kinglet foraged more heavily on inner portions of spruce (more than 20% of the time) than the parula (6%). The kinglet also concentrated its foraging at a lower height (average of 8.0 m compared with 10.0 m), although there was considerable overlap in foraging heights of all species examined. Nonetheless, a considerable amount of foraging was done by the Golden-crowned Kinglet in the same areas as the Northern Parula, and some of the same types of movements were made in the tips of foliage. The Northern Parula spent 91.7% of its foraging time in spruce trees, 2.5% by flycatching, 8% in deciduous trees, and 0% on the ground. In spruce, 48.3% of its time was spent at the tip of foliage: 32.9% by gleaning, 5.0% by stretching, 7.5% by hovering, 2.1% by hover-walking, and 0.8% by hanging. In addition, 23.3% of time was spent on twigs 5 mm

or smaller in diameter, 2.9% on dead twigs (2.5% gleaning and 0.4% hovering), 2.1% gleaning on dead branches, 5.0% on lichen-covered branches, 3.8% on the distal portion of branches, 6.3% on the proximal portion of branches, and 0% on the trunk. The Black-throated Green Warbler showed more similarities in foraging to the Northern Parula than any other warbler. It foraged at the most similar height (average 11.8 m), hovered more frequently than any other warblers, and also attained the highest density of any of the warblers. The Black-throated Green, Blackburnian, and Yellow-rumped warblers did not use the tips of foliage as much as the Northern Parula, but the use of this habitat by the 3 warblers combined was heavy. In an area with equal numbers of spruce and birch, the Northern Parula foraged significantly more frequently on spruce (119 times) than birch (23 times) in the first half of June. By mid-July, it foraged somewhat less in conifers (51 times) than birches (66 times). By this time, the young had fledged and birch leafminer sawflies probably resulted in a superabundant food supply. Use of deciduous trees minimized competition with the Golden-crowned Kinglet which foraged solely in conifers. In Louisiana, the Northern Parula had no competitors and ranged widely through the canopy and also in the understorey once the young fledged. In spruce forests in Maine, the Golden-crowned Kinglet was the primary competitor, followed by the Black-throated Green Warbler and Blackburnian Warbler. The Yellow-rumped and Magnolia warblers did not appear to be significant competitors. Morse (1971b) studied the foraging strategies of warblers on small islands in Maine. Islands supported either 3 species of warblers (Black-throated Green Warbler, Yellow-rumped Warbler, and Northern Parula), the Yellow-rumped Warbler and Northern Parula, or just the Northern Parula. The parula showed a stronger tendency than the other 2 species to use deciduous foliage and to forage at the tips of vegetation. It preferentially selected birch trees infected with defoliating insects. Males foraged higher than females, but both sexes foraged lower in vegetation when the Black-throated Green Warbler was present. Where the Black-throated Green Warbler was absent, female Northern Parulas and male Yellow-rumped Warblers had higher foraging diversity, but no clear-cut relationship was detected for male parulas. When the Northern Parula was the only warbler species on an island, it exhibited much greater foraging diversity to include both coniferous and deciduous trees, a wider range of heights, and small limbs as well as the tips of branches. Foraging diversity declined on 1 island where it was the sole occupant because it concentrated on foraging in deciduous trees with high concentrations of insects. The Black-throated Green and Yellow-rumped warblers may restrict the foraging strategies of the Northern Parula, but it exhibits a greater level of foraging plasticity and was therefore able to occupy the smallest islands. Morse (1989) concluded that the Northern Parula may be more limited by the presence of kinglets and other warblers than by the availability of beard lichen for nesting.

Although the foraging strategies of the Northern Parula are well documented, there is limited information on its diet, particularly during the breeding season. Young have been fed small green caterpillars, mayflies, and other winged insects. Prey delivered to nestlings tends to be larger than what is generally available. During the breeding season, adults consume mostly insects and spiders and rarely bud scales. It feeds heavily on spiders and caterpillars and accesses tent caterpillars by tearing a hole in the tent with its bill. In New Hampshire, 6 stomachs contained an average of 1.3 spruce budworms. It ate a low to moderate number of budworms compared with other species. In New Brunswick, it showed no response to increasing numbers of budworms. During a spruce budworm outbreak in Maine, stomachs contained 83% and 16% budworm larvae and pupae in 2

years. In another Maine location, it fed heavily on birch leafminer sawflies. Beetles constitute a large proportion of the winter diet, but they are not as prevalent in the breeding season diet. It also consumes moths, ants, wasps, bees, flies, locusts, scale insects, plant lice, lacewings, and mayflies. Four wintering birds in Florida had consumed mostly hymenopterans (ants, bees, and wasps) and spiders, and lesser amounts of caterpillars, maggots, beetles including weevils, scale insects, bugs, and grasshoppers (Bent 1953; Crawford and Jennings 1989; Graber and Graber 1951; Mitchell 1952; Moldenhauer and Regelski 2020; Morris et al. 1958; Morse 1967, 1971b; Mousley 1924).

The Northern Parula is an infrequent host of the Brown-headed Cowbird. The nest shape and side entrance may inhibit entrance by the cowbird and some nests may not be sturdy enough to support a cowbird. In Ontario, there is little overlap in the ranges and habitat preferences of this warbler and the cowbird. Parasitism has been reported in Florida, Kansas, Virginia, Missouri, Oklahoma, New Jersey, New York, Pennsylvania, Connecticut, Delaware, and Maryland. The Northern Parula may build over nests containing cowbird eggs, but has been observed feeding cowbird fledglings in Delaware, Oklahoma, and Maryland (Lemieux et al. in Gauthier and Aubry 1996; Moldenhauer and Regelski 2020).

Direct habitat loss does not currently appear to be a major concern in Ontario, but the Northern Parula has largely been eradicated due to habitat destruction in southern Michigan, southern Wisconsin, and the Mississippi River lowlands of Missouri. Draining of bogs and other moist wooded areas were implicated in its decline in southern Wisconsin (Moldenhauer and Regelski 2020).

Indirect effects due to decline or loss of beard lichen appear to be significant limiting factors in some regions. Lichens are sensitive to sulphur dioxide. Air pollution that affected lichen survival has largely extirpated or reduced the Northern Parula in several northeastern states including Massachusetts, Connecticut, New Jersey, New York, and Vermont. Old-growth balsam fir forests with high densities of beard lichen are very vulnerable to the spruce budworm, which also provides an excellent food source for the Northern Parula. To protect balsam fir forests from budworm outbreaks, foresters recommend that forests not be allowed to mature to this stage and, if an outbreak is imminent, that the timber be harvested immediately. The shorter rotations and pesticides are detrimental to the Northern Parula's habitat and prey (Lemieux et al. in Gauthier and Aubry 1996; Moldenhauer and Regelski 2020).

Forest management may be detrimental or beneficial to the Northern Parula, depending upon the prescription used. Clear-cutting temporarily eliminates habitat, but high densities may occur in clear-cuts as young as 6 years in northern Ontario. Short rotations that preclude development of beard lichen and minimize the presence of spruce budworms are detrimental (Lemieux et al. in Gauthier and Aubry 1996; Welsh and Fillman 1980). Vanderwel et al. (2009) studied the effects of partial tree harvest on the Northern Parula, with particular reference to the Boreal Forest Region of Ontario. There was no change in its abundance with removal of 30% of trees, but it declined when 50-70% of trees were removed. In the Canadian Shield of Ontario, there was no difference in its abundance in early successional and mid-successional clear-cuts and burns in the same seral stages. It was significantly less abundant in both early successional and mid-successional stands than in mature stands (Zimmerling et al. 2017). Haché et al. (2013) studied the effects of selection harvesting in northern hardwoods in New Brunswick. Forty percent of the BA was removed and canopy

coverage was reduced by 20%. The authors expected the parula to decline due to its preference for mature trees, but there was no measurable effect. The Northern Parula expanded its range into Tennessee, North Carolina, and Virginia only after the dense virgin spruce forests were cut (Moldenhauer and Regelski 2020). This may have created the edge habitat that it prefers when dominant competitors are present. In South Carolina bottomland forests, Harrison and Kilgo (2004) examined the response of the Northern Parula to clear-cutting and to clear-cutting where residual patches of trees and snags were retained. It completely disappeared from the clear-cut habitat. In the patch-retention clear-cuts, it declined the first year after harvest but recovered in the second year. In Illinois, Robinson and Robinson (1999) created openings of 0.02-0.4 ha in a 2,000-ha forest through selection thinning. It was significantly more abundant in selectively cut areas than in unharvested forest. Bowen et al. (2007) concluded that creation of small gaps in the forest through selection harvesting increased habitat diversity and usage by the Northern Parula, and that this was particularly beneficial in stands with a sparse understorey due to a dense canopy.

In North Carolina pine-oak forests, the Northern Parula responded positively to fire but occurred more frequently only after low-intensity fires (Rose and Simons 2016).

Declines in the Maritime Provinces prior to 1966 were attributed to the widespread use of DDT (Moldenhauer and Regelski 2020).

Heavy rains can result in nests being abandoned or failing. A newly completed nest was abandoned following 3 days of continuous rain. At least 2 Maine nests containing young collapsed as a result of extended rainstorms (Morse 1971b; Mousley 1928).

Blake et al. (1992) studied the effects of drought on the Northern Parula in Wisconsin. It exhibited no significant variation in relation to any moisture indices.

Price (2004) predicted that the breeding range of the Northern Parula might contract in southern Ontario if the average summer temperature increased by 2°C.

Status

Anecdotal information suggests that the Northern Parula may have been more common in the early 1900s than it is currently. At that time, it was a very common to abundant spring migrant (Fleming 1907; McIlwraith 1894) and was apparently more common as a breeder then in Parry Sound and Muskoka districts (Mills 1981). It was more abundant there and in many other areas of the province when extensive old-growth forests existed. By the 1960s, there were only 0-3 reports annually in Algonquin Provincial Park, but there was a major increase in numbers and distribution in the 20 years preceding Tozer's (2012) book. Baillie and Harrington (1937) reported that it occurred locally during the breeding season throughout most of the eastern half of the province from Lake Erie to northern Hastings County north to at least Lake Abitibi and probably to the western end of Lake Superior. The only breeding record for the province at that time was from Algonquin Park where adults were observed feeding young on 9 July 1934. During the first atlas, the breeding range was determined to extend from the Bruce Peninsula and Manitoulin Island along the southern edge of the Canadian Shield and throughout much of the Canadian Shield, with a more spotty distribution in the northwest portion of the Boreal Forest Region. Even in the heart of its range, it was found in only 33-50% of squares. There were only 4 scattered records in the Carolinian Forest Region,

suggesting a possible range retraction in this area since Baillie and Harrington's (1937) publication. Highest concentrations occurred in the Algonquin Highlands with other concentrations on the southern side of Manitoulin Island, near Sault Ste. Marie, and on the Bruce Peninsula (Helleiner in Cadman et al. 1987). James (1991) considered the Northern Parula a rare to uncommon breeder across the province north to Red Lake, Lake Nipigon, and Timmins, and south to Bruce and Peterborough counties. There are sight records north to Big Trout Lake and south to Chatham-Kent.

The second atlas demonstrated that the breeding distribution was essentially the same as during the first atlas. An exception was that the Northern Parula disappeared from the northern shoreline of Lake Erie except for a single record in Niagara Region. Its probability of observation increased significantly province-wide and in all regions except the Hudson Bay Lowland and Carolinian Forest Region, where it rarely occurs. Increases were most evident on Manitoulin Island, north of Lake Huron, and in the area surrounding Algonquin Park. Highest densities occurred in the Algonquin Highlands, east of Lake Superior, and in the region from Thunder Bay to Kenora (McLaren in Cadman et al. 2007).

Breeding Bird Survey (BBS) data for 1980-2007 indicate a more robust population of the Northern Parula than for most neotropical migrants. Significant increases were recorded during this period for Ontario, Maine, Illinois, Michigan, Missouri, and New Hampshire (Moldenhauer and Regelski 2020). These authors noted that these results should be interpreted with caution, but they are consistent with trends determined by the second atlas. BBS data for 1970-2021 indicate that it increased at annual rates of 3.2% in Canada and 5.32% in Ontario. Trends for 2011-21 were annual increases of 3.73% in Canada and 3.96% in Ontario. Results were highly reliable for the Canadian trends, of medium reliability for the long-term Ontario trend, and of low reliability for the short-term Ontario trend (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

After the young leave the nest, the female and fledglings move through the canopy at a lower level than the male, who continues to sing. Once the young fledge, there is a tendency for both adults and fledglings to move to early successional areas, such as small forest gaps created by selective thinning and clear-cuts 3-9 years old. During the postfledging period in South Carolina, all observed birds were in or at edges of forest gaps with none observed in forest interior. In Missouri, none were seen in oak-hickory forests during the postfledging period, although the Northern Parula nested within this habitat. Numbers declined from the breeding to postfledging seasons in mature riparian forests, although it continued to occur in this habitat. Numbers increased from the breeding to postfledging seasons in a 9-year-old clear-cut. It did not breed in 3-year-old clear-cuts, but was present during the postfledging period (Bowen et al. 2007; Moldenhauer and Regelski 2020; Pagen et al. 2000).

Porneluzi et al. (2014) netted during the postfledging period in a Missouri oak-pine-hickory forest 2-15 years after it was clear-cut. The Northern Parula was captured in low numbers each year and showed no significant trend over time.

MIGRATION

The Northern Parula is a nocturnal migrant that spends the day in mixed flocks with other warblers, chickadees, titmice, and other woodland birds (Harrison 1984; Moldenhauer and Regelski 2020).

Spring arrival may be correlated with increasing temperatures. The mean maximum temperature at arrival in Wisconsin and Michigan was 5°C. Males arrive on the breeding grounds before females to establish a territory, but the timing differential of the sexes has not been quantified. In southern and central Ontario, most migrants arrive in the first week of May and have passed through by the end of the month. Rarely, individuals may arrive in the last week of March or mid-April, and stragglers may persist until the first week of June (Black and Roy 2010; Curry 2006; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Mills 1981; Moldenhauer and Regelski 2020; Tozer 2012; Weir 2008).

Autumn migration may be triggered by temperature with the mean temperature upon departure from Wisconsin being 7.2°C. Birds begin to leave the breeding grounds in August. Males cease singing in late July and birds become very inconspicuous, making it difficult to track departure times. In the southern Shield, most leave by the first week of September, but some remain until the end of September. In the south, migrants arrive in the last week of August or first week of September and may remain until mid-October (Black and Roy 2010; Curry 2006; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Mills 1981; Moldenhauer and Regelski 2020; Tozer 2012; Weir 2008).

During migration, the Northern Parula is less discerning in its habitat selection than during the breeding season. During migration, it occurs predominantly in deciduous trees, but may use almost any species of tree or shrub. It prefers deciduous woodlands, but may occur in roadside and shade trees, in parks and residential yards, and in orchards and shrubby areas. In Illinois, most spring and autumn migrants were detected in bottomland forests, but it also occurred in forest edges and upland forests. In North Carolina, it was not observed in thickets during spring migration. It occurred in a variety of forest types including those dominated by pine, pine-hardwoods, oak-hickory, beech, and floodplain forests. It was seen most frequently in beech forests and this appeared to be preferred habitat. During spring migration in Ohio, it was significantly more abundant in riparian than upland forests. Riparian forests were dominated by sycamore, Manitoba maple, silver maple, sugar maple, white ash, cottonwood, hackberry, white elm, and honey locust. Upland forests were dominated by sugar maple, red and white oak, white ash, white elm, and hickory. Riparian stands had significantly lower percent shrub coverage (19% compared with 39%), higher percent canopy cover (83% compared with 74%), and fewer trees larger than 8 cm DBH than upland stands. The Northern Parula and Baltimore Oriole were the only migrants that were more abundant in riparian than upland stands. The Northern Parula appeared to actively select for riparian forest habitat during spring migration. In South Carolina bottomland forests, it was 5 times more abundant in and at edges of small gaps created by selective thinning than in unbroken forest. In autumn, all observations were in and at edges of forest gaps indicating a preference for small forest gaps. During migration, it tends to move high in the canopy and in the crowns of lower trees. During spring migration in North Carolina, 51.5% of observations were in the canopy, 45.6% were in low trees, 2.9% were in shrubs, and 0% were on the ground. In the canopy, 24.6% of all observations were at the top of the crown, 19.6% in the inner crown, 7.3% in the lower crown, and 0% on the bole. In low trees, 17.4% of observations were at the top of the crown, 21.7% in the inner crown, 6.5% in the lower crown, and 0% on the bole. In shrubs, 1.5% of observations were at the top of the crown, 0.7% in the inner crown, and 0.7% in dense thickets, with no observations in the lower crown, brush piles,

or grasses (Bent 1953; Bowen et al. 2007; Graber et al. 1983; Moldenhauer and Regelski 2020; Parnell 1969; Rodewald and Matthews 2005).

During autumn migration in New York, Lebbin et al. (2007) observed the Northern Parula searching for food at night in trees illuminated by lights from a football stadium. Many individuals and species of warblers foraged simultaneously within the same trees, interacting with each other as is typical in mixed-species flocks during the daytime.

The Northern Parula is commonly killed during migration by striking television towers and other tall objects (Bent 1953; Graber et al. 1983; Moldenhauer and Regelski 2020).

In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season for 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming occurred during the second period. The Northern Parula arrived significantly earlier during the second period but there were no significant differences in its autumn departure dates or length of the breeding season.

James (1991) considered the Northern Parula a rare to uncommon migrant in Ontario. There are indications that numbers of migrants may be lower now than they were historically. Fleming (1907) considered it an abundant migrant and McIlwraith (1894) stated that it was a very common migrant. In Elgin County, it was an uncommon migrant in 1891 and 1954 but by 2000 it was a rare spring and very rare autumn migrant (Lancaster et al. 2004). In the Hamilton area, it was documented in larger numbers prior to the 1950s (Curry 2006).

Magnolia Warbler

Setophaga magnolia

BREEDING SEASON

Habitat Requirements

Ontario Magnolia Warbler nests were in open and dense woods. It preferred mixed woods (62.1% of nests) to coniferous (31.0%) and deciduous (6.9%) stands. It inhabited both mature and second-growth forests. Nests were usually at woodland edges or openings that had dense understories of small coniferous, and less frequently, deciduous trees and shrubs (Peck and James 1987). James (1984b) concluded that it occupied mostly mixed and coniferous forests. Occupied stands may range from very young to very mature but presence of young coniferous trees, usually with dense deciduous shrubs, is essential. In more mature forests, it prefers open woods, edges, or clearings.

In the Boreal Forest Region near Pickle Lake, the Magnolia Warbler occurred in disturbed edges of coniferous forests (James 1980). From Pickle Lake north to the Wetico Hills, it was most abundant in mixed scrub followed by deciduous scrub and mixed forest, deciduous forest, coniferous forest with an understorey, coniferous scrub, and coniferous forest without an understorey. It was absent in heath and tundra habitat (McLaren and McLaren 1981). Near Lake Nipigon, it was one of the dominant species in spruce–balsam fir forests, particularly in immature stands with frequent openings dominated by shrubs. It was also common in black spruce–white cedar–alder stands,

mixed spruce-fir-deciduous stands, and in clear-cuts (Kendeigh 1947; Sanders 1970). Near Manitouwadge, it occurred in all age classes of forests but was most abundant in stands 1-23 years old (Venier et al. 2009). Near White River, it was most frequent in stands 18-20 years old, but not significantly (Venier and Pearce 2005). Welsh (1993) considered it a species that occupied all age classes of forest and documented it in stands 3-220 years old. Near Quetico Park, Apfelbaum and Haney (1985) reported it in stands 1-370 years old. In the Clay Belt of Ontario, Welsh and Lougheed (1996) found the Magnolia Warbler in every stand they surveyed. It was most abundant in balsam fir–spruce stands followed by those dominated by jack pine, trembling aspen, and balsam poplar. It occurred in wet to dry sites, but less frequently in wet stands and was present in stands that covered the entire spectrum of nutrient levels. Near Hearst, it occurred in upland mixed and lowland coniferous stands. It occurred in clear-cuts as young as 3 years old and in all older clear-cuts and uncut forests. It reached very high densities and was the dominant species in 2 stands. In many other stands, it was second in abundance to the Tennessee Warbler which was extraordinarily abundant due to a spruce budworm outbreak. On the northeast shore of Lake Superior, Baillie and Hope (1943) found it mostly in mixed woods, particularly where there were small spruces present.

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Magnolia Warbler tended to avoid pure jack pine stands near Gogama and preferred edges of mixed forests. It occasionally nested in jack pine stands 15-25 years old where there were openings with some small spruce growing. It was more common in 15-30-year-old mixed stands where small spruce or balsam fir were interspersed at edges or openings (James and Peck 1995a). Kirk et al. (2012) reported that it occurred in mature and old-growth stands of white pine, and was slightly more common in mature stands. It was the fifth-most abundant bird species in these communities and represented 4.7% of all bird sightings. In white pine stands in Algonquin Park, it was present in clear-cuts 2-9 and 10-16 years old and in stands with no recent history of harvesting (Kingsley and Nol 1999). In Algonquin Park, Martin (1960) reported the Magnolia Warbler in stands dominated by black spruce, black spruce–white cedar, white birch–poplar, hemlock, and balsam fir–spruce-hardwoods, and in plots at edges of forests. He considered it characteristic of boreal forest and did not record it in pure deciduous or immature white pine stands. In poplar-birch stands, it was active from the ground to the treetops but concentrated its activities at heights of 1.5-9 m, from the mid-level of shrubs to the mid-canopy. In black spruce–white cedar, territories ranged from the ground to 9 m, midway up the height of the cedars. In hemlock stands, it ranged from 1.5-6 m, entirely below the canopy. In balsam

fir–spruce-hardwood stands, it was second in abundance, but occurred at higher density in pure coniferous stands. In plots at edges of mixed forests, it was second in abundance to the Red-eyed Vireo. Tozer (2012) reported that it often nested in Algonquin Park in young coniferous growth such as balsam fir and white spruce. In Muskoka and Parry Sound districts, it preferred balsam fir and spruce forests (Mills 1981). In tolerant hardwood stands near Sault Ste. Marie, it was associated with the number of hardwood saplings (mostly sugar maple) and the percent coverage by hardwood seedlings less than 50 cm tall (Holmes and Pitt 2007).

No detailed information has been compiled on the Magnolia Warbler's habitat requirements in the Great Lakes–St. Lawrence Forest Region south of the Shield. In this area, it also prefers mixed and coniferous forests, especially where there are small conifers present. The structure of its habitat is similar to that of the Chestnut-sided Warbler. Both species require young, dense patches of shrubs or saplings, with the Chestnut-sided Warbler preferring deciduous species and the Magnolia Warbler preferring conifers. The Magnolia Warbler may also breed in coniferous plantations in this region (LaForest 1993; Weir 2008).

Sutherland (1986) described breeding habitat in the Carolinian Forest Region in Halton Region and Middlesex and Norfolk counties. Breeding habitat in Halton consisted of the interface between a regenerating wet meadow and a white cedar–tamarack stand. The meadow was almost completely covered with dense regeneration of white cedar and tamarack, with lesser numbers of trembling aspen, balsam poplar, and beaked willow. In Middlesex County, the Magnolia Warbler was found in an intermediate-aged coniferous plantation bordering the Dorchester Swamp. In Norfolk County, it has been encountered regularly in the extensive, mature coniferous plantations at St. Williams and Turkey Point. There are also breeding season records from Long Point in white pine and white cedar woodlands. In southwestern Ontario, it may occur in larger cedar swamps and older coniferous plantations. In the Hamilton area, it has been observed since the 1990s in coniferous plantations, but many of these are maturing to the point where they are no longer suitable habitat (Curry 2006). It is more the structure of plantations than their age that determines their suitability. The Hamilton plantations are intermediate in age and have not been thinned extensively; consequently they have few shrubs and saplings in the understorey. The Norfolk County plantations that are inhabited are mature and have been managed for timber harvest. Many of these have evolved into mixed forests with a well-developed understorey. In Elgin County, it nests in ravines dominated by hemlock (Lancaster et al. 2004).

Throughout its range, the Magnolia Warbler nests mostly in mixed and coniferous forests and, to a much lesser extent, deciduous forests. In deciduous forests, it typically seeks out patches of conifers but nests in pure deciduous forests in the southern portion of its range. It is characteristically associated with spruce and balsam fir stands, in either pure stands of these species, in stands where these species codominate, or in spruce-fir stands mixed with varying amounts of poplar and birch. South of the more boreal stands of spruce and fir, it is most common in hemlock stands, often in ravines. Other conifers that it may be associated with include white cedar, white pine, pitch pine, and junipers. It appears to be a habitat generalist at the forest community level, occurring in a wide range of vegetation communities on soils that range from dry to very wet. It also inhabits a range of stand ages from very young clear-cuts to old-growth forests. In some areas, it nests in coniferous

plantations, particularly those dominated by spruce. It occasionally inhabits shrubby fields (Back 1979; Beals 1960; Bent 1953; Brooks 1940, 1947b; Campbell et al. 2001; Capen 1979; Chapman 1907; Crawford and Titterington 1979; Cumming 2004; Dawson 1979; Dunn and Hall 2020; Erskine 1977; Freedman and Johnson 1999; Harrison 1984; Hedge et al. 1996; Hoffman 1989a; Kendeigh 1947; Kirk et al. 1996; Kotesovec 1994a; Lamoue and Morrier in Gauthier and Aubry 1996; Nice 1926; Parker et al. 1999; Sabo 1980; Schieck et al. 1995; Sinclair et al. 2003; Temple et al. 1979).

Forest structure is probably more important to the Magnolia Warbler than forest type. It is a warbler of dense shrubs and saplings, and presence of young conifers is the most predictable aspect of its habitat. Consequently, it is associated with young stands, including fields regenerating with conifers and clear-cuts, and forests with open canopies that allow coniferous regeneration. Territories may include both mature forests and clear-cuts. In New Jersey, it was the first warbler to colonize regenerating old fields. Densities in New Brunswick plantations were very low until tree-sized plants became established at about age 13 years. Once plantations form a closed canopy they become unsuitable until harvesting opens up the canopy and allows regeneration to occur. In northern hardwood stands, it is more abundant in disturbed and early successional habitats than in mature undisturbed areas; it is uncommon in this type of habitat. In Quebec black spruce stands, it was associated with younger development stages such as recent clear-cuts and burns, although it also occurred in lower densities in forests 120-200 years old. Over a 30-year period at a site in New York, it disappeared as a breeding species. This was attributed to natural succession, with the formerly open canopy becoming closed and shading out the shrub layer. In dense, young stands of spruce and balsam fir, it is often the dominant warbler or even dominant species, except for the spruce-budworm specialist warblers during an outbreak. Riparian areas dominated by alders or willow shrubs are another habitat that it readily occupies. Over 35 years of succession in New York, the Magnolia Warbler increased significantly in an open agricultural field that transitioned to a second-growth forest. Over 33 years, it remained stable in an undisturbed mixed forest. In a Christmas tree plantation where the trees were well spaced but grew taller over 25 years, it increased significantly (Bent 1953; Brooks and Bonter 2010; Campbell et al. 2001; Dunn and Hall 2020; Erskine 1977; Freedman and Johnson 1999; Imbeau et al. 1999; Lent and Capen 1995; Litwin and Smith 1992; Morgan and Freedman 1986; Morse 1989; Niemi and Pfannmuller 1979; Noon et al. 1979; Thompson et al. 1999).

In Ontario, the Magnolia Warbler inhabits all ages of forests from very young clear-cuts to mature stands. Studies in other areas often found that it preferred certain age classes of forest, but the preferences often differed in the same geographic region suggesting that the preferences are related more to stand structure and species composition than age. In the Prairie Provinces, Kirk et al. (1996) found no significant differences in its abundance in stands 0-9, 15-20, 40, or 80 years old, although it was more abundant in 15-20-year-old stands. Schieck et al. (1995) reported it only in aspen-dominated stands that were older than 120 years in Alberta. It was significantly more abundant in forests older than 140 years than in younger stands in Saskatchewan. The older stands had a higher proportion of conifers and higher percent coverage by shrubs (Cumming and Diamond 2002). The studies in the prairies were conducted in the Boreal Forest Region, where Erskine (1977) stated that it was more common in young than mature coniferous forests. The Prairie Boreal Forest Region is often dominated by poplars, with conifers occurring predominantly in more

mature stands which may explain differences in preferences for stand age. In mixed forests in the northeast, it was associated with late succession and mature stands (Temple et al. 1979). In Maine, Titterington et al. (1979) found it in all age classes of spruce–balsam fir stands, from clear-cuts dominated by slash and bare ground to dense forests with a closed canopy and open understorey. It was significantly more abundant in the mid-stage of succession which was characterized by deciduous regeneration taller than 2 m with a well-developed but slower growing coniferous regeneration layer. It was one of the dominant species in this stage of succession. In Pennsylvania, it occurred in 100% of old-growth hemlock–white pine–hardwood stands, 15.1% of woodlots statewide, and in 31.5% of woodlots in the Appalachian Plateau. Haney (1999) considered it to have old-growth affinities.

Collins (1983a) found no differences in the habitat preferences of the Magnolia Warbler in Maine and Minnesota. It was associated with more than average coverage by conifers and moderately sized trees that were mostly larger conifers. It was in a guild that inhabited forest and forest edge with a high percentage (70%) of ground cover and moderate canopy closure. In Wisconsin, the Magnolia Warbler was in a guild associated with yellow birch and all conifers (spruce, balsam fir, white cedar, and hemlock) except pine (Beals 1960).

Despite its usage of young and often very small stands, the Magnolia Warbler appears to prefer landscapes that are heavily forested. In Quebec, the mean forest cover within 500 m of territories was 56.5%. This value may be biased upwards because the entire study area was heavily forested (Bourque and Desrochers 2006; Dunn and Hall 2020).

Some studies examined the Magnolia Warbler's preference for riparian and nonriparian balsam fir stands in Newfoundland and Quebec, and in coniferous forests in British Columbia. In 1 Newfoundland study, there was no significant difference in its abundance in riparian areas, in forest interior, or at forest edges distant from riparian areas, although it was most abundant in the latter habitat. Another Newfoundland study found that it was significantly more abundant in 30-m-wide riparian buffer strips than in undisturbed strips 50 m wide. In Quebec, it was more abundant in riparian than nonriparian stands, but not significantly; riparian habitat consisted of meadow marsh and shrub thickets. During the breeding season in British Columbia, it was positively correlated with riparian willow and alder thickets, but not significantly (LaRue et al. 1995; Whitaker and Montevecchi 1997, 1999; Wiebe and Martin 1998).

Ralston et al. (2019) surveyed for the Magnolia Warbler in 20 plots in boreal forest habitat in New York, Vermont, Maine, Nova Scotia, and Newfoundland. It occurred at 14 of the sites indicating broad habitat preferences and an ability to use multiple boreal forest habitats. It was found throughout low- and high-elevation sites at low latitudes.

Some studies identified microhabitat preferences of the Magnolia Warbler. In Minnesota, average habitat characteristics were 51.1% ground cover, 76.1% shrub coverage, 61.1% canopy coverage, 16.9 m canopy height, 40.0% coniferous coverage, 4.6 tree species in the surrounding 0.04-ha circle, 18.0 trees 7.5-15 cm diameter at breast height (DBH), 12.4 trees 15.1-23 cm DBH, 8.9 trees 23.1-30 cm DBH, 3.8 trees 30.1-38 cm DBH, 2.1 trees 38.1-53 cm DBH, 0.6 tree 53.1-68 cm DBH, and 0.2 tree larger than 68 cm DBH. It occurred in a broad range of habitat, but always had some dense growth of spruce or balsam fir saplings within its territory. Presence of small conifers was the

most predictable component of its habitat. It appeared to be a habitat generalist but was restricted to a narrow species-specific subset of habitat resources (Collins et al. 1982). In Vermont, it occurred in habitats with dense vegetation less than 3 m tall and no overhead tree canopy. It was associated with a very dense understorey in clear-cuts and also in pole-sized stands. Mean habitat characteristics were 76.3% green ground cover, 6.7% ground cover by slash, 48.3% canopy closure, 11.2 m canopy height, 11.0 m^2 basal area (BA) deciduous cover, and 9.7 m^2 BA coniferous cover (Thompson and Capen 1988). In subalpine areas of New Hampshire, it occurred where there were wet depressions with means of 7.9 m canopy height, 59% canopy closure, 72% coniferous foliage volume, and 10 cm DBH for live trees (Sabo 1980). In subalpine areas of New Hampshire and Maine, abundance of the Magnolia Warbler was negatively correlated with total foliage volume of deciduous stems smaller than 2 cm DBH (DeGraaf et al. 1998). In the mid-Atlantic states, its presence was positively correlated with percent coverage by conifers, percent ground cover, and forest cover within 2 km. It was negatively correlated with the number of snags larger than 3 cm DBH and foliage density between 2 and 3 m (Robbins et al. 1989).

Without any documentation, Freemark and Collins (1992) designated the Magnolia Warbler a forest-interior species. This is not the case and, if anything, the opposite may be true in many areas. In Maine, Morse (1967) found it both at forest edges and in forest interior. In Newfoundland, Whitaker and Montevecchi (1999) considered it a species of forest edges and open areas rather than a forest generalist or forest-interior species. Bent (1953) stated that it avoided forest interior in favour of more open spaces.

Freemark and Collins (1992) stated that the Magnolia Warbler was classified as area-sensitive by some authors but not by others. No references to its being area sensitive were found. It was not identified as area-sensitive in Maryland or the mid-Atlantic states (Bushman and Therres 1988; Robbins 1979; Robbins et al. 1989). In Maine, it nested on islands as small as 1 ha (Morse 1989) and it was not restricted to larger islands in Wisconsin (Beals 1960).

Ontario nests were in living trees and shrubs with the exception of one in a dead tree. The Magnolia Warbler greatly preferred conifers (91.0% of nests in 7 species) over deciduous species (9.0% in 4 species). A more recent nest was found in common juniper to bring the total number of coniferous nest-tree species to 8. It greatly preferred nest-tree species shorter than 3 m (86.4% of nests) to those 3-6 m tall (4.5%) and larger trees (9.1%). The DBH of 3 nest trees ranged from 2.5 to 7.5 cm. The most common nest-species were spruce (59 nests), balsam fir (19), hemlock (5), white cedar (4), maple (3), and alder (3). Nests may be either distant from the trunk on a limb, usually within several branchlets or a crotch, or against the trunk. Ten nests were 0.6-2.4 m from the tree trunk. Four nests were on lateral branches between the trunks of 2 adjacent small trees. Nest heights were 0.25-6 m, with most 0.8-1.5 m from the ground (Peck and James 1987, 1998a). A nest near Campbellville was in a dense clump of white cedars 8-10 m tall. It was 2.25 m above ground near the end of an upturned lower bough of a small cedar (Sutherland 1986).

Nests elsewhere are typically elevated a short distance above the ground in a living tree, where they are usually well concealed. Most nests are in conifers, particularly balsam fir and various spruce species (black, white, red, and Norway). Further south, hemlock is a preferred nest-tree species; of 50 Pennsylvania nests, 49 were in hemlock. Other nest-species include meadowsweet, juniper,

blackberry, witch-hazel, pin cherry, sugar maple, willow, and birch. Nests were 0.15-10.7 m from the ground, but were seldom higher than 5 m and usually under 3 m. Of 33 Maine nests, 54.5% were less than 1.5 m from the ground, 39.4% were 1.5-3.0 m up, 6.1% were 3.0-4.6 m up, and 0% were higher than 4.6 m. These results are typical for the species. The nest is on a lateral branch or crotch at or distant from the trunk (Bent 1953; Campbell et al. 2001; Chapman 1907; Cruickshank 1956; Dunn and Hall 2020; Harrison 1984; Kotesovec 1994a; Mills 1981; Mousley 1916a, 1924, 1946; Nice 1926; Sinclair et al. 2003; Stanwood 1910a).

Males establish a territory immediately upon arrival and maintain them until the young fledge, but the intensity of defence wanes in the latter part of the nesting cycle. Most activities are conducted within the territory but females sometimes go well beyond the territorial boundaries during incubation. The function of this is unknown because this is past the period when females may seek extra-pair copulations. Near Quebec City, territories were significantly autocorrelated, or clumped, at scales of 250, 350, 450, and 550 m. Near Lake Nipigon, 7 territories averaged 0.57 ha (range 0.40-0.65 ha). Few observations were made of individual birds, so territories could have been larger. In Algonquin Park, average territory size was 0.30 ha (range 0.26-1.69 ha). In New York, 15 territories averaged 0.73 ha. The smallest (0.24 ha) was in a dense shrubby area. The largest (1.2-1.6 ha) included a pine-spruce plantation where the nest was located. In subalpine habitat in New Hampshire, territories averaged 0.7 ha. On 2 Maine Islands, average territory sizes over 6 years were 0.70-0.75 ha and 0.75-0.88 ha and 9 territories in spruce forest on the mainland averaged 0.72 ha (range 0.51-1.05 ha; Bourque and Desrochers 2006; Dunn and Hall 2020; Kendeigh 1945, 1947; Martin 1960; Morse 1976, 1977; Sabo 1980).

No information is available on natal philopatry, but it is probably low. No information is available on the proportion of adults that exhibit breeding season site fidelity. Nine birds banded in their probable breeding location were recovered at the original banding site in subsequent years indicating some level of site fidelity (Dunn and Hall 2020).

Limiting Factors

Peck and James (1987, 1998a) reported eggs in Ontario nests from the last week of May until the third week of July, with most present in the last 3 weeks of June. In Algonquin Park, nests are under construction from late May to late June, eggs are present from late May to mid-July, nestlings are present from early June to early August, and dependent fledglings have been seen from mid-June to late August (Tozer 2012).

It is uncertain if nest construction is initiated immediately after the female arrives or if some time elapses. Nests take approximately 6 days to construct. The first egg is laid 1-3 days after the nest is complete. Incubation may begin after the second egg is laid but typically not until the clutch is complete. The incubation period of Ontario nests was 11-13 days. Overall, incubation periods of 10-15 days have been reported but the Ontario range is more typical. Young may leave the nest when they are 8 days old when they are incapable of flight, but more frequently at age 9-10 days (Bent 1953; Dunn and Hall 2020; Morse 1989; Mousley 1924; Nice 1926; Peck and James 1998a; Stanwood 1910a).

A single brood is raised annually. There are indications of possible second broods in New York and Pennsylvania, but double brooding has not been conclusively documented. One New York

study reported that second broods were attempted regularly, but this may have been referring to replacement clutches. The Magnolia Warbler renests regularly if a clutch is lost and 1 or 2 replacement clutches may be laid in an attempt to raise a brood. Clutches of 2-5 eggs were reported in Ontario (average 3.78 eggs). Four-egg clutches were most abundant and constituted 64.8% of clutches. In other areas, clutches of 3-6 eggs have been reported, with only 1 author reporting a 6-egg clutch. Four eggs is the typical clutch size. An analysis of North American clutches revealed that 90% consisted of 4 eggs, 7% held 3 eggs, and 3% contained 5 eggs (Bent 1953; Campbell et al. 2001; Chapman 1907; Dunn and Hall 2020; Harrison 1984; Kendeigh 1945; Mousley 1916a, 1924; Peck and James 1987; Stanwood 1910a).

The mating system is monogamous and pairs remain intact throughout the breeding season. Both sexes are probably capable of breeding at age 1 and every year thereafter. Many populations contain a sizable population of nonbreeding floaters, suggesting that some first-year males may not be successful in attracting a mate (Dunn and Hall 2020; Nice 1926).

Mills (2007) studied the foraging strategies of the Magnolia Warbler during different seasons in Parry Sound District. During the breeding season and autumn, it was associated with conifers, hardwoods, and early successional habitats. It was associated more with early successional habitats in mid-summer (which may have included the postfledging period). Habitat selection during the breeding season and autumn allowed it access to a wider range of tree species. Foraging occurred at heights of 3.9-11.8 m during the breeding season and 3-11.9 m in autumn. Most authors concur that the Magnolia Warbler forages predominantly in the shrub and subcanopy levels rather than in the upper canopy, although a small proportion of foraging occurs there. Females may also forage in the herbaceous layer. In Saskatchewan, it used subcanopy trees more than any other species and had the lowest average foraging height. It mostly used young regenerating trees. Average foraging heights are consistent throughout its range: 7.3 m in Maine (range 0.0-13.7 m); 5.8 m in conifers and 6.9 m in deciduous species in Saskatchewan; 7.4 m in northern Ontario; 5.4 m in Mackenzie District; and 72.6% of observations 2-8 m from the ground in New Hampshire (Cumming 2004; Greenberg et al. 1999; Kotesovec 1994a; LaRue et al. 1995; Morse 1967; Sabo 1980). In Maine, there was considerable overlap in the foraging heights of the sexes, but males tended to forage higher than females. Males foraged lower than their song perches but still well above females. Male foraging height was associated more with the level of their singing perches than that of the nest; females foraged lower near the nest level. Feeding at the same level of the nest probably saves the female energy. Higher foraging by the male allows him to be conspicuous and facilitates territory defence (Morse 1968). The Magnolia Warbler may exhibit preferences for tree types and species and where it forages within trees. These preferences differ geographically, probably in response to which competitive species are present and to local prey availability. In Saskatchewan, it foraged more than expected in white birch based upon its availability and less than expected in trembling aspen. It used spruce and balsam fir in proportion to their availability. In northern Ontario, 47.0% of foraging occurred in conifers compared with only 28.0% in Mackenzie District; 72% of foraging occurred on conifers in subalpine New Hampshire. In Saskatchewan conifers, it was significantly more abundant in the middle of the tree with no usage of the extreme top or bottom. In deciduous trees, the inner parts of branches near the trunk were used significantly less than the 2 outer zones and there was no difference in usage among the vertical zones (Cumming 2004; Greenberg et al. 1999; Sabo 1980).

Most feeding occurs where the overhead foliage can be reached, predominantly from a small twig. About 58% of foraging occurs on the undersurface of leaves, 22% on the tops of leaves, and 20% on twigs. Gleaning is the preferred foraging technique but hovering, including some flycatching, is sometimes as common as gleaning (Dunn and Hall 2020; Kotesovec 1994a; Morse 1967, 1968; Sabo 1980).

Some studies compared the Magnolia Warbler's foraging strategies with those of other warblers and species. In Maine, Morse (1967) concluded that its foraging was not particularly similar to that of the Golden-crowned Kinglet, Northern Parula, Blackburnian Warbler, or Black-throated Green Warbler. In Saskatchewan, the Magnolia Warbler had a 95% overlap with the Boreal Chickadee and Yellow-rumped Warbler in conifers and an 88% overlap with the Tennessee Warbler in deciduous species. Two thirds of observations of the Boreal Chickadee and Magnolia Warbler were in subcanopy trees, but the Yellow-rumped Warbler was found significantly more in canopy trees than these 2 species. Two thirds of observations of Tennessee, Blackburnian, and Black-throated Green warblers were in canopy. Use of subcanopy trees by the Magnolia Warbler mostly segregated its habitat from potentially competitive warbler species (Cumming 2004). In New Hampshire, Sabo (1980) identified the Magnolia and Yellow-rumped warblers as a transition group from conifer and large substrate use to the more generalized species and distinct from the kinglets on fine substrates and the Red-breasted Nuthatch on the bole. The Black-throated Green Warbler aggressively displaced the Magnolia Warbler. Density of the Magnolia Warbler was higher in similar habitats where the Black-throated Green Warbler was absent. Both the Magnolia and Yellow-rumped warblers foraged low in trees but differed somewhat in habitat selection.

Nestlings are fed mostly caterpillars, but also grasshoppers, miscellaneous insects, and spiders. Adults eat mostly insects, predominantly caterpillars, and some spiders. There is 1 record of the Magnolia Warbler feeding on cultivated grapes. Adults have eaten aphids, leafhoppers, beetles (weevils, soldier beetles, and leaf beetles), flies, brown and green lacewings, caddisflies, beetle larvae, scale insects, sawfly larvae, ants, moths, and locusts. It eats later instars of the black-headed budworm and takes considerable numbers of spruce budworms when they are at epidemic levels. In New Hampshire and Maine, it was 1 of 4 species that ate the most budworms along with the Cape May, Bay-breasted, and Blackburnian warblers. Despite its high consumption of spruce budworms, the breeding density of the Magnolia Warbler often declines during budworm outbreaks. This has been documented in Ontario near Lake Nipigon and in New Brunswick and Maine. Near Manitouwadge, there was either no response or possibly some evidence for a positive response to budworm numbers. The inverse relationship with budworm populations has been attributed to competition with more common and aggressive species such as the Bay-breasted Warbler. Forty-nine stomachs collected in Maine during a spruce budworm outbreak contained 48% and 39% budworm larvae and pupae by volume in 2 years. The diet of 4 adults from the Lake Nipigon area consisted of 30.3% beetles (weevils, click beetles, and soldier beetles), 29.4% spiders and harvestmen, 12.9% lepidopterans, 11.3% aphids, 7.4% flies (house flies and march flies), 5.8% green and brown lacewings, and 2.9% leafhoppers (Bent 1953; Crawford and Jennings 1989; Dunn and Hall 2020; Gage et al. 1970; Kendeigh 1945, 1947; Kotesovec 1994a; Mitchell 1952; Morris et al. 1958; Mousley 1924; Nice 1926; Venier et al. 2009).

The Magnolia Warbler is an infrequent host of the Brown-headed Cowbird. It is unknown what effect parasitism has on its reproductive success. It may successfully fledge cowbirds. Although the current rate of parasitism is low, there are concerns that parasitism may be increasing. In Ontario, 12 of 122 nests (9.8%) were parasitized. The actual frequency of parasitism is probably lower because large areas of the Magnolia Warbler's range in Ontario have few or no cowbirds. In Quebec, 6 of 147 nests (4.1%) were parasitized; 3 of 15 nests (20.0%) in British Columbia were parasitized; 6 of 31 nests (19.4%) in Maine and Pennsylvania were parasitized; and 1 of 164 nests (0.6%) reported to the Western Foundation of Vertebrate Zoology was parasitized (Bent 1953; Campbell et al. 2001; Dunn and Hall 2020; Harrison 1984; Hedge et al. 1996; Mousley 1946; Peck and James 1998a).

Habitat loss and degradation do not appear to be significant issues for the Magnolia Warbler. It has been suggested that it is more common now than prior to European settlement because forest clearing created suitable habitat. This may not be the case in southern Ontario because the original forest cover should have been more favourable than the current agricultural landscape with scattered woodlots. Clear-cutting and other forest management practices in the Canadian Shield improve habitat, but it has declined in Algonquin Park and other areas as a result of fire suppression and forest maturation, which result in the loss of the shrub layer. In the south, coniferous and mixed plantations may provide suitable breeding habitat. Browsing by white-tailed deer may reduce or eliminate the shrub layer in forests. On Anticosti Island, the Magnolia Warbler was able to use the ground layer vegetation where deer densities were high. Nonetheless, it was recommended that deer density not exceed 7.5 per km^2 and large areas of southern Ontario support higher densities than that target (Cardinal et al. 2012; Dunn and Hall 2020; Lamoue and Morrier in Gauthier and Aubry 1996; Tozer 2012).

In Ontario, forest harvesting is beneficial for the Magnolia Warbler. In the Boreal Forest Region, Vanderwel et al. (2009) concluded that it increased when 30%, 50%, or 70% of the tree cover was removed. In Quebec black spruce stands, Imbeau et al. (1999) concluded that it would benefit from short logging rotations. Near Sault Ste. Marie, selection harvesting in northern tolerant hardwoods resulted in an increase in its abundance 2-3 years after harvesting. Postharvest numbers were inversely related to the amount of residual BA (Holmes and Pitt 2007). In the Canadian Shield of Ontario, it was significantly more abundant in early successional and mid-successional clear-cuts than in burns in the same seral stages. It was significantly less abundant in early successional and mid-successional stands than in mature stands (Zimmerling et al. 2017). In Minnesota, it was one of the most responsive species to harvesting, increasing in abundance in clear-cuts and partial cuts relative to control areas (Hanowski et al. 2005). Forest clearing may reduce populations if conifers are eliminated or if the habitat becomes permanently fragmented. In Saskatchewan aspen stands, it was most abundant in stands older than 140 years old because these contained higher proportions of coniferous cover. The rotation age was 80-90 years, and it was concluded that it could decline if stands older than rotation age were completely lost from the landscape (Cumming and Diamond 2002; Dunn and Hall 2020).

Abnormally cold or wet periods may depress populations. Extended periods of fog may also reduce breeding success (Dunn and Hall 2020; Morse 1968).

In Alberta, Bayne et al. (2008) observed no differences in occupancy rates at noisy compressor stations and quiet well pads. The Magnolia Warbler apparently exhibited no response to chronic noise.

In Alberta, the Magnolia Warbler was significantly less abundant at pipelines than in adjacent forest interior. There were no significant differences in its abundance at seismic lines or well pads than in forest interior adjacent to these features (Bayne et al. 2016).

Price (2004) predicted that the summer range of the Magnolia Warbler might exclude southern Ontario if the average summer temperature increased by 2°C. In southern Quebec, it was associated with cooler and wetter summers and was considered sensitive to climate change. In central Quebec and Labrador, it was associated with stands having the warmest summer temperatures and would probably benefit from climate change (DesGranges and LeBlanc 2012; DesGranges and Morneau 2010). The Quebec results underscore the difficulties in predicting effects of climate change on species over broad geographic areas.

Status

Presumably the Magnolia Warbler was always a common breeder in the province, although earlier ornithologists discussed its status as a migrant only. Baillie and Harrington (1937) considered it common in coniferous forests north from about latitude 44°N to the Albany River, where it was the most abundant warbler. It bred from southern Georgian Bay and Frontenac County west to Thunder Bay and probably to Lake of the Woods. They expected that it would breed in the south because it had nested in New York adjacent to the St. Lawrence River. James et al. (1976) reported it to be common from Guelph north to Big Trout Lake and Fort Albany. During the first atlas, the Magnolia Warbler had a continuous range throughout the Canadian Shield, Manitoulin Island, the Boreal Forest Region, and the southern portion of the Hudson Bay Lowland. It was also found in scattered locations south of the Shield, mostly in the Great Lakes–St. Lawrence Forest Region. A few breeding records were obtained in the Carolinian Forest Region near Long Point, near the Thames River, and on the Lake Huron shoreline (Welsh in Cadman et al. 1987). Sutherland (1986) concluded that it was a very rare breeder in southwestern Ontario, despite recent records from Halton Region and Middlesex and Norfolk counties. It may have been more common in the south previously, with records from Middlesex, Perth, Wellington, and York 1884-1944. It was previously much more abundant in Algonquin Park after extensive fires and heavy logging created suitable habitat (Tozer 2012). James (1991) considered the Magnolia Warbler a common summer resident from southern Georgian Bay and Ottawa north to Big Trout Lake and Fort Albany; occasional and rare north to Sutton Lake and Fort Severn; and occasional and rare south to Norfolk County.

The second atlas indicated no significant change in the breeding distribution of the Magnolia Warbler, although there were isolated records from the Tundra Region. Its probability of observation increased significantly province-wide and in all atlas regions except the Hudson Bay Lowland, where it experienced a nonsignificant increase. Large increases occurred south of the Shield, with it reported in many new squares. Increases were attributed to succession of retired farmland to young forests in the south and forest harvesting in the north. It was one of the most abundant species in the province. Highest densities occurred in the Boreal Forest Region south of latitude 51°N and the

western portion of the Great Lakes–St. Lawrence Forest Region in the Shield. This corresponds with the area where most clear-cutting operations take place (McLaren in Cadman et al. 2007).

Much of the Magnolia Warbler's range is not sampled by the Breeding Bird Survey (BBS). BBS results suggest that it is increasing, with a significant rangewide increase of 1.3% per year 1966-2007. There was a significant increase of 3.4% 1966-79 and a nonsignificant increase of 0.06% 1980-2007 (Dunn and Hall 2020). BBS data indicate that it increased at an annual rate of 9.49% in Canada and decreased at an annual rate of 0.169% in Ontario 1970-2021. The trends for 2011-21 were annual decreases of 1.57% in Canada and 3.87% in Ontario. The results were of medium reliability except that the short-term Canadian trend was highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young leave the territory shortly after fledging, but may be attended by the adults until they are 25 days old. Once they are independent, juveniles often join other birds in loose flocks (Bent 1953; Dunn and Hall 2020). During the postfledging period in Pennsylvania, Stoleson (2013) found almost identical numbers of Magnolia Warblers in mature forests and adjacent clear-cuts. It could conceivably have bred in both habitats, so it was unknown whether there were any movements from breeding to postfledging habitats.

MIGRATION

Most migration by the Magnolia Warbler is nocturnal, but it may move during the day to correct for displacement by winds during the night. During the day, it occurs in mixed flocks of small passerines, particularly those centred around the Black-capped Chickadee. It may also occur in flocks as large as 50 comprised solely of Magnolia Warblers. Three birds banded at the Long Point Bird Observatory (LPBO) were recovered in Cuba, the Honduras, and Guatemala. Birds of both sexes tracked during spring migration that were captured at LPBO moved predominantly northward toward the southern tip of Georgian Bay. Some females moved northeastward to the shoreline of Lake Ontario between Toronto and Kingston (Brewer et al. 2018; Dunn and Hall 2020; Morbey et al. 2018).

Males arrive on the breeding grounds prior to females by as much as 7-10 days in New York and Ohio (median date of 19 May for males and 26 May for females) but the difference is not as pronounced in Ontario. At Prince Edward Point, mean arrival for males was 21.2 May compared with 24.1 May for females. In spring at LPBO, mean capture dates for males were 16.9 May for after-second-year birds, 20.4 May for second-year birds, and 18.9 May for those of undetermined age. Mean capture dates for females were 21.4 May for after-second-year birds, 23.9 May for second-year birds, and 23.0 May for those of undetermined age. For both sexes, after-second-year birds arrived significantly earlier than second-year birds. In Ohio, adult birds also arrived significantly earlier than yearlings. Mean capture dates were 13 May for adult males, 17 May for yearling males, 21 May for adult females, and 23 May for yearling females. At a Minnesota site, average stopover time was 4 days in both spring and autumn. At Long Point, the midpoint of spring migration was 21 May. In southern Ontario, the Magnolia Warbler typically arrives in the first or second week of May and is common until the end of May. A few may arrive in late April. The peak of migration is in the last half of May with most migrants gone by the end of May, but a few remain into early June. In the southern Shield, most arrive in the last half of May (Black and Roy 2010; Boone et al. 2010; Curry 2006; Dunn

and Hall 2020; Fleming 1907; Francis and Cooke 1986; Keast 1980; LaForest 1993; Lancaster et al. 2004; Mills 1981, 2005a; Stewart et al. 2002; Tozer 2012; Weir 2008).

Most birds leave the breeding grounds by mid-August and juveniles initiate autumn migration 1-2 weeks earlier than adults. At LPBO, juveniles preceded adults by an average of 16 days in 1 year and 5 days in another year. At Moosonee, single birds observed on 31 July and 7 September were considered migrants. In the southern Shield, migration peaks in early September with the latest records in late September or early October. In the south, autumn migrants are present from mid-August to early or mid-October, with rare records as late as mid-November. The midpoint of autumn migration at Long Point is 7 September (Black and Roy 2010; Curry 2006; Dunn and Hall 2020; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Mills 1981, 2005a; Tozer 2012; Weir 2008; Wilson and McRae 1993; Woodrey and Chandler 1997).

Dunn and Hall (2020) stated that spring arrival dates of the Magnolia Warbler were 0-4 days earlier than they were historically. At Long Point, Mills (2005a) compared first spring arrival and last autumn departure dates 1974-2002. There was a tendency toward earlier spring arrival but this was not significant. There was also no significant difference in arrival times of the sexes. There were no differences in autumn departure dates.

Boone et al. (2010) used stable isotopes as an indicator of the wetness of wintering habitat used by spring migrants captured in Ohio. For some species, wetness of wintering habitat can affect migration timing. The Magnolia Warbler overwintered in both mesic and xeric habitats and there was no relationship between winter habitat moisture and migration timing, energetic condition at capture, or moult and breast-streaking conditions.

During migration, the Magnolia Warbler occurs in a variety of habitats including forests and forest edges, bottomland forests, riparian shrub thickets, shrubby pastures and fields, city parks, backyards, orchards, and farmyards. It tends to be associated more with shrubs and forest edge. In forests, it uses treefall gaps where there is more shrub cover than in the surrounding forest and tends to remain low in the canopy and in shrubs. During spring and autumn in Illinois, it was most abundant in forest edge habitat and shrubby areas. In spring, small numbers occurred in bottomland forests but higher usage of this habitat occurred in autumn. During both migration periods, but particularly autumn, some birds were detected in upland forests, orchards, marshes, and pastures. During spring migration in Ohio, it was significantly more abundant in mature upland than mature riparian forests. Upland forests had a more open canopy (74% compared with 83%) and more than twice as much shrub coverage (39% compared with 19%). It was positively correlated with riparian habitat during migration in British Columbia, particularly in autumn when this relationship was significant. Riparian habitat consisted of willow and alder shrubs; the nonriparian habitat was coniferous forest. In both Ohio and British Columbia, the Magnolia Warbler appeared to select areas with extensive shrub coverage. During autumn migration in Pennsylvania, it was significantly more abundant in forest edges, forest-agricultural edges, shrub-sapling-stage forests and suburban forests than in pole-stage forests and forest interior (Bent 1953; Campbell et al. 2001; Chapman 1907; Dunn and Hall 2020; Graber et al. 1983; Leighton et al. 2002; Rodewald and Brittingham 2002, 2004; Rodewald and Matthews 2005; Wiebe and Martin 1998).

Prey availability is important in determining whether Magnolia Warblers gain or lose weight during migratory stopovers, particularly in spring. At Long Point, the earliest spring migrants lost weight at the tip and midpoint of the peninsula, but gained mass at the base of the peninsula. By the peak of migration, birds experienced a net gain in weight at the midpoint. At the tip, birds continued to lose weight, but conditions improved as the season progressed. Due to the coldness of the lake, there is marked retardation of phenology at the tip of the peninsula. Although large numbers of birds occur there, it is not necessarily good habitat for refuelling. During the peak of autumn migration, it gained mass at all 3 sites at Long Point, probably because prey is not limiting at this time (Dunn 1998, 2000). Emerging midges along the Great Lakes shorelines can be an important source of prey in spring. Along the Lake Huron shoreline in Michigan, the coast was an important resource-rich area with more arthropods near than distant from the shoreline. Emerging midges appeared to be responsible for creating high-quality stopover habitat and spiders were also more abundant at the shore (Smith et al. 2009). On the southwestern shore of Lake Erie in Ohio, there was no difference in abundance in midge biomass inland and at the shoreline. As spring progressed, birds at both inland and shoreline sites consumed more aquatic insects and experienced greater refuelling performance later in the day. There was no association between midge biomass and refuelling performance, but the Magnolia Warbler opportunistically supplemented its diet with midges. The lack of relationship for this warbler may be because it has a later, narrow migratory window when terrestrial food resources are more abundant. Refuelling was influenced more by foraging opportunities later in the day than by midge availability (MacDade et al. 2011).

During migration, the Magnolia Warbler forages in low trees, the subcanopy, and shrubs. During autumn at Prince Edward Point, it foraged at heights of 1.5-9 m. During spring migration in South Carolina, 4.6% of foraging occurred in the canopy, 77.3% in low trees, 18.2% in shrubs, and 0% on the ground. In the canopy, 0% of foraging occurred in the upper crown, lower crown, or on the bole, and all 4.6% occurred in the middle of the crown. In low trees, 59.1% of foraging occurred in the inner crown, 18.2% in the lower crown, and 0% in the upper crown or on the bole. In shrubs, 13.6% of foraging occurred in the inner crown and 4.6% in the lower crown, and 0% in the upper crown, dense thickets, brush piles, and grasses. During autumn migration at Prince Edward Point, 43% of foraging occurred on outer leaves, 8% on twigs and inner leaves, 14% on outer branches, 20% on sapling foliage, 10% on sapling branches, 3% on small shrubs, and 0% in the air, on inner branches, the trunk, and the ground. In New York during autumn migration, it was suspected that it was foraging nocturnally in trees illuminated by artificial lights, but this could not be confirmed (Graber et al. 1983; Keast 1980; Lebbin et al. 2007; Parnell 1969).

During migration, the Magnolia Warbler's diet consists almost entirely of invertebrates. Five found dead near Prince Edward Point in autumn had eaten approximately 15 beetles each. In autumn in Ohio during cold, wet weather, it fed on honeysuckle fruit. A week later, the fruit had been depleted and 2 were seen creeping through the lawn, apparently plucking tiny arthropods off the undersides of grass blades and violet leaves (Keast 1980; Tramer and Tramer 1977).

The Magnolia Warbler is a common victim of strikes at buildings and other tall structures. At the Lennox generating station chimneys near Kingston, 2,485 were killed 1972-82, with 230 and 760

mortalities on 5 and 6 September 1981. In Wisconsin, 1,346 were collected at a television tower 18-30 September 1963. On Padre Island, Texas, 1,109 of 2,421 mortalities (45.7%) at lighted buildings and wires were Magnolia Warblers (Graber et al. 1983; Dunn and Hall 2020; Weir 2008).

The Magnolia Warbler is susceptible to blood parasites that are transmitted by black flies. Infection has the potential to cause a delay in spring arrival, increased probability of nest desertion, and decreased clutch size, hatching success, and fledgling success. Two Ohio studies examined the incidence of infection during spring migration, and 36.3-39.5% of birds were infected. The intensity and the probability of infection were not related to energetic condition, capture date, or sex. After-second-year birds were more likely to be infected than second-year birds (Boone et al. 2010; DeGroote and Rodewald 2010).

In Pennsylvania, an outbreak of the viburnum leaf beetle resulted in almost complete mortality of the southern arrowwood, which was formerly the third most abundant shrub species. Prior to the infestation, spring migrating Magnolia Warblers gained significant mass after sunrise, but no weight gains occurred after the infestation (Smith and Hatch 2017).

Strode (2003) studied the effects of climate change on the migration of the Magnolia Warbler in Illinois and North Dakota. Over 100 years, there was no significant spring temperature change in Illinois, but spring advanced an average of 8.6 days in North Dakota since 1961. Spring also advanced north of Illinois. The Magnolia Warbler exhibited no response to changing temperatures and now has as many as 20 fewer days to travel between southern Illinois and northern Minnesota. In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming occurred during the second period. The Magnolia Warbler arrived significantly earlier, departed significantly later, and had a significantly longer breeding season during the second period.

James (1991) considered the Magnolia Warbler an abundant migrant in Ontario. Hussell et al. (1992) reported a nonsignificant decline in migratory Magnolia Warblers of 1.4% per year at LPBO 1961-88. Trends by period were: 1961-70, −8.9%; 1970-79, +9.8%; and 1979-88, −2.0%. Variations in trends by decade may have been related to spruce budworm populations. More recent data from migration counts across Canada 1997-2006 indicate general stability or small increases at most sites (Dunn and Hall 2020).

Bay-breasted Warbler

Setophaga castanea

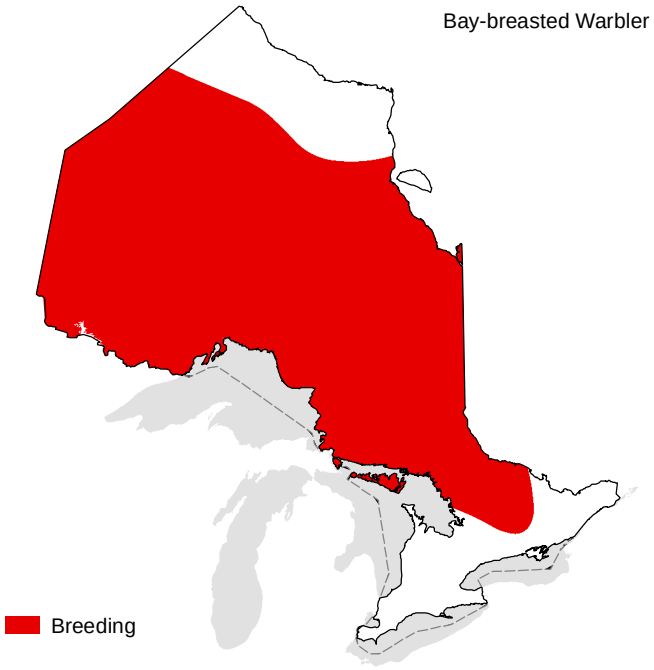
BREEDING SEASON

Habitat Requirements

Ontario Bay-breasted Warbler nests were in coniferous and mixed forests. This warbler showed a distinct preference for open coniferous stands with a dense deciduous understorey (66.7% of nests). Nests in denser mixed (20.0% of nests) and coniferous (13.3% of nests) forests were usually near water or clearings (Peck and James 1987). It requires tall, mature, and dense conifers with live branches in the shade of the forest canopy. Occupied stands usually have a dense understorey of deciduous or coniferous shrubs in the forest or at edges. Nesting may occur in lowland or upland forests (James 1984b).

In the Hudson Bay Lowland near Moosonee, the Bay-breasted Warbler nested in a lichen-rich spruce forest bordering a stream (Wilson and McRae 1993).

Most information on the Bay-breasted Warbler's habitat requirements in Ontario is from the Boreal Forest Region, which constitutes most of its range in the province. From Pickle Lake north to the Wetico Hills, it was most common in mixed forests followed by deciduous forests, coniferous forests without an understorey, and coniferous forests with an understorey. It was absent in scrub, heath, and tundra habitats (McLaren and McLaren 1981). James (1980) observed it regularly in small



numbers in mixed forests near Pickle Lake. It is associated with older, closed stands of mixed woods where there is little interspersion between young and old forests and higher amounts of intact older forests (Rempel 2007; Rempel et al. 2007). Near Lake Nipigon, it was strongly associated with white spruce and balsam fir. Black spruce was not favoured because it is not attractive to spruce budworms. Balsam fir supported the highest densities of budworms and this warbler (Kendeigh 1947). In the same area during a period when spruce budworms were scarce, it nested in low density in an overmature stand that was 30 m tall with a broken canopy dominated by 60-cm diameter at breast height (DBH) trembling aspen. This stand had a scattered understorey of white birch and white spruce and dense thickets of balsam fir regeneration and mountain maple (Sanders 1970). Near Hearst, it nested in mature upland mixed forests and clear-cuts in lowland coniferous and upland mixed stands. It occupied clear-cuts as young as 6 years were in upland stands. The youngest occupied lowland stand was 24 years old (Welsh and Fillman 1980). At Quetico Park, it was rare to uncommon in stands 1-23 years old but common in stands 67-73, 112-176, and 367-370 years old. In the 67-73-year-old communities, Bay-breasted and Blackburnian warblers were the dominant species. In the heavier white spruce and balsam fir cover in the 112-year-old stand, the Bay-breasted Warbler was the most abundant species and it and the Blackburnian Warbler were the most important species in the 175- and 176-year-old stands (Apfelbaum and Haney 1999). Welsh (1993) considered the Bay-breasted Warbler a late-succession species. Highest densities occurred in stands older than 50 years. Much lower densities were present in stands 20-30 years old, and it was absent or sparse in stands younger than 20 years. Near Manitouwadge, it occurred predominantly in mature stands, but occupied intermediate-aged and young stands when spruce budworms became abundant. It altered its habitat choices when food was extraordinarily abundant (Venier et al. 2009). In the Clay Belt, it was most abundant in white spruce stands, followed by those dominated by tamarack or white cedar, white spruce–balsam poplar, and black spruce. It was uncommon in jack pine stands. It occurred in stands that were poor to rich in nutrients and wet to dry, but was more common in damp, nutrient-rich stands (Welsh and Lougheed 1996).

In white pine stands in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, the Bay-breasted Warbler inhabited both mature and old-growth stands. It was slightly more abundant in mature than old-growth stands (Kirk et al. 2012). In white pine stands in Algonquin Park, it was uncommon in stands with no recent history of harvesting and in cuts 2-16 years old (Kingsley and Nol 1999). In Algonquin Park, Martin (1960) did not observe it in black spruce or black spruce–

white cedar stands, but recorded it in low density in hemlock stands. He considered it characteristic of hemlock stands. Near Gogama, it was common in jack pine forests 40 years and older, but only when the jack pine budworm was present in epidemic numbers. It was present every year in adjacent mixed forests that supported spruce trees, a habitat that it clearly preferred over jack pine (James and Peck 1995a).

The Bay-breasted Warbler nests predominantly in the Boreal Forest Region, so its habitat preferences elsewhere are similar to those in Ontario. It is consistently present in spruce forests only when spruce budworms are abundant but may be found in balsam fir stands even when budworms are absent. Regularly used forest types include those dominated by white or red spruce, balsam fir, a mix of spruce and balsam fir, and spruce–balsam fir mixed with trembling aspen, balsam poplar, and white birch. It has nested in spruce plantations in New Brunswick. Seldom-used stands include those dominated by white pine, hemlock, white cedar, tamarack, and northern hardwoods. In British Columbia, it nested in mature trembling aspen stands at edges of mature white spruce forests. Extralimital nesting occurred in southern Manitoba during a forest tent caterpillar outbreak. The habitat was uncharacteristic, consisting of a narrow ridge of pure deciduous species dominated by peach-leaved willow, Manitoba maple, cottonwood, and green ash. The shrub layer was dominated by sandbar willow, red elderberry, pin cherry, and red-osier dogwood (Back 1979; Bent 1953; Campbell et al. 2001; Dawson 1979; Erskine 1977; Freedman and Johnson 1999; Harrison 1984; Kirk et al. 1996; Mendall 1937; Noon et al. 1979; Sabo 1980; Sealy 1979; Sequin in Gauthier and Aubry 1996).

Several studies described the characteristics of forests inhabited by the Bay-breasted Warbler. In Quebec balsam fir–white cedar stands, it was associated with mature forests. It was equally abundant in nonriparian stands and riparian stands with a wetland band of alder and grasses (LaRue et al. 1995). Parker et al. (1999) found significantly higher densities near streams in New Brunswick, although it also occurred in nonriparian areas. In the taiga area of British Columbia, it inhabited mixed stands of white spruce and trembling aspen with a multilayered canopy, frequent openings, and a dense understorey of highbush cranberry and white birch. Breeding habitat includes mature and old-growth stands of white spruce, including those interspersed with trembling aspen, white birch, balsam poplar, willow, and alder, and with a poorly to moderately developed shrub layer. Typical habitat includes trees taller than 20 m with a DBH greater than 50 cm and a shrub layer of highbush cranberry, prickly rose, and alder. In more upland areas, it selects mature spruce or mixed stands with an understorey of highbush cranberry and white birch (Campbell et al. 2001). In the Yukon, the Bay-breasted Warbler nests in dense, tall, old-growth white spruce forests along rivers and also in old-growth spruce stands mixed with trembling aspen and balsam fir both in and distant from riparian areas. These forests are characterized by high structural complexity with a shrubby understorey, standing and fallen dead timber, and abundant woody debris (Sinclair et al. 2003). In the Prairie Provinces, Kirk et al. (1996) considered it an old-forest species associated with stands rich in nutrients growing on dry soils. In Saskatchewan, it was most abundant in stands older than 140 years (Cumming and Diamond 2002). In Newfoundland, it was associated with young stands (40 years old) that were nutrient poor (Thompson et al. 1999). On an island in Maine, it was common only where there were dense growths of lichen-covered lower branches of spruce in the shade of the forest canopy. This habitat does not appear until the forest becomes dense and contains large

trees. When this island became infested with spruce budworms, the Bay-breasted Warbler was the dominant species and also occupied dense young stands of conifers (MacArthur 1958). In Maine spruce–balsam fir stands, it was absent in early successional areas and first appeared in low density when hardwood regeneration was taller than 4.5 m and both deciduous and coniferous trees were 10-15 cm DBH. It was most abundant in stands with a dense canopy of spruce and balsam fir and an open forest floor (Titterington et al. 1979). Erskine (1977) concluded that it was characteristic of mature stands in the Boreal Forest Region and that it was scarce or lacking in young coniferous stands. When spruce budworms are abundant, it expands into young and intermediate-aged stands in response to the abundant food. It may inhabit mixed-wood stands as young as 8 years (Venier et al. 2020).

Near Quebec City, Drolet et al. (1999) did not find the Bay-breasted Warbler in any areas where there was less than 55% forest cover within the surrounding 100-ha landscape. They concluded that forest remnants as small as 5 ha embedded in a clear-cut dominated landscape may be inadequate to support it. In Saskatchewan, it was absent in a fragmented landscape but common in nearby contiguous forest (Venier et al. 2020). A 5-ha stand near Great Slave Lake supported the Bay-breasted Warbler (Erskine 1977).

Other studies described microhabitat preferences of the Bay-breasted Warbler. In subalpine forests in New Hampshire, it was a mid-slope species that preferred some wet depressions in its territory. Average habitat characteristics were 11.3 m tall canopy, 75% canopy coverage, 59% conifer foliage volume, 19% conifer foliage volume 0-2 m from the ground, 44% deciduous foliage volume above 5 m, and 13 cm DBH of live trees (Sabo 1980). In New Brunswick, it selected areas with high densities of large deciduous trees (Parker et al. 1999). In Maine spruce–balsam fir forests, it was significantly correlated with the number of hardwood and softwood stems 10-15 cm DBH and the number of coniferous stems larger than 20 cm DBH, the largest size category.

Ontario nests were in conifers: 60.0% in black spruce, 20.0% in white spruce, 13.3% in balsam fir, and 6.7% in jack pine. Nests were situated from the lowest branch of taller trees to near the tops of trees, with most in the lower third. Nests were on horizontal branches, usually among numerous branchlets. Nests were 0.3-2.4 m from the trunk with most 0.9-1.5 m distant; 4 nests were near or at the trunk. Nest height was 2.5-7 m with most 3.5-5.5 m up (Peck and James 1987). Mills (1981) reported a nest near Bala that was 1.2 m from the ground in a roadside maple.

Throughout its range, most Bay-breasted Warbler nests are in spruce and balsam fir trees, much less frequently in pines or hemlock. During extralimital nesting in deciduous habitat in Manitoba, 9 nests were in Manitoba maples and 1 was in green ash. Nests are typically on a horizontal limb 1.5-3 m from the trunk but occasionally at or near the trunk. Fifty-four Canadian nests averaged 4.9 m from the ground (range 1.2-9 m). Some nest trees were beside roads, in small clumps of trees in forest openings, and within 20 m of a building. Nests are not very well concealed and some are remarkably out in the open, but they blend in so well with their surroundings that they are difficult to find (Bent 1953; Campbell et al. 2001; Chapman 1907; Cruickshank 1956; Harrison 1984; Mendall 1937; Philipp and Bowdish 1917; Sealy 1979; Sequin in Gauthier and Aubry 1996; Sinclair et al. 2003; Venier et al. 2020).

Territories are established immediately upon arrival in spring. In New Brunswick, populations increased 5.7-fold during a spruce budworm outbreak but the mean territory size remained constant. Initially there had been unoccupied interstices between territories that became filled in as the population increased (MacArthur 1958). In Manitoba, 9 nests were clumped together and one was 510 m from the group. The non-random dense clumping occurred despite availability of other similar habitat (Sealy 1979). Near Lake Nipigon, 88 territories averaged 0.15 ha (range 0.04-0.49 ha), the smallest territory size of the warbler species present. Few measurements were taken so territories could have been larger than reported; territories could have been as large as 0.88 ha. Average territory sizes on 4 plots were 0.32, 0.17, 0.15, and 0.12 ha (Kendeigh 1947). Average territory size in subalpine forests in New Hampshire was 1.5 ha (Sabo 1980).

No information is available on natal philopatry. On the Gaspé Peninsula of Québec, 6 of 57 adults (10.5%) returned the following year. Spruce budworm larvae were abundant in each year. Results indicated that the Bay-breasted Warbler has low site fidelity even when spruce budworms are plentiful (Moisan Perrier et al. 2021). It is a good example of a fugitive species that is dependent upon periods of superabundant food supplies. It is often absent in large geographic areas for long periods of time until a budworm outbreak occurs. It may then become the most abundant breeding bird species, but leaves when the outbreak has run its course. The invasion of deciduous habitat in Manitoba during an outbreak of forest tent caterpillars suggests that it responds directly to prey abundance rather than to vegetation. The Manitoba forest tent caterpillar population remained high the year after the area was occupied by the Bay-breasted Warbler, but the warblers were present in only 1 year (MacArthur 1958; Morse 1989; Sealy 1979).

Limiting Factors

Nests with eggs have been reported in Ontario from the second week of June through the first week of July (Peck and James 1998a). In Algonquin Park, nestlings are present from late June until the second week of July and dependent fledglings have been observed from mid-June to mid-July (Tozer 2012).

It is unknown how much time elapses after the female arrives until nest building commences, and the time it takes to build a nest is unknown. Eggs are laid at the rate of 1 a day. It is uncertain when incubation starts but it appears to occur early in the laying period. The incubation period at 1 nest was slightly over 12 days and young hatched over a period of 2 days. Nestlings fledge when they are 10-12 days old. They may remain in the vicinity of the nest for 9 days (Harrison 1984; Mendall 1937; Venier et al. 2020).

A single brood is raised annually. It is unknown if replacement clutches are laid if the first is lost. Ontario nests contained clutches of 4-6 eggs (average 5.38 eggs). These included 6 each of 5- and 6-egg clutches and a single clutch of 4 eggs. Clutches of 3-8 eggs have been reported, with 5 and 6 eggs the most common clutch sizes with a typical range of 4-7 eggs. The mean size of 49 New Brunswick clutches was 5.43 eggs (range 4-7 eggs). During spruce budworm outbreaks, the Bay-breasted Warbler occasionally lays 6-8 eggs, more than any other warblers except the Tennessee and Cape May warblers, 2 other budworm specialists. The Bay-breasted Warbler lays more eggs during budworm outbreaks (average of 5.8 eggs) than when budworms are scarce (average of 5.1 eggs). In Manitoba, 2 unparasitized clutches contained only 3 eggs. The small clutches may have

been because the birds were nesting in atypical habitat and the cowbird parasitism rate was high (Bent 1953; MacArthur 1958; Mendall 1937; Morse 1989; Peck and James 1998a; Philipp and Bowdish 1917; Sealy 1979; Venier et al. 2020).

The age at first breeding is unknown, but is probably 1 year. The mating system is assumed to be monogamous. In atypical habitat in Manitoba, 1 male mated with a second female after the first disappeared. This male may have mated polygynously, but this was not confirmed. One female built a nest, abandoned it, and took over another unfinished nest and mated with a different male. Pair bonds were quickly established and may have been quite transitory (Sealy 1979; Venier et al. 2020). In Maine, Hensley and Cope (1951) removed breeding males and females from the population. There was an increase in population after removal, possibly due in part to increasing spruce budworm numbers. There appeared to be a large surplus floating population of Bay-breasted Warblers.

The Bay-breasted Warbler is a slow and methodical forager that spends 76% of its time creeping along branches smaller than 10 mm in diameter. It regularly works from the lichen-covered bases of branches well out to their tips, although the largest amount of time is spent in the interior of the tree. When spruce budworms are abundant, it frequently remains motionless on a branch and catches the caterpillars as they descend on their threads; this can be a highly effective foraging technique. Foraging movements within a tree are in a radial pattern and most foraging occurs mid-height in the tree. In conifers in Saskatchewan, only 0-4.9% of foraging time was spent in the top one fifth and bottom two fifths of the tree. In the 2 middle zones, more than 15% of the time was spent in the inner part of the tree with large branches mostly devoid of needles, more than 15% in the central layer of older needles and larger branches, and 5-9.9% of time in the outer layer with new growth, fresh needles, and small twigs. In deciduous trees, 0-4.9% of foraging time was spent in the top third of the tree, and more than 15% in the middle zone. In the lower third of the tree, 5-9.9% of time was spent in the inner zone and 10-14.9% of time was spent in the central and outer zone. It used all tree species in proportion to their availability but tended to favour white spruce and avoid white birch. It used small twigs at ends of branches and treetops significantly less than their abundance. Mean foraging height was 10.3 m in conifers and 11.8 m in deciduous trees. The Bay-breasted Warbler and Black-throated Green Warbler foraged significantly higher than the Blue-headed Vireo and Magnolia Warbler in conifers. The Bay-breasted Warbler tended to occur more frequently in canopy than subcanopy trees. The Bay-breasted Warbler and Blue-headed Vireo favoured foraging on large inner and middle branches that were seldom used by other species. Similar foraging techniques and uses of different parts of trees were used in Maine, where the Bay-breasted Warbler foraged more than expected in red spruce. In that state, there were no significant differences in the foraging movement patterns of Bay-breasted and Blackpoll warblers, but they were significantly different from other warbler species. Most warblers fed in different areas of trees in different manners. The Bay-breasted Warbler obtains most prey by gleaning from conifer needles or from the top and occasionally bottom of small deciduous leaves. Hawking and hovering are rare foraging techniques. In Maine, different warbler species behaved in a manner such that they were exposed to different foods by feeding in different positions in trees, indulging in hawking and hovering to different extents, moving in different directions through trees, and moving at differing rates. They also probably have the greatest need for food at different times due to differing nesting

chronologies (Cumming 2004; Greenberg et al. 1999; MacArthur 1958; Morse 1978; Sabo 1980; Venier et al. 2020).

Limited data suggest that young are fed mostly caterpillars and moths (Venier et al. 2020). McMartin et al. (2002) examined the diet and food-niche overlap among the Bay-breasted, Tennessee, and Cape May warblers near Longlac during a spruce budworm outbreak. They examined the diet during 2 periods: 7-11 June and 18-28 June. In the early period, the Bay-breasted Warbler's diet consisted of 75.7% beetle adults, 5.7% caterpillars, 8.6% flies, 2.9% spiders, and 7.1% other invertebrates (soft-winged bugs, hymenopteran larvae and adults, true bugs, beetle larvae, snails, odonates, caddisflies, and neuropterans). Diet during the late period consisted of 29.6% adult beetles, 57.7% caterpillars, 5.6% flies, 2.8% spiders, and 4.2% other invertebrates. The diet during the 2 periods was significantly different, being dominated by adult beetles early in the season and by caterpillars later. The food-niche breadth for the Bay-breasted Warbler doubled from early to mid-season but declined by two thirds for the other 2 warblers. In the early season, the 3 species differed in their consumption of adult beetles, caterpillars, and flies, with the Bay-breasted Warbler consuming the most beetles. Later, the only difference in diet among the 3 species was in the amount of adult beetles consumed, with the Bay-breasted Warbler again eating the most. The different diets were probably a reflection of the tendency of the species to forage in different locations within trees, and beetles are found mostly in the interior portions of trees. The limited consumption of caterpillars early in the season was because of their small size. Kendeigh (1947) summarized the diet of 6 Bay-breasted Warblers near Lake Nipigon during a spruce budworm outbreak. They had consumed 37.3% lepidopterans (including geometer moth larvae), 23.1% flies (including march and crane flies), 12.4% spiders, 12.4% mayflies, 7.8% soft-winged bugs (including aphids and planthoppers), 6.2% beetles (including click and scarab beetles), and 0.7% true bugs (including stink bugs). In Maine, Mitchell (1952) examined the contents of 135 stomachs during a spruce budworm outbreak. They contained 51% and 35% budworm larvae and pupae by volume in 2 years. In Manitoba, Bay-breasted Warblers were observed feeding on forest tent caterpillars that were less than 20 mm in length, and on flying insects that were probably midges. Two stomachs contained mostly midges, but also leaf beetles, ichneumonid wasps, plant bugs, chewing lice, and seeds (Sealy 1979). The Bay-breasted Warbler has also eaten house flies, gall flies, ants, lacewings, moth cocoons, cankerworms, geometer moth and other caterpillars, grasshoppers, locusts, and dragonflies (Bent 1953; Venier et al. 2020). In Maine, the Bay-breasted and Black-throated Green warblers tended to eat more caterpillars than Cape May, Yellow-rumped, and Blackburnian warblers. Otherwise, the diet of the Bay-breasted Warbler was most similar to that of the Blackburnian Warbler, and the feeding habits of these species are similar.

Food abundance is a limiting factor to the Bay-breasted Warbler and significantly affects its abundance and distribution. It is a spruce budworm specialist, colonizing areas or significantly increasing during budworm outbreaks and declining or disappearing when the outbreak is over. It may be absent to uncommon when budworms are scarce and be the most abundant species during outbreaks. It also responds to outbreaks of the black-headed budworm, jack pine budworm, and forest tent caterpillar. Near Lake Nipigon during a spruce budworm outbreak, it was the most abundant species, representing 28.8% of all birds present. Habitat appeared to be saturated for it. A later study in the same area when there were no budworms determined that it was almost absent.

Near Manitouwadge, it experienced an enormous increase in territory density from 1979 to 1983 as budworm populations increased. There was a 4.7-fold increase in its density in mature forest over 5 years and it became much more abundant in young and intermediate-aged stands where it was formerly uncommon. In 1 area of Maine, the response to budworm populations was direct, immediate, and strong, with the population increasing 12-fold. Another study in Maine and New Hampshire found no population increase in association with a budworm outbreak, but the study was conducted in only 1 or 2 years in the 2 study areas. The Bay-breasted Warbler was one of the species that consumed the most budworms, along with Blackburnian, Cape May, and Magnolia warblers. When budworm populations are high, food is superabundant and the entire bird population has little effect on it. In Maine and New Hampshire, all birds combined consumed 84% of budworms when the budworm population was low (100,000 per ha), but only 22% when populations were 550,000 per ha. Budworm abundance also affects social dominance among warbler species. When budworm populations are low, the Black-throated Green Warbler is dominant to the Bay-breasted Warbler. When budworms and the Bay-breasted Warbler are abundant, this warbler also inhabits younger coniferous stands, forcing the Black-throated Green Warbler to abandon spruce stands and occupy ridges dominated by mixed growths of hardwoods and hemlock. When it is abundant, the Bay-breasted Warbler is dominant to the Blackburnian Warbler and can depress populations of Blackburnian and Magnolia warblers and other species (Crawford and Jennings 1989; Gage et al. 1970; James and Peck 1995a; Kendeigh 1947; MacArthur 1958; Morris et al. 1958; Morse 1978, 1989; Sanders 1970; Sealy 1979; Venier et al. 2009).

The Bay-breasted Warbler is a rare host of the Brown-headed Cowbird because there is little overlap in the 2 species' distribution. In a Manitoba extralimital nesting effort in atypical deciduous forest habitat, 4 of 6 nests were parasitized. Prior to the Manitoba records, only 4 cases of parasitism were known: 2 in Quebec and 2 in Alberta. Of 65 nests reported to Canadian nest records schemes, only 1 (1.5%) was parasitized (Sealy 1979; Venier et al. 2020).

Most major threats to the Bay-breasted Warbler are related to forest management. Shorter rotation periods have been adopted in eastern Canada, thereby reducing the area of mature forest that it prefers. Younger stands are also less likely to support spruce budworm outbreaks. Planting of black spruce and jack pine, which are more resistant to the spruce budworm, diminishes breeding habitat quality. In Saskatchewan, the Bay-breasted Warbler was most abundant in stands older than 140 years, but rotation age is only 80-90 years. It may suffer some population density reduction if stands older than rotation age are completely lost from the landscape. Populations also appear to decline with partial harvest techniques, when as few as 30% of trees are removed. Eighty-two percent of the breeding population occurs in Canada's Boreal Forest Region and almost a third of this area is allocated to timber companies. A 1995 forest management plan for New Brunswick projected that mature spruce–balsam fir forest will decline from 46% of the landscape to 8% in 40 years. The Bay-breasted Warbler has been demonstrated to avoid riparian and upland leave strips (buffers) 32-132 m wide. Modelling determined that Bay-breasted Warbler populations would not be maintained in Ontario's Boreal Forest Region even if all harvesting guidelines for key species were followed (Cumming and Diamond 2002; Rempel et al. 2007; Vanderwel et al. 2009; Venier et al. 2020; Wells 2007). In the Canadian Shield of Ontario, it was significantly more abundant in early successional clear-cuts than in early successional burns, but was equally abundant in mid-

successional clear-cuts and burns. It was significantly less abundant in early successional than mature stands but equally abundant in mid-successional and mature stands (Zimmerling et al. 2017). Fire suppression may have a positive effect, allowing more stands to become mature and more vulnerable to spruce budworm predation (Sequin in Gauthier and Aubry 1996).

Spruce budworm populations have declined recently and this has resulted in a decline of the Bay-breasted Warbler. Declines have been evident on both the Breeding Bird Survey (BBS) and migration monitoring data. In the 1960s, no budworm outbreaks of any consequence occurred. A massive outbreak began to build in 1970 that peaked in the early 1980s. The budworm population has fallen since then with 2 resurgences in the mid-1980s and early 1990s. Budworm defoliation in Ontario peaked at 18,850,000 ha in 1980 and declined to 28,000 ha in 2004. Spraying for budworms was an annual event from 1952 until the early 1990s, but there is little evidence that it was effective in reducing outbreaks. Areas sprayed were only a small proportion of the infested area and probably had no effect on Bay-breasted Warbler populations. Its numbers may have stabilized somewhat because of budworm control programs and shorter harvest rotation periods that keep budworm populations at low to moderate levels over long periods of time instead of massive outbreaks followed by tree defoliation and death and a crash in the budworm population. During the first Quebec atlas, breeding evidence for the Bay-breasted Warbler was obtained most frequently in areas that were subjected to budworm outbreaks. Once outbreaks subsided, populations of both budworms and warblers appeared to be greater in balsam fir stands that had been treated with insecticides than in untreated stands (Anonymous 2013; McCracken 2004; Morse 1989; Sequin in Gauthier and Aubry 1996; Venier et al. 2009, 2020).

In 1989 in New Brunswick, birds collected 3 days after spraying with fenitrothion had an average brain acetylcholinesterase inhibition rate above the level that is considered life threatening. In the early 1990s, fenitrothion was replaced by Bt and is no longer used (Venier et al. 2020).

Expansion of the forest industry further into the Boreal Forest Region could have adverse effects on the Bay-breasted Warbler. Other potential threats include prospecting for minerals, oil, and natural gas and building hydroelectric facilities. Winter habitat is also being lost to agriculture (Anonymous 2013; Wells 2007).

In Alberta, the Bay-breasted Warbler was significantly more abundant at seismic lines than in adjacent forest interior. There was no difference in its abundance at pipelines and well pads than in forest interior adjacent to these features (Bayne et al. 2016).

Venier et al. (1999) compared the Ontario breeding distribution of the Bay-breasted Warbler with 24 climate variables. Results suggested a strong influence on its breeding distribution that was probably related to the effects of climate on vegetation distribution. It was negatively correlated with variation in monthly precipitation and the timing of the end of the growing season. Price (2004) concluded that the Bay-breasted Warbler might become extirpated as a breeding species in southern Ontario if the average summer temperature increased by 2°C. In Saskatchewan, Cumming et al. (2014) determined that the northern limits of Bay-breasted Warbler distribution appeared to be associated with a July minimum temperature isotherm. Subject to that constraint, higher abundance was associated with closed mixed forests and open coniferous forests. Within those vegetation communities, abundance was highest when the mean April temperature was higher

than –1.6°C, when the April leaf area index was less than 215 (an indicator of mixed forest), or when the standard deviation of the April minimum temperature was more than 2.0°C. In southern Quebec, the Bay-breasted Warbler was correlated with cooler and wetter summers. DesGranges and Morneau (2010) considered it very sensitive to climate change. In central Quebec and Labrador, it showed no strong relationship with climate variables, but occurred in stands with a moderate number of growing-degree days (DesGranges and LeBlanc 2012).

Status

Baillie and Harrington (1937) considered the Bay-breasted Warbler a fairly common breeder in certain localities between the northern portion of the Bruce Peninsula and the transcontinental railway. At that time, numerous summer records from Cochrane, Kenora, Temiskaming, Nipissing, Parry Sound, and Thunder Bay districts and Victoria County indicated that it was more common and widespread than formerly supposed. The most northerly records were from Moose Factory and latitude 53-54°N along the Manitoba border. The first atlas demonstrated that it ranged throughout the Canadian Shield and in the Hudson Bay Lowland to Attawapiskat in the northeast to the northwest corner of the province. Distribution was spotty in the Great Lakes–St. Lawrence Forest Region in the Shield and on Manitoulin Island. Budworm populations peaked in the province just prior to the first atlas and the range determined by it was considered maximal. Densities were probably more than 100 per km^2 throughout the Boreal Forest Region such that the Ontario breeding population was probably several million during the first atlas (Welsh in Cadman et al. 1987). James (1991) considered the Bay-breasted Warbler to be common across the north as far north as Sandy Lake and Fort Albany; uncommon in the Algonquin Highlands; occasional and rare north to near Fort Severn and Attawapiskat, and south to Muskoka District and Renfrew County.

The second atlas was conducted during a period of low budworm abundance. There was no significant change in the distribution of the Bay-breasted Warbler between atlases, but it was more spottily distributed at the northern and southern extremes of its range. There was no significant difference in its overall probability of observation between atlases. Significant declines in the Hudson Bay Lowland and the Shield portion of the Great Lakes–St. Lawrence Forest Region (consistent with the observed northern and southern range contractions) were offset by a significant increase in the Boreal Forest Region. It was most abundant in the Boreal Forest Region, particularly in a band from Little Sachigo and Sandy lakes east to the Clay Belt. Numbers outside the Boreal Forest Region were very low or 0 on point counts (Zimmerling and Nicoll in Cadman et al. 2007).

BBS data suggest that the Bay-breasted Warbler is declining. The United States reported nonsignificant annual declines of 1.9% 1966-2007 and 0.5% 1980-2007. Using different analytical techniques, Environment Canada reported significant declines of 3.0% and 5.2% for the same periods. Declines of the Bay-breasted Warbler are probably linked to declines of the spruce budworm (Venier et al. 2020). Populations also fluctuate in non-infested areas, so it is difficult to assess changes in status and how these are related to budworm populations (Harrison 1984). BBS results indicate that it increased at an annual rate of 0.155% in Canada and decreased at an annual rate of 0.419% in Ontario 1970-2021. Trends 2011-21 were an annual increase of 2.08% in Canada and an annual decrease of 2.39% in Ontario. The long-term Canadian trend was of medium reliability; the other trends were of low reliability (A.C. Smith et al. 2023).

MIGRATION

The Bay-breasted Warbler is a nocturnal migrant. During the day, particularly in autumn, it may forage in mixed-species flocks, especially those containing Blackpoll Warblers. Autumn migration is triggered by favourable conditions such as high pressure, clear skies, and strong north to northeast winds (Bent 1953; Brewer et al. 2018; Chapman 1907; Venier et al. 2020).

The Bay-breasted Warbler is a late spring migrant, possibly because of its northern breeding range. Spring migration is rapid with stopovers of short duration, often a single day or 2 at most. Males arrive a few days earlier than females. At Long Point, mean capture dates for males were 16.5 May for after-second-year birds, 20.0 May for second-year-birds, and 18.9 May for those of undetermined age; adults arrived significantly earlier than yearlings. Mean capture dates for females were 19.6 May for after-second-year birds, 20.1 May for second-year-birds, and 22.6 May for birds of undetermined age; there was no significant difference in timing of arrival of age classes. At Prince Edward Point, the mean date of capture was significantly earlier for males (23.3 May) than for females (24.7 May). In southwestern Ontario, spring migration spans all of May to mid-June. Spring migration in southeastern Ontario occurs over less than 2 weeks beginning in mid-May, with the peak in the third week of May when females arrive. In the southern Shield, most birds pass through in the third and fourth weeks of May. First arrival near Lake Nipigon was 25 May (Black and Roy 2010; Curry 2006; Francis and Cooke 1986; Keast 1980; Kendeigh 1947; LaForest 1993; Lancaster et al. 2004; Mills 1981; Stewart et al. 2002; Tozer 2012; Venier et al. 2020; Weir 2008).

Autumn migration is more protracted and birds may linger longer at stopover sites than in spring. In West Virginia, adults and juveniles migrated simultaneously. Autumn migration may begin in late July shortly after nesting is completed. In the southern Shield, autumn migrants are usually present from mid-August to mid-September, with some arriving in early August and others remaining until the first week of October. In southern Ontario, migration occurs from the end of July until the end of October with the peak in mid-August (Black and Roy 2010; Campbell et al. 2001; Curry 2006; Keast 1980; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Venier et al. 2020; Weir 2008).

In British Columbia, migration habitat is similar to breeding habitat. In most other areas, the Bay-breasted Warbler occupies a greater diversity of habitat during migration and is not restricted to using conifers (Campbell et al. 2001; Venier et al. 2020). During spring migration in Illinois, it preferred upland oak-hickory forests over bottomland forests and shrubby areas. It also occurred in forest edges in both spring and autumn. In autumn, it occupied all woody habitats, but was least common in shrub and pine habitats in southern Illinois. In central Illinois, it was most numerous in shrubs (Graber et al. 1983). During spring migration in Ohio, it was significantly more abundant in mature upland forests than in mature riparian forests. These habitats were structurally similar, except that upland forests had significantly less canopy cover (74% compared with 83%) and 39% shrub coverage compared with 19% (Rodewald and Matthews 2005). During autumn migration, it was not observed in pole-stage forest habitat. From most to least abundant, it occurred in forest edges, forest interior, shrub-sapling-stage forests, forest-agricultural edges, and suburban forests. There was no significant difference in its usage of habitats (Rodewald and Brittingham 2002). In addition to

forested and shrubby areas, the Bay-breasted Warbler may occur in urban parks and rural residential yards (Leighton et al. 2002).

Keast (1980) examined the foraging strategies of the Bay-breasted Warbler at Prince Edward Point during autumn migration. It fed at heights of 1.5-18 m, but mostly at 5-13 m with a peak at 10 m. It occasionally fed for part of the day at 17-18 m, then in the tops of saplings, subsequently descending for short periods into shrubs. Similar to the breeding season, it fed radially and slower than other warblers, approaching the foliage along branches. Foraging time was equally spent on outer leaves, on sapling foliage, and on sapling branches. Foraging was not observed on twigs, inner leaves, outer branches, inner branches, the trunk, low shrubs, or the ground. During autumn migration in New York, Lebbin et al. (2007) observed it foraging at night in an area illuminated by football-stadium lights. It made aerial sallies after insects and appeared to glean insects from foliage. One spring day in Illinois, several foraged on urban plantings of Norway spruce and Scotch pine, hovering at branch tips in the manner of parids (Graber et al. 1983).

The Bay-breasted Warbler is predominantly insectivorous during migration, but occasionally eats fruit during autumn migration. Mueller and Mueller (1976) observed several feeding on flowering dogwood berries in North Carolina. During cold, inclement weather in Ohio, Tramer and Tramer (1979) observed 4 Bay-breasted Warblers eating the fruit of yews. After the fruit was depleted, they foraged by creeping through the lawn, apparently gleaning tiny arthropods from the undersides of grass blades and violet leaves. It has also eaten Virginia creeper berries during autumn migration (Venier et al. 2020).

The Bay-breasted Warbler is one of the more common victims at television towers and other tall structures. It was the seventh most commonly killed species at the Long Point lighthouses 1961-2001. From 1972 to 1982, 2,408 were killed at the Lennox generating station chimneys with peak kills of 831 and 758 on 5 and 6 September 1981. The Bay-breasted Warbler represented 3.7-12.6% of warbler kills at towers in Michigan, Ontario, and Wisconsin; 3.1-6.9% in Maryland and Tennessee; and 1.6% in Georgia and Florida (Anonymous 2013; Venier et al. 2020; Weir 2008).

James (1991) considered the Bay-breasted Warbler a common migrant in Ontario. This is true for most of the province, but it appears to be uncommon during spring in Niagara Region and uncommon during both migration periods in Elgin County (Black and Roy 2010; Lancaster et al. 2004). In Hamilton, McIlwraith (1894) observed that it was abundant in some springs but rare or entirely absent in others. This may have been related to spruce budworm abundance or perhaps varying weather conditions. He rarely saw more than 3 or 4 together but observed a flock of 50 or more feeding in a clump of willows overhanging Hamilton Bay in spring 1885. In most areas, it is more abundant during autumn than spring migration. This is probably due to the addition of juveniles to the population but it may be partially because birds remain in stopover locations longer, allowing numbers to build up. In the Hamilton area on 21 May 1960, a fallout of this warbler occurred during wet, foggy weather. A single person observed an estimated 350, but there were probably thousands over the city. During migration in Ontario, typical daily maxima are 20-30 in spring and 50-300 in autumn (Black and Roy 2010; Curry 2006; LaForest 1993; Mills 1981; Tozer 2012; Weir 2008).

Similar to the BBS, migration monitoring data indicate a decrease in the Bay-breasted Warbler. Population indices at LPBO are closely related to the extent of spruce budworm outbreaks in

Ontario. Significant decreases have been observed since the outbreaks began to ebb. In the 15 years prior to 2004, autumn numbers at LPBO decreased by as much as 51%. Levels at that time were slightly below the pre-budworm 1960s. McCracken (2004) concluded that there was no need for alarm provided that budworm infestations continue to occur. Hussell et al. (1982) reported that it decreased at LPBO 1961-70 at a rate of 12.2% per year. It increased 19.8% annually 1970-79 and decreased 5.1% annually 1979-88. Overall, it experienced a nonsignificant decrease of 0.8% per year 1961-88. These population changes were related to budworm abundance. Budworm numbers have remained low with a resultant decrease in Bay-breasted Warbler numbers at LPBO. It decreased significantly 0.84% per year 1967-2004 and at a rate of 4.2% 1994-2004. The annual decrease between 1981-86 and 2001-06 was 3.4%. A significant decrease of 7.4% per year was experienced at the Thunder Cape migration monitoring site (Venier et al. 2009, 2020). The decrease is not restricted to Ontario, but is widespread. In Michigan, numbers banded in autumn peaked at 126 in 1981. Results in subsequent years were 23 in 1982, 14 in 1983, 1 in 1984, 5 in 1993, 0 in 1994, and 3 in 1995 (Venier et al. 2020).

Blackburnian Warbler

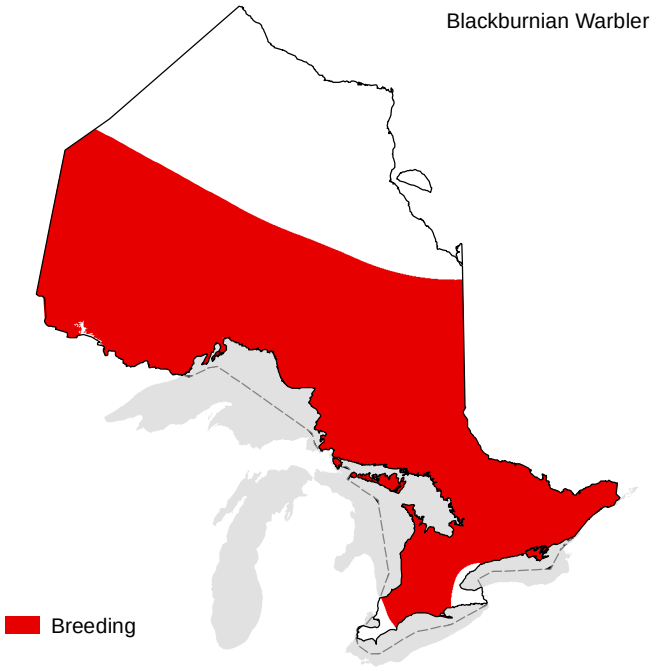
Setophaga fusca

BREEDING SEASON

Habitat Requirements

Ontario Blackburnian Warbler nests were in coniferous (60.0% of nests) and mixed (40%) forests. One was in a spruce bog and another was in a recent burn (Peck and James 1987). It prefers undisturbed coniferous and mixed forests and selects mature stands that are somewhat open with old to overmature large trees. It nests in both upland and lowland sites and prefers areas with balsam fir and hemlock (James 1984b).

In the Boreal Forest Region of Ontario, Blackburnian Warbler habitat consists of mature conifers in closed mixed-wood forests, with little interspersion between older and young forests and high amounts of forest older than 80 years. It was associated with high canopy closure, moderately tall stands, and high amounts of hardwoods (Rempel 2007; Rempel et al. 2007). In northwestern Ontario, it was widespread in most forest stand types except pure spruce and pure hardwood stands, but was abundant in only red pine and white pine stands. It also occurred in stands dominated by jack pine, trembling aspen–white birch, and white spruce–balsam fir (Welsh 1993). Near Lake Nipigon, it inhabited coniferous forests and stands dominated by white cedar, poplar-birch, and spruce (Kendeigh 1947). On the northeast shore of Lake Superior, it occurred only in large mature mixed



stands (Baillie and Hope 1943). Near Quetico Park, it occurred in all age classes of forest, but was least abundant in stands 1-23 years old. In stands 67-73 years old, it and the Bay-breasted Warbler were the dominant species. These were closed-canopy forests with a sparse, park-like understorey. These 2 warblers continued to be the most important in stands 112, 175, and 176 years old, and the Blackburnian Warbler was the most abundant species in stands 112 years old. The stands in which it dominated were comprised of jack pine and poplar. In jack pine stands near White River, it was most abundant in stands 40-100 years old, but not significantly. It was not a significant indicator for any age class. Its abundance was strongly negatively associated with coarse woody debris with 25-75% of the wood soft but with the shape still intact (Venier and Pearce 2005). Near Hearst, Welsh and Fillman (1980) reported it in uncut upland mixed woodlands and lowland conifers, where it was most abundant in upland stands. It also occurred in clear-cuts in upland stands 6-24 years old and in 24-year-old lowland cuts. In the Clay Belt, it was most abundant in balsam fir–white spruce–balsam poplar stands followed by those dominated by balsam poplar, balsam fir–spruce, tamarack or white cedar, and black spruce. It was most common in wet, nutrient-rich stands but also occurred in nutrient-poor stands (Welsh and Lougheed 1996).

The Blackburnian Warbler was common in mature and old-growth white pine stands in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield. It was slightly more abundant in old-growth stands than mature stands, but not significantly. It was the third-most abundant species. It used both white pine and red pine stands extensively, preferring mature or old-growth stands. It was not observed in stands younger than 66 years. The density of supercanopy pine trees was the most important variable in determining its presence and abundance. It was correlated with basal area (BA) of conifers, total BA, stand age, and presence of medium-sized and large pines (Kirk et al. 2012). It also nests in younger pine stands. Kingsley and Nol (1999) observed it in 71.4-100% of uncut white pine stands in Algonquin Park compared with 70-81.8% of stands 10-16 years old and 7.5% of stands 2-9 years old. Near Gogama, James and Peck (1995a) considered the Blackburnian Warbler characteristic of jack pine forests as well as mixed forests where pines represented at least 40% of the tree cover. It did not colonized areas until pines were at least 10 m tall. It was never numerous until pines attained a height of 12 m. It was common in older pine forests, usually where trees were dense and uniform and there were few tall shrubs. In northern hardwood stands near Sault Ste. Marie, the Blackburnian Warbler was associated with short shrubs in the understorey. Near Pimisi Bay, Lawrence (1953b) found it predominantly in mature conifers, including white pine, white spruce, hemlock, and red pine in order of importance. These stands had some scattered poplars and

white birch within them. In other areas, she observed it in climax stands of conifers with sparse or no undergrowth and with deciduous trees and shrubs only around the edges of the stands. In Algonquin Park, it was most abundant in hemlock stands and characteristic of hemlock. In hemlock stands, it occurred at heights of 3-24 m, from 3 m below the bottom of the canopy to the top of the canopy. It was the most abundant species in hemlock stands. Other stand types it occurred in included black spruce–white cedar, balsam fir–spruce, white birch–poplar, white birch–poplar–balsam fir–spruce, and immature white pine. In mixed forests, it was not observed above 12.2 m, which represented the top of the coniferous forest cover, although the deciduous trees extended above this. In balsam fir–spruce stands, it occupied the central portion of the canopy. In black spruce–white cedar stands, it occurred at heights of 3-17.7 m. These heights represented the bottom of the canopy and top of the shrubs to above the white cedar layer but 3.5 m from the top of the spruce (Martin 1960). In Parry Sound District, it was associated predominantly with conifers during the summer but moved to areas of conifers and white birch later in the season (Mills 2007). In Haliburton County and Muskoka District, the Blackburnian Warbler occurred mainly in mature forests, especially coniferous stands where there was limited understorey. It was associated with intermediate levels of canopy volume and slightly less than the mean tree density. It was associated with tall canopies. It occurred mostly in undisturbed forests or on cottage lots in mature woods where the canopy layer had not been disturbed (Clark et al. 1983).

In the off-Shield portion of the Great Lakes–St. Lawrence Forest Region, Speirs and Orenstein (1975) found the Blackburnian Warbler in a mature white pine plantation that included a small relict of red maple–red oak forest. They considered it associated with pines. At Presqu'ile, it nested in a stand of planted and natural conifers (LaForest 1993).

In the Carolinian Forest Region, the Blackburnian Warbler nested for many years in hemlock in Milton Heights (Curry 2006). In Elgin County, breeding birds occur in mature woodlands, especially those containing pine. It also nests in pine plantations and ravines dominated by hemlock (Lancaster et al. 2004).

The Blackburnian Warbler nests in a wide diversity of habitats throughout its range. In the eastern Boreal Forest Region, it is characteristic of balsam fir and spruce stands, but is seldom found in pure spruce stands. It is characteristic of mature coniferous stands and is scarce or lacking in young stands. It inhabits the most fertile coniferous stands available whether they are hemlock, balsam fir, or spruce amidst poplar. It is one of the most regular and common species in white pine and red pine stands, and also pitch pine stands in Ontario (Erskine 1977). In the western Boreal Forest Region, it is also associated with coniferous species, but is characteristic of white spruce stands. It occurs in mature drier sites that are rich in nutrients (Kirk et al. 1996). In Quebec, its probability of observation is high in deciduous forests with conifers and in mixed forests, especially where balsam fir occurs. It becomes less common as the percentage of conifers increases and where pure coniferous stands are found, particularly those dominated by spruce (Lanoue and Dauphin in Gauthier and Aubry 1996). In Maine, it is common in almost pure coniferous forests dominated by white spruce and red spruce. It inhabits only stands with tall or supercanopy spruce and its density is directly related to the volume of tall conifers. It inhabits the highest strata of the treetops, especially where the socially dominant Black-throated Green Warbler is present. The Blackburnian Warbler avoided small islands

forested with spruce in Maine, but occurred on similarly sized islands in New York and Minnesota where the conifers were 4 m taller. In Maine, it avoided areas of blowdown and small groves of white birches among the spruce, although in other areas it may be common in conifers mixed with poplars and birch (Kendeigh 1945; Morse 1967, 1976, 2020). In Maine, Vermont, and other areas, it may occur in low densities in clear-cuts in deciduous and mixed forests (Lent and Capen 1995; Titterington et al. 1979). On islands in Wisconsin, it was most abundant in stands dominated by pines, including jack, white, and red pines. Densities were the same in stands dominated by white birch–yellow birch–white cedar and hemlock–yellow birch, with lesser numbers in red maple–yellow birch stands. It was highly associated with pines and its numbers increased with increasing importance of conifers (Beals 1960). In New York and many other areas, the Blackburnian Warbler prefers spruce draped with beard lichen (Morse 2020). In New Brunswick, it breeds in spruce plantations older than 20 years and in mixed forests of red spruce, red maple, balsam fir, trembling aspen, white pine, and white birch in decreasing order of abundance. It is one of the most abundant species there. It was associated with high densities of large coniferous trees. It selected, in order of preference, stands dominated by pine, a mix of tolerant and intolerant hardwoods with spruce, mixed spruce and intolerant hardwoods, and spruce–balsam fir. It avoided stands of mixed tolerant and intolerant hardwoods, intolerant hardwoods, and intolerant hardwoods mixed with spruce (Freedman and Johnson 1999; Parker et al. 1999). In Quebec, it occurs predominantly in mixed forests and particularly in mature balsam fir stands where it seeks tall trees towering over the canopy. It is common in balsam fir–white cedar stands and occurs in 6-15-year-old strip-cuts through both deciduous and coniferous forests. It is absent in final strip-cuts and clear-cuts (Falardeau et al. 1999; Lanoue and Dauphin in Gauthier and Aubry 1996; LaRue et al. 1995). Further south in its range, the Blackburnian Warbler prefers stands dominated by or containing hemlock. It attains its highest density within hemlock stands. In the extreme southern portion of its range, it nests in deciduous stands where conifers are completely lacking or scarce. These forests may be dominated by northern hardwoods such as sugar maple, beech, and yellow birch or more southern species such as oaks. Early in the period when the chestnut tree was being attacked by blight, it was common on dry ridges dominated by chestnut sprouts. Presence of large trees is less of a requirement in deciduous stands because there is less likely to be competition from the Black-throated Green Warbler, although the 2 species occasionally nest together in hardwoods. Even where conifers are present or even dominant, the Blackburnian Warbler may occasionally nest in low densities in deciduous stands dominated by northern hardwoods or poplar-birch. In Ohio, a female foraged predominantly in a walnut tree in the lawn of an urban park but nested in Norway spruce planted at the edge of the lawn. A Massachusetts nest was in an open growth of white cedar 36 m from a house, but the male usually sang from a mature pine and hemlock forest 137 m distant. A Minnesota nest was directly over the entrance to a cabin; it was in a cedar tree (Back 1979; Bent 1953; Brooks 1940, 1947b; Capen 1979; Chapman 1907; Erskine 1977; Harrison 1984; Holmes and Schultz 1988; Kotesovec 1993; Morse 2020; Nice 1932b).

Several studies examined microhabitat preferences of the Blackburnian Warbler. In New Brunswick, territory density was determined by the density of mature red spruce and yellow birch. It foraged and sang in both mature coniferous and deciduous species, but avoided immature conifers (Young 2004). In Michigan, 90% of Blackburnian Warblers were in coniferous stands,

predominantly in sawlog-sized stands, although some occurred in pole-sized stands. Stand types it nested in included hemlock, white spruce–balsam fir, white pine, white cedar, upland hardwoods, mixed coniferous swamp, and red pine. Occupied sites had dominant trees that were 60-167 years old with a high BA (10.6 m^2 for conifers and 3.2 m^2 for deciduous species), high canopy closure (80.1%), low understorey coverage (15.8%), and low herbaceous cover (38.5%). It inhabited older, medium to high density, mesic, conifer-dominated forests (Doepker et al. 1992). In Maine, it was associated with a coniferous overstorey and larger conifers. It was positively correlated with deciduous trees less than 10 cm diameter at breast height (DBH) and taller than 4.5 m, negatively associated with conifers the same size, and positively correlated with conifers larger than 20 cm DBH (Titterington et al. 1979). In northern Wisconsin mesic forests, it first appears when forests become sawtimber-sized (trees larger than 23 cm DBH). Occupied stands had a mix of deciduous and coniferous species with a predominantly closed canopy and an understorey of saplings (Hoffman 1989a). In New Hampshire and Maine, DeGraaf and Chadwick (1987) concluded that the Blackburnian Warbler was associated with sawtimber-size spruce–balsam fir forest. They considered it a size-class obligate species that preferred 1 size class but occurred in others. In subalpine areas of these 2 states, its abundance was negatively correlated with percent ground cover, the number of deciduous trees 2-10 cm DBH, and the number of woody stems per ha (DeGraaf et al. 1998). In northeastern mixed forests, Temple et al. (1979) considered it associated with mature forests and increasing amounts of pine. Niemi and Pfannmuller (1979) placed the Blackburnian Warbler in a guild that was common in mature upland coniferous stands, uncommon in mature lowland coniferous stands, and very uncommon in alder, mature deciduous upland forest, disturbed shrubby areas, young plantations, aspen regeneration, and recent clear-cuts. It was associated with increasing numbers of trees and saplings and moderate numbers of low shrubs. The average habitat characteristics of the Blackburnian Warbler in Minnesota were 56.7% ground cover, 41.0% shrub cover, 77.3% canopy cover, 16.1 m canopy height, 55.0% coniferous cover, 6.1 tree species per 0.04-ha circle, 16.1 trees 7.5-15 cm DBH per circle, 11.7 trees 15.1-23 cm DBH, 9.5 trees 23.1-30 cm DBH, 4.9 trees 30.1-38 cm DBH, 2.7 trees 38.1-53 cm DBH, 0.4 tree 53.1-68 cm DBH, and 0.2 tree larger than 68 cm DBH. It was associated with mature, mostly undisturbed forests containing coniferous cover and preferred moderate ground and shrub coverage with more than 75% canopy cover. Territories consistently contained more than 50% conifers, usually spruce or balsam fir, mostly in the large tree-size categories (Collins et al. 1982). Collins (1983a) compared the habitat usage of the Blackburnian Warbler in Maine and Minnesota and found that usage of areas with trees 7.5-15 cm DBH and 15.1-23 cm DBH differed significantly in the 2 areas. In Minnesota, it occupied habitats with tall canopies, moderate coniferous cover, few small trees, and more large trees. In Maine, it selected areas with high canopy closure, variable coniferous cover, and many trees in the smaller size class. Despite this, the Blackburnian Warbler was associated with large conifers in both states.

Most authors concluded that the Blackburnian Warbler requires mature stands, and 2 studies quantified this. In Saskatchewan, Cumming and Diamond (2002) demonstrated that it was most frequent in forests older than 100 years. Its probability of detection on point counts was 20-49% in 50-60- and 80-90-year-old forests, more than 100% in forests 100-110 years old, and 80-100% in forests 140 or more years old. In Pennsylvania, it occurred in 100% of old-growth hardwood-hemlock-pine forests compared with 18.6% of forests statewide and 35.0% of forests on the

Appalachian Plateau. Haney (1999) considered it to have old-growth affinities and it achieved particularly high densities in the oldest mixed forests.

It is possible that the Blackburnian Warbler is area sensitive in the west but not in the east. In Saskatchewan, it was more common than expected in mature white spruce stands that were large but isolated. The relationships between its abundance and forest type and the amount of forest within 5 km were significant, but the relationship with forest size was not (Hobson and Bayne 2000). In Maine, it was absent on islands smaller than 1 ha, but occurred on similarly sized islands in Minnesota and New York where there were tall white pines or spruce available. Avoidance of small islands in Maine was likely because the trees were too short rather than because the habitat patches were too small (Morse 2020). A Wisconsin study found that it was not confined to large islands (Beals 1960). In Minnesota, it nested on 0.5-1.1-ha islands, but was not documented on smaller islands (Howe 1979). There appear to be no studies that have conclusively demonstrated that the Blackburnian Warbler is area sensitive.

Freemark and Collins (1992), Hobson and Bayne (2000), and Morse (2020) all concluded that the Blackburnian Warbler was a forest-interior species, but provided no documentation, although Morse (1967) stated that it was typically an inhabitant of forest interior in Maine. In Quebec balsam fir–white cedar stands, it was significantly more abundant in nonriparian than riparian habitat. This may have been more a function of habitat suitability than edge avoidance. Riparian areas contained open wetland strips of alder–reed grass or sweet gale, habitat that is unsuitable (LaRue et al. 1995). In Maine, its abundance was correlated with distance from an interstate highway even after accounting for variation in habitat. This suggested that the highway was exerting a negative influence on this warbler (Ferris 1979). It was not determined if this was an edge-avoidance effect or due to noise, disturbance, predation, or other factors. During 1 breeding season, a male Blackburnian Warbler defended a territory at the edge of the St. Williams Forest, often singing from trees at the extreme edge (personal observation). Nests have been found at the very edge of stands and even in sparse tree cover near buildings but adjacent to coniferous or mixed habitat in Manitoba, Minnesota, and Massachusetts (Bent 1953; Nice 1932b). There appears to be no evidence that the Blackburnian Warbler is an obligate forest-interior species.

All Ontario nests were in living coniferous trees: 55.2% in pines, 20.7% in hemlock, 17.2% in spruces, 3.4% in balsam fir, and 3.4% in white cedar. Most nests were in the top portions of trees, although some were at mid-level and some were in lower branches. Usually they were on horizontal branches, often among smaller branchlets or at crotches; 17.6% were near or against the trunk. Nests were 0.9-5 m from the trunk with most 1.8-2.4 m from the trunk. Heights of nests from the ground were 2.4-17.4 m, with most 6-12 m up (Peck and James 1987, 1998a). Three nests in the Pimisi Bay area were 8.0-16.8 m from the ground, with 2 in white pine and 1 in white spruce. All were on a horizontal branch 2.4-3 m from the trunk. The bottom of 1 nest was not affixed to the limb, resting loosely upon it, half suspended and attached to 4 short, stiff twigs by spider silk. Another nest was in a crotch of 3-cm diameter branches (Lawrence 1953b).

Nests are almost invariably placed in conifers although there is 1 record of a nest in a chestnut tree. The Blackburnian Warbler occasionally nests in pure deciduous stands, so it is likely that nests in deciduous trees are more prevalent than the literature suggests. In Canada and New England,

most nests are in spruce, white pine, and balsam fir; hemlock is greatly preferred further south. Lesser numbers of nests have been reported in white cedar and tamarack. Red and white spruces are favoured nest trees. It may use black spruce in the north and planted Norway spruce in the south. In addition to white pine, it has nested in jack pine, and it is likely that it also uses red pine and pitch pine. Nests are almost always on a horizontal branch, occasionally near the trunk, but more frequently some distance from it and occasionally at the extreme outer tips of branches. In white cedar, nests may be at the very top of trees. Nests have been reported at heights of 1.5-25.6 m from the ground, with most above 9 m (Bent 1953; Chapman 1907; Cruickshank 1956; Kendeigh 1945; Kotesovec 1993; MacArthur 1958; Morse 2020; Nice 1932b).

Males establish territories are established as soon as they arrive and maintain them only until the young fledge. At Pimisi Bay, no territories were defended beyond late July. There is 1 report of the Blackburnian Warbler nesting in colonies but examination of the data reveals that birds were simply present in moderate to high density with no evidence of clustering of territories. At Pimisi Bay, these warblers did not nest close together. Near Quebec City, territories were significantly clumped at scales of 450 and 550 m. Its distribution there was probably related to the clustered distribution of ground cover and the percent coverage of deciduous trees, at least at the 250-m scale. Although the amount of available food does not affect territory size, there is a close relationship between foliage volume at high levels in trees and territory size. The Blackburnian Warbler concentrates its activities in treetops where there is only about 40% of the foliage volume per unit area than in the level frequented by the Black-throated Green Warbler. The density of the Blackburnian Warbler is typically almost 40% of that of the Black-throated Green Warbler. Near Lake Nipigon, 4 territories averaged 0.85 ha (range 0.81-0.89 ha), but few observations were made, so territories could have been larger. Average territory size in Algonquin Park was 0.18 ha (range 0.04-0.96 ha). At Mirabel, Quebec, territories averaged 1.0 ha (range 0.6-1.7 ha). Nine New York territories averaged 0.53 ha. In Maine, territories averaged 0.4-0.6 ha in white and red spruce forests and 1.1 ha in largely deciduous forests (Bent 1953; Bourque and Desrochers 2006; Kendeigh 1945, 1947; Lanoue and Dauphin in Gauthier and Aubry 1996; Lawrence 1953b; Martin 1960; Morse 1976, 1977, 1989, 2020).

No information is available on natal philopatry and little information is available on adult site fidelity. At Pimisi Bay, 3 territories were occupied in 3 consecutive years. These birds were not banded so it is unknown if the same individuals were present each year (Lawrence 1953b). In New Brunswick, Zitske et al. (2011) banded 205 males over 7 years and 54 (26.3%) were resighted at least once. Two males (7.7%) dispersed 65-650 m from where they were originally captured. It is possible that reproductively unsuccessful birds emigrated in search of better habitat quality.

Limiting Factors

Eggs have been reported in Ontario nests throughout June and in the first week of July (Peck and James 1987). Dependent fledglings are regularly observed in Algonquin Park from late June to mid-August, and occasionally until the end of August (Tozer 2012).

Two first nests at Pimisi Bay took 4 and 6 days to build and it took 3 days to build a replacement nest. The first egg was laid in one of these nests 2 days after it was completed. Presumably 1 egg is laid per day, although this has not been confirmed. Incubation probably starts with the laying of the

last egg. The incubation period at 1 Ontario nest was 12 days and possibly 13 days at another. There is no other information on the incubation period. It is unknown how old young are when they leave the nest (Bent 1953; Lawrence 1953b; Morse 2020; Peck and James 1987).

A single brood is raised annually, but renesting may occur if the first brood is unsuccessful. At Pimisi Bay, no third nesting attempts were made after 2 failures. In Ontario, clutches of 4 or 5 eggs have been reported (average 4.29 eggs, mode 4 eggs). Elsewhere, clutches of 3-5 eggs have been reported with 4 eggs most common. The mean size of 44 clutches from Maine and Vermont was 3.96 eggs. There is no evidence that clutch size varies with spruce budworm populations (Bent 1953; Chapman 1907; Lawrence 1953b; MacArthur 1958; Morse 2020; Peck and James 1987).

The age at first breeding is unknown, but is probably 1 year. Some populations contain vagrant nonbreeding individuals and these are most likely yearling males that were unsuccessful in defending a territory or attracting a mate. The mating system is monogamous. There is no evidence of extra-pair copulations, although this has not been studied in any detail. Silent second males have been observed on territories and it is possible that they were seeking extra-pair copulations. Pairs remain together until the young fledge. There is no evidence of pairs rejoining in subsequent years (Morse 1976, 2020).

Some studies determined where the Blackburnian Warbler forages in conifers in Maine, Vermont, and Saskatchewan. Conifers were divided into 5 vertical zones and 3 horizontal zones. The inner horizontal zone consisted of large-diameter branches that were largely devoid of needles, the central zone contained fairly large branches with old needles, and the outer zone had new growth of fresh needles and small twigs. In all areas, it consistently fed in the top 2 zones, mostly in the outer zone and also in the central portion of the zone second from the top. It made limited use of the central zone and used the 2 bottom zones less than expected with almost no usage of the lowest zone. Within conifers, it moved in a radial direction, similar to the Bay-breasted Warbler, but significantly different from the Cape May, Black-throated Green, and Yellow-rumped warblers in Maine and Vermont. In Saskatchewan, the Blackburnian Warbler exhibited one of the least diverse foraging patterns in trees along with the Blue-headed Vireo, but there was 0% overlap with the vireo with respect to other foraging techniques. The Blackburnian Warbler foraged significantly higher in conifers than all other warblers except Bay-breasted and Black-throated Green warblers. In Saskatchewan, there was an 85% overlap in foraging between Blackburnian and Bay-breasted warblers, significantly higher than for most other pairs of warblers. The Blackburnian Warbler was intermediate between the Bay-breasted and Black-throated Green warblers in its method of foraging, usually moving out from the base of branches to the tips in the manner of the Bay-breasted Warbler, occasionally hopping about rapidly on the foliage at the tips of branches looking for insects, and even hovering occasionally. It seldom hawked flying insects. Warblers in coniferous forests tended to feed in different places within trees and in different manners and were therefore probably exposed to different prey items, thus reducing competition. Competition is further reduced by differing times for peak food requirements, with the Blackburnian Warbler nesting considerably sooner than the Bay-breasted Warbler. The Blackburnian Warbler can only persist in large numbers when the forest is sufficiently old that the primary feeding zone of the dominant Black-throated Green Warbler stops well below the treetops where the Blackburnian Warbler prefers to feed

(Cumming 2004; MacArthur 1958). In Maine, Morse (1967) studied the foraging of the Blackburnian Warbler and other species in spruce. It foraged at an average height of 15.2 m (range 10.7 to more than 19.8 m). It usually foraged at greater heights than the Northern Parula, Magnolia Warbler, Yellow-rumped Warbler, and Golden-crowned Kinglet and, to a lesser extent, the Black-throated Green Warbler. The Blackburnian Warbler did not use the tips of foliage as frequently as the Northern Parula, yet foraged more similarly to the Northern Parula and Black-throated Green Warbler than to the Magnolia and Yellow-rumped warblers. Foraging by the Blackburnian Warbler was 19.8% at the tips of foliage (16.7% by gleaning and 3.1% by hovering), 48.9% on live twigs as large as 5 mm, 2.1% on dead twigs, 2.1% on dead branches, 4.2% on the distal portions of branches, 15.6% on the proximal portions of branches, and 3.1% by flycatching. Only 4.2% of foraging occurred on deciduous species. Studies were completed in Saskatchewan and New Hampshire on the foraging tactics of the Blackburnian Warbler in deciduous trees, where there may be a different suite of potential competitors. In Saskatchewan, the average foraging height in deciduous species was 15.7 m, the same as in conifers. Its foraging height was significantly higher than that of the Blue-headed Vireo and Magnolia Warbler, but not significantly different from Yellow-rumped and Tennessee warblers. The most overlap in foraging tactics in deciduous trees with the Blackburnian Warbler was with the Yellow-rumped Warbler. The Blackburnian Warbler spent 89.9% of its foraging time in the canopy, 10.1% in the subcanopy, and 0% in the shrub and herbaceous layer (Cumming 2004). In Minnesota, the Blackburnian Warbler foraged at heights of 1-15 m, but predominantly at 6-12 m. Eighteen percent of foraging occurred in red pine, 51% in white pine, 19% in deciduous trees, 2% in balsam fir, and 4% each in spruce and other species (Howe 1979). In New Hampshire, Robinson and Holmes (1982) considered the Blackburnian Warbler a near-surface searcher that predominantly gleaned small to medium-sized, often cryptic, insects. Others in this group included the Black-throated Green Warbler, which also gleans from leaves in the canopy, and Black-throated Blue Warbler, which forages similarly but exclusively in the understorey. The Blackburnian Warbler made 77.0% of its prey attacks on leaves and 14.4% on bark. It captured 1.8% of prey by hawking and 6.0% by flush-chasing. Holmes and Schultz (1988) compared the foraging strategies of 10 species in northern hardwood stands in New Hampshire, including their tree-species preferences. The 3 main tree species used by the Blackburnian Warbler for foraging were beech, sugar maple, and yellow birch. Forty-two percent of prey attacks were on upper leaf surfaces, 47% on lower leaf surfaces, 2% on leaf petioles, and 9% on twigs. The proportional use of these substrates varied among tree species. Prey was obtained predominantly by gleaning (70% of prey attacks) and 30% by hovering with little difference among tree species. Unlike in conifers, it did not concentrate its foraging in any particular strata. All 10 species differed significantly from each other in their use of foliage substrates, of tree species, and of petioles and small twigs combined. The Blackburnian Warbler did not change its use of attack manoeuvres significantly in different tree species. It foraged preferentially in yellow birch, which had the highest densities of caterpillars. In yellow birch, it and the Black-throated Blue Warbler and Rose-breasted Grosbeak overutilized upper leaf surfaces in proportion to their availability and underutilized lower leaf surfaces. In beech, the Blackburnian Warbler significantly overutilized upper leaf surfaces. It and the Black-throated Blue Warbler and Black-capped Chickadee differed from other species in directing proportionally more manoeuvres toward upper leaf surfaces. The Blackburnian and Black-throated Blue warblers consistently changed foraging patterns in the same manner among tree species. The Blackburnian Warbler, Black-capped Chickadee, Black-

throated Green Warbler, and Rose-breasted Grosbeak predominantly gleaned from foliage close to their perches. The only species that hovered to any extent were the Least Flycatcher and Blackburnian Warbler in beech and the Rose-breasted Grosbeak in yellow birch. In sugar maple, only the Blackburnian Warbler, Black-capped Chickadee, Scarlet Tanager, and Rose-breasted Grosbeak foraged in proportion to the distribution of available insects. In coniferous habitat in Maine, male Blackburnian Warblers foraged higher than females, lower than their song perches but higher than the nest. Females foraged closer to the nest height. Both sexes foraged predominantly at heights of 9.4-12.2 m, but males spent significantly more time in this level. Females foraged to a maximum height of 15.5-18.3 m; males foraged at heights in excess of 18.6 m. Males hawked significantly more than females and females hovered more than males. Females may not normally hover more than males because 65% of the hovering motions were conducted by 2 females seen in close proximity on a single day. When these 2 females were removed from the analysis, there was no significant difference in the amount of hovering by the sexes (Morse 1968). Holmes (1986) conducted a similar study in deciduous habitat in New Hampshire. There was no significant difference in the average foraging heights of the sexes: 15.1 m for males and 14.4 m for females. When G-tests were applied, females used a higher stratum proportionally more than males. Males foraged at heights of 6-26 m with a peak at 14 m; females foraged 2-26 m from the ground with a peak at 20 m. Similar to Maine, male foraging heights were correlated with song perch heights and female foraging heights were correlated with nest height. Both sexes were predominantly leaf gleaners that foraged with equal frequency in proximal and distal portions of canopy trees. The sexes differed significantly in their usage of tree species, with females exhibiting high selectivity for coniferous trees. Tree species usage by females was 8.5% for beech, 5.8% for sugar maple, 52.4% for yellow birch, 3.7% for white ash, and 29.6% for conifers. Male tree species usage was 14.0% for beech, 7.3% for sugar maple, 65.4% for yellow birch, 2.0% for white ash, 10.0% for conifers, and 1.3% for other maple species. Conifers represented only 1% of the available trees. In the Clay Belt of Ontario, 57.0% of foraging was in conifers at an average height of 13.6 m at 72% of tree height. Eighty-three percent of prey attacks were on foliage: 40.1% by aerial attacks, 4.8% by hanging, 22.0% by hovering, and 18.4% by reaching (Greenberg et al. 1999). In Parry Sound District, foraging height was 5-16 m during the breeding season and 4-13.5 m during autumn migration. Based upon foraging heights and general foraging strategies, the foraging manoeuvres of the Red-eyed Vireo and 6 warbler species were essentially indistinguishable (Mills 2007).

Nestlings near Pimisi Bay were fed green caterpillars and mayflies. Young at an Ohio nest were fed larvae, caterpillars, and winged insects. Two males near Lake Nipigon had consumed 196 prey items: 31.1% flies, including march flies; 28.6% beetles, including weevils and soldier beetles; 11.7% lepidopterans; 6.6% conifer sawflies; 6.6% ichneumonid wasps; 5.1% spiders; 4.6% brown lacewings; 3.6% short-horned grasshoppers; and 2.0% planthoppers. In New Hampshire, adults captured 75.0% caterpillars, 16.6% adult lepidopterans, 4.2% flies, 2.1% beetles, and 2.1% spiders. It was also likely that they preyed heavily on soft-winged bugs, particularly leafhoppers. Other prey the Blackburnian Warbler has eaten during the breeding season includes ants, wasps, crane flies, leaf beetles, spruce budworm caterpillars, and saddled prominent caterpillars. Birds offered gypsy moth larvae in an aviary experiment all refused to eat them (Bent 1953; Crawford and Jennings 1959; Holmes and

Schultz 1988; Holmes and Sturges 1975; Kendeigh 1947; Kotesovec 1993; Lawrence 1953b; Robinson and Holmes 1982; Whelan et al. 1989).

The Blackburnian Warbler may exhibit variable responses to spruce budworm outbreaks. It does not alter its clutch size when budworm numbers are high and its population may remain static, increase, or decrease during budworm outbreaks. Data from 2 areas in Ontario indicate that it was more abundant during outbreaks than when budworms were scarce or lacking. Near Lake Nipigon during an outbreak, density of the Blackburnian Warbler averaged 14.8 per km^2 (Kendeigh 1947). It was absent or rare in the same area when budworms were absent (Sanders 1970). Near Manitouwadge, density increased by 42% in mature stands during a budworm outbreak, but it continued to be absent in young and intermediate-aged stands (Venier et al. 2009). In New Brunswick, it exhibited a direct but weak response to increasing budworm numbers. It responded almost immediately to the outbreak, but to a lesser extent than the Bay-breasted Warbler. The Blackburnian Warbler apparently did not respond to an earlier outbreak in the same area (Morris et al. 1958). During a spruce budworm outbreak in New Hampshire and Maine, Blackburnian Warbler stomachs contained an average of 3.0 budworms, third highest of any species. It had densities almost twice as high as the Magnolia, Bay-breasted, and Cape May warblers and consequently consumed more budworms per ha than any other species. These populations of the Blackburnian Warbler did not increase with budworm populations, but the studies were done in outbreak years so densities could not be compared to periods when budworms were absent (Crawford and Jennings 1989). In Maine during a spruce budworm outbreak, 19 stomachs contained 20% and 26% budworm larvae and pupae by volume in 2 years (Mitchell 1952). Blackburnian Warblers may decline during budworm outbreaks if populations of Bay-breasted and/or Cape May warblers increase significantly. These 2 species are dominant to the Blackburnian Warbler (Morris et al. 1958; Morse 1989). The Blackburnian Warbler is most likely to be adversely affected by these 2 warblers during budworm outbreaks in areas lacking supercanopy trees. Where very tall trees are present, the Blackburnian Warbler may reduce competition by foraging above the preferred heights of the other warblers. In New Hampshire, Holmes and Sturges (1975) attributed an increase in Blackburnian Warblers to an outbreak of saddled prominent caterpillars.

The Blackburnian Warbler is an uncommon host of the Brown-headed Cowbird because this parasite avoids extensive mixed and coniferous forests, especially in more northern areas. The high nest height of the Blackburnian Warbler is not a deterrent to the cowbird. The highest nest reported (25.6 m) was parasitized. As of 1977, only 10 parasitized nests had been reported. Many parasitized nests are at edges of forests. The effects of parasitism on the reproductive success of the Blackburnian Warbler are unknown, but it has successfully fledged cowbirds. In Ontario, 4 of 12 nests (33.3%) were parasitized (Morse 2020; Peck and James 1998a). It is likely that parasitism rates are lower in the Boreal Forest Region.

Forest fragmentation at the landscape and local scales can affect Blackburnian Warbler abundance and survival rates. In New Brunswick, habitat loss was associated with a decrease in the number of individuals within a landscape. Annual survival rate increased with increasing amount of habitat within 100 m and there was some evidence for increased survival as habitat increased at the 2-km scale. Within-season survival was 12 times greater in landscapes with 85% habitat than those

with 10% habitat. The differential survival related to habitat abundance may be partly responsible for the lower probability of occurrence in landscapes with low amounts of habitat. There was little support for a relationship between area of mature forest and survival rates (Zitske et al. 2011).

Forest management practices that remove mature conifers are detrimental to the Blackburnian Warbler. In the Boreal Forest Region of Ontario, removal of 30% of trees within stands had no apparent effect but numbers decreased when 50% or 70% of trees were removed. By modelling current harvest prescriptions and natural disturbance regimes in the Boreal Forest Region of Ontario, it was predicted that the Blackburnian Warbler would experience a decrease over the next century. Two studies in Algonquin Park found no significant change in abundance as a result of single- and group-selection harvesting. In Michigan and New Brunswick, rotation periods in coniferous and mixed forests are typically 50 years or less. This is insufficient time for stands to mature to provide Blackburnian Warbler habitat. In addition, the high level of mechanization used to harvest pulpwood kills most of the advanced spruce–balsam fir regeneration. In Saskatchewan, rotation age is longer at 80-90 years, but this warbler is significantly more abundant in stands 100 or more years old. The older forests also contain a higher proportion of conifers than younger stands. In this area, the Blackburnian Warbler is likely to suffer some reduction in its population density if stands older than rotation age are lost from the landscape. Densities are low in retained riparian strips adjacent to clear-cuts (Cumming and Diamond 2002; Doepker et al. 1992; Jobes et al. 2004; Morse 2020; Rempel et al. 2007; Tozer et al. 2010; Vanderwel et al. 2009; Zitske et al. 2011). In the Ontario Canadian Shield, there was no difference in its abundance in early successional clear-cuts and burns, but it was significantly less abundant in mid-successional clear-cuts than in mid-successional burns. It was significantly less abundant in both early successional and mid-successional stands than in mature stands (Zimmerling et al. 2017). In northern hardwoods near Sault Ste. Marie, it had fairly high abundance in a stand where 42.0% of its total BA was removed, approximately 30% higher than the one third recommended in the silvicultural guidelines (Holmes and Pitt 2007). Webb et al. (1977) considered the Blackburnian Warbler a true species of undisturbed forest in New York northern hardwoods. It was most abundant in uncut stands and exhibited high and significant levels of decline at all intensities of logging. In Muskoka District and Haliburton County, it was negatively affected by even low levels of disturbance to forest structure (Clark et al. 1983).

Numbers of Blackburnian Warblers are thought to have declined during the periods of heavy use of persistent pesticides. Mortality was documented with application of DDT for control of Dutch elm disease. A decline and probable mortality was associated with use of fenithrothian for control of spruce budworms in New Brunswick (Morse 2020).

Weather factors such as late snow, cold, or extensive rain during the breeding season can depress populations. Under these circumstances, numbers may be reduced through scarcity of prey or mortality of nestlings due to exposure or starvation. A male continued to feed nestlings at a Pimisi Bay nest where the female had been killed. The young perished, most likely because the male failed to brood them (Lawrence 1953b; Morse 2020).

Factors outside Ontario may affect Blackburnian Warbler populations. Populations breeding in hemlock are at risk because of the woolly hemlock adelgid which attacks and kills hemlock (Morse 2004). In New Jersey and Pennsylvania over a 15-year period, hemlock declined from representing

56% of the total basal area to 46% as a result of the hemlock woolly adelgid; the amount of deciduous understorey increased. It was adversely affected by hemlock decline and decreased (Toenies et al. 2018). The hemlock woolly adelgid has recently colonized southern Ontario. Deforestation in the wintering grounds is serious and may affect populations (Morse 2020).

Venier et al. (1999) determined that climate had a strong influence on the breeding distribution of the Blackburnian Warbler in Ontario. Important factors determining its distribution included maximum diurnal, mean seasonal, and annual ranges in temperature; annual precipitation; range in precipitation; and total precipitation during the growing season. Price (2004) concluded that the Blackburnian Warbler might disappear as a breeding species from southern Ontario if the average summer temperature increased by 2°C.

Status

Baillie and Harrington (1937) considered the Blackburnian Warbler a fairly common summer resident throughout the province north from Lake Erie and Ottawa to Hudson Bay. The first atlas indicated a more constrained distribution. Although it still ranged from Lake Erie to Ottawa in the south, distribution south of the Canadian Shield was spotty. It was absent in Essex, Chatham-Kent, Lambton, and Middlesex and there were only 1 or 2 records each for Elgin County and Niagara Region. There were no records from the Hudson Bay Lowland during the first atlas, with the northern extent of breeding occurring roughly from Sandy Lake to south of Moosonee (Crins in Cadman et al. 1987). It is likely that the population south of the Shield declined between the time of Baillie and Harrington's (1937) publication and the first atlas due to deforestation. It is less likely that there was a change in the northern extent of its range. The range determined by the atlas was similar to that depicted by Godfrey (1986), who acknowledged that the northern limits of its range were uncertain. James (1991) considered the Blackburnian Warbler a common summer resident across the province north to Sandy Lake and Cochrane, but with sight records to Fort Severn. He considered it rare south of the Shield to Elgin County.

The second atlas revealed that there had been no significant changes in the breeding range of the Blackburnian Warbler since the first atlas. Its probability of observation increased significantly since the first atlas for the entire province, mainly because of a significant increase in the Boreal Forest Region and the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region. Although not significant, trends in all other regions were positive. There was considerable infilling of its range south of the Shield, particularly in the Great Lakes–St. Lawrence Forest Region, but also to some extent in the Carolinian Forest Region (Crins in Cadman et al. 2007). No explanation is evident for its increase. The increase in the Shield portion of the Great Lakes–St. Lawrence Forest Region may be because populations of the Bay-breasted and Cape May warblers declined significantly in this region. These species compete with the Blackburnian Warbler and are dominant to it. Their decline was likely related to decreases in spruce budworm populations, and Blackburnian Warbler populations may decline during budworm outbreaks due to competition from more dominant spruce-woods warblers. South of the Shield, numbers may have increased slightly due to maturation of mixed and coniferous forests. Highest densities occurred in the Shield portion of the Great Lakes–St. Lawrence Forest Region, with isolated areas of high density in the Boreal Forest

Region. Areas of high density coincided with the distribution of mixed forests with a strong coniferous component (Crins in Cadman et al. 2007).

The Blackburnian Warbler may experience annual fluctuations in its abundance. This has been documented in Maine, New Hampshire, and Wisconsin. Changes in abundance in Wisconsin were unrelated to drought and changes in annual precipitation (Blake et al. 1992; Holmes and Sherry 2001; Morse 1976). Changes in annual populations are most likely related to food supplies and competition from species that are dominant to it, especially the Bay-breasted, Cape May, and Black-throated Green warblers.

The overall population of the Blackburnian Warbler appears to be holding steady despite deforestation pressures in its wintering grounds and portions of the breeding grounds. Breeding Bird Survey (BBS) data for both 1966-2002 and 1993-2002 indicated no significant changes. It is probably underrepresented on the BBS because of its roadside count method and the fact that there are few roads in the core of its breeding range (Morse 2020). BBS results indicate an annual increase of 0.123% in Canada and an annual decrease of 0.459% in Ontario 1970-2021. Trends for 2011-21 were annual decreases of 0.547% in Canada and 1.02% in Ontario. Results were highly reliable except that the short-term Ontario trend was of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

At Pimisi Bay, the onset of the postnuptial moult occurs in the third week of July. At this time, singing ceases abruptly and birds move out of their territories, often pursued by fledglings still begging for food. At this time, both young and old birds join flocks of warblers that are passing through (Lawrence 1953b). The male and female may each care for half the brood, moving independently of each other with no evidence of subsequent regrouping. Fledglings in Maine soon drift away from the natal area, often leaving spruce forests to seek nearby groves of white birch which often support large numbers of leafrollers and other caterpillars (Morse 2020). Central Ontario birds also moved to areas containing more white birch late in the season (Mills 2007). Fledglings from an Ohio nest remained in deciduous shrubbery shortly after leaving the nest (Kotesovec 1993). In Minnesota, Streby et al. (2011b) captured both juveniles and adults in 2-10-year-old regenerating deciduous clear-cuts during the postfledging period. No birds were captured in this habitat during the breeding season.

MIGRATION

The Blackburnian Warbler is a nocturnal migrant, but occasionally exhibits some daytime movement. During autumn migration, it is likely to join mixed flocks of other warblers as well as chickadees and other resident species (Morse 2020).

Males arrive in spring before females. At Long Point, the mean capture dates for males were 16.5 May for after-second-year birds, 20.0 May for second-year birds, and 18.4 May for males of undetermined age. For females, mean capture dates were 22.1 May for after-second-year birds, 26.4 May for second-year birds, and 25.4 May for females of undetermined age (Stewart et al. 2002). At Prince Edward Point, the mean date of arrival was 21.6 May for males and 27.0 May for females (Francis and Cooke 1986). Males are present there from 10 May to 7 June and females are present 15 May to 14 June; peak numbers occur 25-31 May (Keast 1980, 1990). In southern and central Ontario, the peak of migration occurs around mid-May, with average arrival in the first week of May.

Most have passed through by the end of May, but migrants may be present from the last week of April until mid-June (Black and Roy 2010; Curry 2006; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). At Pimisi Bay, first arrivals occurred from 5 to 17 May (mean 12 May, median 13 May). Females arrived 3-23 days after males (median 9 days, average 11 days). The median of 9 days was considered more representative than the average (Lawrence 1953b). The Blackburnian Warbler was first observed on 20 May near Lake Nipigon (Kendeigh 1947).

During autumn migration in Virginia and West Virginia, juveniles passed through earlier than adults, although few adults were seen. Juveniles were observed from 3 September until 20 October; adults were observed 23-30 September (Stewart 1986). In the southern Shield, autumn migration is evident by mid-August and peaks in the first half of September with stragglers until mid-October (Lawrence 1953b; Mills 1981; Tozer 2012). Autumn migrants appear in the south by mid-August. The flight is heaviest in the first half of September but may extend into late September in the southeast. Migrants may arrive in mid- to late July and remain into early October, with rare stragglers remaining into November or even January (Black and Roy 2010; Curry 2006; Fleming 1907; Keast 1980, 1990; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008). Sheppard (1939) reported one in his garden in Niagara Falls 5-11 November.

During migration, the Blackburnian Warbler occurs in a variety of treed habitats, including deciduous, mixed, and coniferous forests. It has been stated that it prefers to forage in hemlock and pines, but it frequently occurs where there are no conifers. In Illinois, it showed no consistent preference for habitat, occupying woody areas such as bottomland and upland forests, forest edges, and shrubby areas equally in both spring and autumn. In addition to wooded and shrubby areas, the Blackburnian Warbler may be found in gardens and rural residential areas provided that some trees are present (Bent 1953; Graber et al. 1983; Morse 2020). During spring migration in Pennsylvania, it was most abundant in suburban forests followed by forest interior, forest-agricultural edges, and pole-stage forests. It was not detected in shrub-sapling-stage forests. It was significantly more abundant in suburban forests than in pole-stage forests (Rodewald and Brittingham 2007). During spring migration in Ohio, it was significantly more abundant in mature upland forests than mature riparian forests. Upland stands had significantly less canopy cover (74% compared with 83%) and more shrub coverage (39% compared with 19%; Rodewald and Matthews 2005). During autumn migration in Pennsylvania, there was no significant difference in its abundance in forest interior, forest-agricultural edges, suburban forests, shrub-sapling-stage forests, or pole-stage forests (Rodewald and Brittingham 2002, 2004). In early November in Niagara Falls, one appeared to roost overnight in a large weeping willow that was still almost in full leaf (Sheppard 1939).

The foraging habits during migration are similar to those used in the breeding season. Because the Blackburnian Warbler is not confined during migration to a territory where it may face competition from other warblers, it may forage at lower heights. During autumn migration at Prince Edward Point, it foraged at heights of 1.5-18 m, with a peak around 7 m. It sometimes fed part of the day at heights of 17-18 m, then in the tops of saplings, subsequently descending for short periods into shrubbery only 1.0-1.5 m tall. It occasionally showed some preference for feeding in conifers but commonly fed in deciduous species. Foraging locations were 5% in the air, 45% on outer leaves,

14% on twigs and inner leaves, 10% on outer branches, 2% on inner branches, 0% on the trunk, 19% on sapling foliage, 3% on sapling branches, 2% on low shrubs, and 0% on the ground. It was predominantly a crown and inner foliage feeder with some foraging conducted in outer branches and minor amounts in the canopy of saplings. During migration, it may modify its foraging behaviour to take advantage of unusual opportunities or to seek atypical prey when conventional prey items are scarce or lacking. During autumn migration in New York, Blackburnian Warblers searched at night for food among the foliage of trees illuminated by lights from a football stadium. It was observed eating insects on the ice of Lake Manitoba. Beetles, midges, other flies, and spiders were on the ice at that time. During a cold spell during spring migration in Massachusetts, it foraged in low shrubbery, grasses, and plowed fields, abandoning these areas later in the day when it warmed up (Bent 1953; Keast 1980; Lebbin et al. 2007; McNicholl and Goossen 1980; Morse 2020).

The Blackburnian Warbler continues to be largely insectivorous during migration, but may occasionally eat fruit when insects are scarce. An early spring migrant in Massachusetts ate ivy berries (Bent 1953; Morse 2020). Midges are abundant near the shorelines of the Great Lakes in spring and these areas provide an abundance of food for migrants. The midges attract large numbers of spiders and the warblers also prey upon them (R.J. Smith et al. 2007). Stomachs of Blackburnian Warblers killed at a hydro tower near Prince Edward Point contained small beetles and some plant material (Keast 1980). A very late autumn migrant at Niagara Falls appeared to be feeding on aphids and possibly aphid eggs on willow trees (Sheppard 1939).

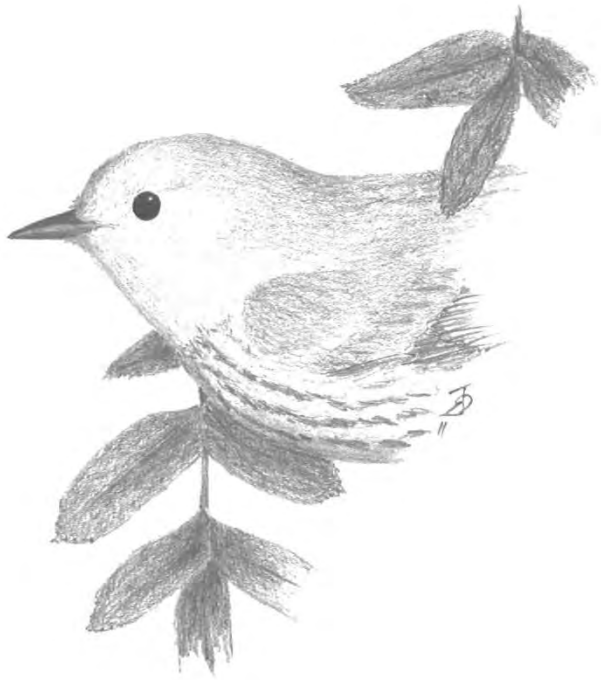
The Blackburnian Warbler is a common victim of collisions at tall structures. From 1972 to 1982, 1,491 were killed at the Lennox generating station chimneys near Kingston. Maximum kills of 136, 500, and 291 occurred on 2, 5, and 6 September 1981, respectively (Weir 2008).

James (1991) considered the Blackburnian Warbler a common migrant in Ontario, although Black and Roy (2010) considered it an uncommon spring migrant in Niagara Region.

Migration monitoring at Long Point indicated a nonsignificant decline in numbers of the Blackburnian Warbler 1961-88. Trends by period were: 1961-70, –8.1%; 1970-79, –14.7%; and 1979-88, –0.8%. Declines in the 1970s were attributed to decreases in the spruce budworm population, and its numbers corresponded closely with budworm numbers (Hussell et al. 1992).

Yellow Warbler

Setophaga petechia

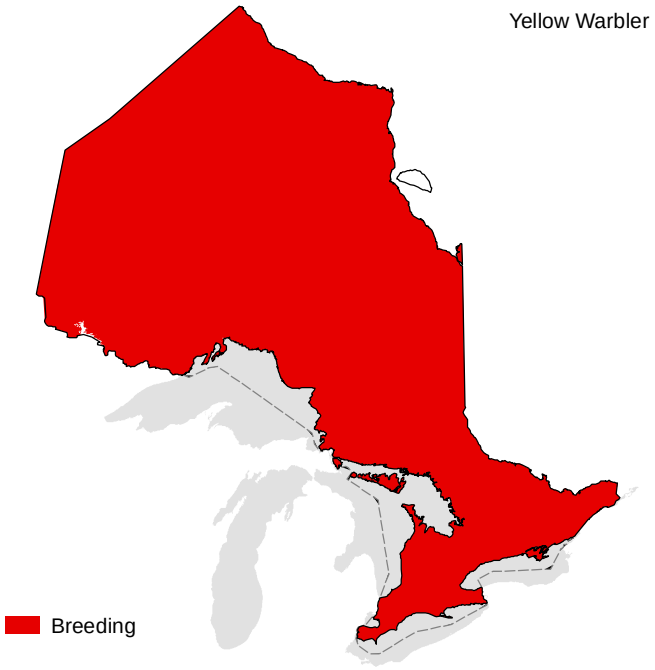


BREEDING SEASON

Habitat Requirements

The Yellow Warbler has one of the most extensive breeding ranges of any warbler, from above the treeline from the Atlantic to Pacific coasts south to Mexico and Venezuela. Forty-three subspecies are currently recognized within 3 main groups. It is likely in future that these 3 groups will be recognized as distinct species. Western populations appear to be genetically distinct from those in the east, so it is possible that they may also be split into individual species (Boulet et al. 2006; Lowther et al. 2020). The habitat preferences of the Yellow Warbler are remarkably similar throughout its range, except that the more southern subspecies nest in mangrove swamps, a habitat that is structurally similar to what is preferred range-wide (Salgado-Ortiz et al. 2008).

Ontario nests were predominantly in open shrubby habitat, most frequently (47.3% of nests) in overgrown fields and pastures. Other nesting habitats included floodplains and shorelines of rivers, lakes, and sloughs (18.8% of nests); in woodlots and at woodland edges (14.4%); in gardens and near cottages (10.6%); in hedges, fencerows, and old orchards (5.5%); in bogs and fens (2.1%); on railroad



and road rights-of-way (1.0%); and in boreal forest burns (0.3%). When the Yellow Warbler used forest cover, it appeared to prefer mixed woods to deciduous stands and only occasionally used coniferous forests. Occupied treed habitats were usually open and consisted primarily of short trees and shrubs. Both wet and dry sites were occupied. Nests were often near water, probably due to its preference for nesting in willow, alder, and dogwood. In tundra habitat, nests were in willow and alder thickets along sloughs and rivers (Peck and James 1987).

In the Tundra Region of Ontario, the Yellow Warbler was a common breeder in alder thickets along the Hudson Bay coast. It also nested in deciduous shrubs in swamps between the spruce forest and barren coastal regions (Manning 1952). At Cape Henrietta Maria, it nested in dense willows bordering tundra sloughs (Peck 1972).

In the Hudson Bay Lowland, the Yellow Warbler nested in alder and willow thickets along the James Bay coast. On islands near Moosonee, it nested in tall willow thickets near the river bank and at edges of barrens (Manning 1952). At North Point north of Moosonee, it nested primarily in wet thickets of willow and grey alder interspersed with common cattail. This habitat was immediately inland from extensive tidal marshes and formed a nearly continuous narrow band along the coast, broken only by scattered cattail marshes (Rimmer 1988).

In the Boreal Forest Region from Pickle Lake north to the Wetico Hills, the Yellow Warbler was most abundant in deciduous scrub, followed by deciduous forest, mixed scrub, mixed forest, and coniferous forest with an understorey. It was not detected in coniferous forest without an understorey, coniferous scrub, heath, or tundra (McLaren and McLaren 1981). In this forest region, it is confined mostly to areas of deciduous shrubs such as forest openings or along the margins of rivers, streams, and open wetlands. It does not usually inhabit clear-cuts, even when they are in the earliest stages of succession.

Habitat in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region is similar to that used in the Boreal Forest Region. James and Peck (1995a) rarely encountered the Yellow Warbler in jack pine stands near Gogama where it occurred only in very young regeneration with a high component of deciduous growth. In Algonquin Park, it was only moderately common in partly open country and at edges of woods (MacLulich 1938). Tozer (2012) concurred, noting that it was limited by the scarcity of willows and the presence of heavily wooded areas. It nests in the park in willows and alders bordering lakes, ponds, and marshes; along an old railway right-of-way; along a hydro corridor; and in roadsides, fields, and clearings. In Parry Sound and Muskoka districts, it nests

in moist thickets of willow and other thickets, which are widely but not commonly distributed. It nests in old fields, small scrubby islands, and wet open areas such as pond margins (Mills 1981). Wilson (1985) reported that it was one of the most common breeding birds on sparsely vegetated bedrock islands in Georgian Bay. North of Kingston on the Frontenac Axis, it nested in a marshy area dominated by willows, cattails, alders, and meadowsweet; in open rocky pasture interspersed with sapling and mature maples, staghorn sumac, and dense clumps of raspberries; and in open areas along a path through mixed forest (Yezerinac et al. 1995).

In Durham Region in the off-Shield portion of the Great Lakes–St. Lawrence Forest Region, Speirs and Orenstein (1975) reported high densities of the Yellow Warbler in a very young pine plantation that was still dominated by willows and meadowsweet, and in an abandoned apple orchard with hawthorn growth and an understorey of grasses.

In the Carolinian Forest Region at Point Pelee, Dodds and Otis (2009) recorded the Yellow Warbler in high densities in mature deciduous forests dominated by hackberry, black walnut, and green ash. One plot was adjacent to a red cedar savannah swamp and a road. In Hamilton, nests were more frequently found in lilac bushes in gardens than in natural habitats (McIlwraith 1894). South of the Shield, it is common in a variety of open habitats. In addition to the alder and willow thickets that it inhabits throughout the province, it occurs in old shrubby fields, lightly grazed pastures, hawthorn meadows, overgrown roadsides, and utility rights-of-way. It is no longer common in residential yards or orchards because these areas tend to be highly manicured now. It is also less frequent in hedgerows than previously, because residual hedgerows tend to be narrow and pass through row crops that do not provide any suitable nesting habitat (personal observation).

Habitat used by the Yellow Warbler throughout its range is very similar to what has been reported in Ontario. It shows a strong affinity for willow thickets with alder and other shrub species also used to a lesser extent. Several studies demonstrated that it increases with shrub density, particularly willow. Above the treeline, it nests in thickets of willows (often tea-leaved willow and bog willow), dwarf birch, and alder. It is characteristic of tundra habitat at the ecotone between tundra and boreal forest, and also characteristic of prairie-forest ecotones. It seldom inhabits the tundra itself except for shrubby areas around tundra sloughs or along rivers and streams. In prairie habitat, it avoids grasslands and nests in shrub thickets and riparian vegetation around pothole wetlands. It avoids vegetation around potholes unless taller trees or shrubs are available as singing perches for the male. In the Boreal Forest Region and other densely forested areas, it avoids forest habitat and occurs in shrubby areas along margins of rivers, streams, and wetlands. Shrubby islands in rivers and lakes may provide ideal habitat and support high densities. It may be present in or near towns in forested areas where it inhabits shrubby areas where forest was cleared. In extensively forested areas, it may occur in deciduous and mixed forests provided that the canopy is open and deciduous shrubs are common in the understorey. In Quebec, it inhabits burns and clear-cuts in extensive forests but usage of these habitats has not been documented elsewhere. These types of habitats are typically used only where they are in floodplains of rivers or bordering lakes. It seldom inhabits forested areas distant. Stand types used most frequently are those dominated by trembling aspen, balsam poplar, cottonwood, green ash, and willow. Dune habitats at Delta Marsh in Manitoba supported the highest reported densities. Tree cover consisted of peach-leaved willow, green ash,

and Manitoba maple with an understorey of sandbar willow. In North Dakota, the Yellow Warbler reached its highest density in willow shrub communities followed by lowland forests of elm, Manitoba maple, cottonwood, black ash, and peach-leaved willow. It was common to abundant in all available habitats, including bur oak forests, trembling aspen forests, and juneberry thickets. On regenerating strip mines in Illinois, it always nested in dense stands of moderately tall black locusts. On Maine islands dominated by spruce, it nested successfully on islands that had sizeable areas not covered by coniferous growth. It nested in deciduous shrubs and saplings at edges of conifers or in large forest openings. On 1 island, it frequented growths of sumacs and small patches of birches. On small islands completely covered with coniferous growth, nesting was unsuccessful and males seldom acquired a mate. There are records of the Yellow Warbler nesting in coniferous forests in Maine. On the mainland, several nested in white spruce 6-9 m tall. On an island, more than 100 nested in white spruce and well into a dense forest of red spruce 18-21 m tall. The only other record of it nesting in conifers appears to be from California where it has nested among fir saplings (Arnold and Higgins 1986; Briskie 1995; Brooks 1940; Campbell et al. 2001; Celada 2004; Chapman 1907; Erskine 1977; Faanes and Andrew 1983; Finch 1989b, 1991a; Gauthier in Gauthier and Aubry 1996; Graber et al. 1983; Hebard 1961; Hobson and Sealy 1989a; Hoffman 1989b; Hutto 1981; Jehl 2004; Jehl and Smith 1970; Karr 1968; Keast 1980; Kirk et al. 1996; Knopf and Sedgwick 1992; Lowther et al. 2020; Manning and MacPherson 1952; Mossman 1988; Morse 1973, 1989; Olechnowski and Debinski 2008; Parnell 1969; Quinlan and Green 2012; Sammler et al. 2008; Sinclair et al. 2003; Taylor and Littlefield 1986; Taylor and Taylor 1979).

The Yellow Warbler is more widely distributed within fragmented landscapes where it frequents a wider variety of habitats than in tundra or forested landscapes. In fragmented landscapes, it still prefers moist to wet habitats rich in nutrients but it also nests in upland areas. Presence of shrubs is a key habitat component. Willows and alders are used universally throughout its range, but other species that form thickets may also be used: apple, hawthorn, raspberries, roses, dogwoods, elm saplings, blueberries, southern arrowwood, sweet gale, bayberry, leatherleaf, elderberries, chokecherry, meadowsweet, and multiflora rose. In addition to riparian areas and wetland borders, it nests in old fields as well as shrubby areas along utility corridors. In New Jersey, it was common in fields 10 and 20 years old but was absent in 40-year-old fields that had become densely overgrown with deciduous saplings and trees. In Minnesota, it was most abundant in shrub habitat along a transmission line corridor followed by tall shrubs in control areas. It was not detected in sedge fens, low shrub communities, or open or closed spruce forests. In Great Lakes coastal meadows in Michigan, it preferred wet meadows where it was associated with greater shrub species diversity and a higher frequency of willows than was generally available. The Yellow Warbler is urban adapted and will nest in shrubby areas in backyards, cemeteries, and urban parks as well as in farmyards, hedgerows, roadsides, and shelterbelts. It occasionally nests in deciduous forests, especially those dominated by early successional species such as poplar and birch. It avoids pole-sized stands dominated by these species because the trees are too dense to provide suitable habitat. In Alberta, it was significantly more abundant in old-growth than young or mature aspen stands and in South Dakota, it was more abundant in mature than immature green ash stands. In the old-growth aspen stands, trees were large and sparse with an open canopy and a moderate density of shrubs. The mature green ash stands had a higher density of chokecherries in the understorey than younger

stands. When it occurs in northern hardwood stands, which is infrequent, it is present only in disturbed or early successional habitats and is absent in mature undisturbed hardwoods. It may occasionally occur in pine stands, but only when they are very young and have a deciduous or shrub component. In Wisconsin, it nests in pine and oak barrens. In these habitats, it was common in shrub prairies, fairly common in pine-dominated barrens and cutovers, and uncommon in nearly forest, diverse barrens, and river terrace barrens. In South Dakota, it was significantly more abundant in contiguous riparian woodlands than small isolated woodlots. It is likely that the woodlots were surrounded by agriculture, providing minimal shrubby habitat (Back 1979; Bent 1953; Brewer 1955; Campbell et al. 2001; Capen 1979; Cilimburg et al. 2002; DellaSala 1985; Gauthier in Gauthier and Aubry 1996; Gentry et al. 2006; Graber et al. 1983; Harrison 1984; Hobson and Bayne 2000; Hoyt 1948; Kirk et al. 1996; Leighton et al. 2002; Mitra 1999; Morse 1989; Mossman et al. 1991; Mousley 1926; Niemi and Hanowski 1984b; Niemi and Pfannmuller 1979; Noon et al. 1979; Riffell et al. 2001; Rumble and Gobeille 1988; Samson 1979; Schieck et al. 1995; Schroeder 1982c; Suthers 1988).

In North Dakota 400-m landscapes with less than 30% tree cover, the Yellow Warbler increased with increasing tree cover within 100 m, attaining a maximum probability of occurrence at 70% tree cover. In landscapes with more than 30% tree cover, there was no response to increasing tree cover from 10% to 60%, with its probability of occurrence remaining stable around 5%. From 60 to 100% tree cover, its probability of occurrence increased to 22%. It may respond more to shrubs or woodland edges than the amount of tree cover. It preferred landscapes that were 42-75% forested; no areas were more than 75% forested (Cunningham and Johnson 2016, 2019).

Some studies examined which areas are settled first by arriving males or compared nest-site patches with random areas, thereby providing insights to microhabitat preferences. At Churchill, most nests were built in the largest shrubs near or at the centre of a willow patch. Nesting in the centre of willow patches helped to compensate against predators because shrubs were leafless and nests were obvious well into the incubation period (Briskie 1995). In Colorado, nests were in shrubs that were taller than random and in shrub patches that were also taller and of more uniform size than occurred in the overall shrub community. Nests occurred in shrubs with a larger radius in patches of greater willow density and more uniform shrub density than random. Nest shrubs were in clumps of closely spaced shrubs. Overall, nest shrubs tended to occur in clumps of uniformly sized shrubs. The Yellow Warbler selected nest sites were selected primarily on patterns of shrub distribution within a vegetation patch and not on factors associated with the shrub itself (Knopf and Sedgwick 1992). In British Columbia, 4 males settled first on territories with a higher percentage of riparian habitat cover, in areas with a greater diversity of shrubs, and in areas with less high canopy cover. Areas selected for nesting had taller and denser shrubs than random areas (Quinlan and Green 2012). In New York, habitat consisted of scattered tall trees but 1 area had little or no vegetation shorter than 6 m. Early in the season, none of the males in the area without shrubbery were successful in attracting a mate but 20% of males in areas with shrubs were mated (Ficken and Ficken 1966). Another New York male in a shrubby area without tall trees for displaying eventually lost his territory to neighbours that had conspicuous singing perches (Ficken and Ficken 1965). In Yellowstone Park, Yellow Warbler abundance increased significantly with willow height. It was 6 times more abundant in willows 225 cm tall than in those 37.5 cm tall. It was also more abundant where willows were structurally more diverse (Olechnowski and Debinski 2008). In Alberta, it

inhabited patches of willows and aspens among mixed grasslands. Willows were used for nesting and foraging; aspens were used for foraging only. Nests were surrounded by greater amounts of willows within 5 m than random points. Territory occupancy and consistency of patch occupancy were affected mainly by the shape and area of the willow patch within a territory, or by the main patch in territories containing multiple willow patches. Warblers also chose patches with ponds supporting Red-winged Blackbirds earlier than patches without blackbirds. Presence of Red-winged Blackbirds reduced the risks of nest predation and parasitism by the Brown-headed Cowbird (Celada 2004). The average habitat parameters of the Yellow Warbler in Michigan were 96.1% ground cover, 38.9% shrub cover, 10.6% canopy cover, 6.0 m canopy height, 2.9% coniferous cover, and 1.1 trees in a 0.04-ha circle around the observation. It inhabited open fields with shrubs and was most common in open marshland with few or no trees, numerous shrubs, and very high ground coverage. It occurred in structurally simple habitat containing patches of shrubs or scattered trees (Collins et al. 1982). In North Dakota, its abundance was negatively correlated with the number of trees 15.1-23 cm diameter at breast height (DBH; Grant and Berkey 1999). In Arizona, it nested in habitats that were intermediate in height and shrub density. It occurred in tall vegetation with more foliage volume above 3 m and fewer trees than average. It used habitat similar to that of the Willow Flycatcher and was considered a habitat generalist (Brown and Trosset 1989).

Collins (1983a) compared habitat usage by the Yellow Warbler in Maine and Minnesota. There were significant differences in canopy cover, canopy height, percent coniferous cover, number of tree species, and number of trees with a DBH of 7.5-15 cm between sites, suggesting that it is adaptable in its habitat selection. Overall, it was associated with high ground coverage, large conifers, very open habitat, and medium-sized deciduous trees.

In Minnesota, Collins (1981) compared vegetation at nest sites and song perches. There were significant differences, with greater numbers of trees at perch sites which increased values for canopy cover, average tree height, and percent coniferous canopy cover.

The Yellow Warbler is not an area-sensitive species. As would be expected in forested habitat, its abundance is either unaffected by patch size or it is more likely to occur in small groves than larger woodlots (Grant and Berkey 1999; Hobson and Bayne 2000; Johns 1993). It is also not area sensitive within its preferred shrubby habitats. In Great Lakes coastal marshes, its abundance was unrelated to patch size and in Wyoming it inhabited significantly smaller patch sizes than were randomly available (Finch 1989b; Riffell et al. 2001). The only potential indication of area sensitivity was provided by Celada (2004) in Alberta. In that study, it inhabited small willow patches. Occupancy and consistency of occupancy were associated with patch size and shape. In this case, some nest patches were smaller than the territories, so the birds were not truly area sensitive.

Schroeder (1982c) prepared a habitat suitability index for the Yellow Warbler. He considered wet shrubby areas to be optimal and upland shrub areas to be marginal, but this may not be the case. Optimum shrub density was considered 60-80%. Completely closed shrub canopies were considered moderate in suitability due to probable restriction of movements by the birds. More recent research indicates that it prefers denser shrub thickets. Shrub heights of 2 m and greater were considered optimal.

In southern Ontario, the Yellow Warbler was significantly more common on conventional than organic farms and was negatively affected by the use of herbicides. The negative relationship with organic farms was possibly because conventional farms had significantly more riparian woodland, a preferred habitat (Kirk et al. 2011).

Nests reported to the Ontario Nest Records Scheme were in shrubs, trees, and vines. Deciduous species were greatly preferred as nest sites to conifers. Twenty-nine deciduous species supported 88.3% of nests; the remainder were in 7 species of conifers. The most frequently used species for nesting were hawthorns (35.0% of nests), willows (23.3%), raspberries (9.9%), white cedar (9.4%), dogwoods (8.5%), honeysuckles (7.2%), and spirea (6.7%). One nest was on a fallen limb and 3 were attached to stems of common reed in dense stands of this species. Most nests were in upright crotches in the central portion of a tree or shrub. Some were on horizontal limbs and a few were suspended from limbs. Four nests were over water. Nests were 0.3-6 m from the ground, with most 0.9-1.5 m up (Peck and James 1987). Wilson (1985) reported 3 nests on an island in Georgian Bay: one each in chokecherry, meadowsweet, and a silver maple sapling. Dance (2008) reported 2 nests in black alder in Oxford County. McIlwraith (1894) reported that nests were frequently found in lilac bushes in residential yards in Hamilton. Most yards are now too manicured to provide any nesting habitat.

Nests throughout the Yellow Warbler's range are usually a short distance above ground in a deciduous tree, shrub, or vine, although 44% of British Columbia nests were in conifers. Willow is a preferred species for nesting throughout its range with all 211 nests reported in Alberta in willow. Willow was the dominant nest-species in British Columbia. At Delta Marsh, more than 50% of nests were in Manitoba maple, which was the second-most abundant tree species behind peach-leaved willow. In Iowa, most nests were in small patches of wolfberry. In addition to the species reported in Ontario, the Yellow Warbler has nested in fox grape, red raspberry, gray dogwood, common elderberry, Allegheny blackberry, tartarian and Japanese honeysuckle, flat-leaved willow, bog willow, hoary willow, limestone willow, dwarf birch, roses, blueberries, southern arrowwood, red maple, ashes, sweet gale, bayberry, poison ivy, apple, crabapple, wolfberry, Manitoba maple, cottonwood, gooseberry, currant, trembling aspen, snowberry, elms, holly, buttonbush, oaks, pear, Saskatoon, autumn olive, multiflora rose, and red-osier dogwood. It appears to select nest sites to minimize predation and parasitism, and branching structure of the nest tree or shrub may be important. In Illinois, there was no significant difference in nest survival rates in native and nonnative shrubs although survival was slightly higher in nonnative species. In Colorado, many birds nested in the same location as the previous year despite the fact that the shrubs had been killed by a fire: nests were obvious at distances of more than 20 m. Branches of willows and other shrubs often overlap within the canopy, so individual shrubs may be indistinguishable to the birds. At a Michigan site, the Yellow Warbler preferentially selected fox grape for nesting. Nests in grape vines were built at a greater height than those in dogwoods, and higher nests had a reduced rate of cowbird parasitism. Dogwoods provided a more stable substrate than vines, with failure in vines due mostly to wind and other events rather than predation and parasitism in dogwoods. Most nests are in crotches of shrubs or saplings. In mangroves in Florida, 35% of nests were on horizontal or diagonal branches and only one was against a trunk. One nest was in the crotch of a dead tree beside an apartment and another was 1.8 m from a door that was used daily. Nests have been reported at heights of 0.2-

18 m, but few are higher than 5 m and most are less than 3 m from the ground. Nest materials may be taken from old Yellow Warbler nests and 1 nest was built of material taken from an active American Redstart nest. Nests may be built in the same crotch as the previous year's nest or even on top of it, but there are no records of old nests being repaired and reused. When nests are parasitized, the Yellow Warbler adds additional layers to its nest to bury cowbird eggs. One 6-tier nest was reported from Illinois (Bent 1953; Bigglestone 1913; Brewer 1955; Briskie 1995; Campbell et al. 2001; Chapman 1907; DellaSala 1985; Enos et al. 2024; Ficken and Ficken 1966; Graber et al. 1983; Hebard 1961; Hoyt 1948; Knopf and Sedgwick 1992; Leighton et al. 2002; MacKenzie et al. 1982; Mitra 1999; Mousley 1926; Prather and Cruz 1995; Rowher 2012; Schrantz 1943; Sinclair et al. 2003).

Males establish territories immediately upon arrival and defend them at least until the young fledge. Territories may be quite small, allowing warblers to pack into small patches of suitable habitat at high densities. There may be some overlap in territories, and birds have been observed travelling as far as 490 m outside the territory to forage. A few males attempt to defend 2 territories that may be as far as 30 m to 1.2 km apart, and some are successful in securing a mate and a nest on both territories. Monogamous males tend to have territories smaller than 0.4 ha and more frequently around 0.2 ha. Average territory sizes at 2 sites in Rhode Island were 0.20 ha and 0.21 ha; averages of 0.15 ha and 0.16 ha have been reported; Utah territories averaged 0.14 ha (range 0.05-0.29 ha); 4 Illinois territories averaged 0.17 ha (range 0.06-0.38 ha); and Quebec territories were 0.2-1.2 ha. In Michigan, 3 polygynous males had territories that averaged 0.78 ha, significantly larger than the 0.21 ha for monogamous males. A polygynous male in Manitoba had a territory size of 0.0474 ha and the 2 females used exclusive areas within his territory that they defended aggressively. The polygynous male's territory was not significantly larger than the average territory size of 0.0429 ha held by monogamous males (Brewer 1955; DellaSala 1986; Ficken and Ficken 1965; Ford 1996; Gauthier in Gauthier and Aubry 1996; Hobson and Sealy 1989a; Lowther et al. 2020; Mitra 1999; Schroeder 1982c).

Limited data suggest that natal philopatry rates are low. In New Jersey old-field habitat, 0 of 55 young returned. In Rhode Island, 3 of 147 nestlings (2.0%) returned to nest. All were males and they were recaptured 250, 900, and 1,000 m from their natal area. Three additional banded birds were observed but not captured. If these were yearlings, the return rate could have been as high as 4.1%. In Quebec, 4.5% of nestlings returned to breed (Lozano and Lemon 1999; Mitra 1999; Suthers 1988).

Adult site fidelity appears to be high. On the James Bay coast of Ontario, 64% of males and 75% of females returned the following year (Rimmer 1988). Only 29.9% of males returned to a study area north of Kingston (Yezerinak et al. 1996). In Quebec, return rates over 3 years were 34.5% for males and 31.5% for females. It was uncertain if there was a relationship between the previous year's breeding success and return rates (Lozano and Lemon 1999). In Rhode Island, 56% of males and 42% of females returned, mostly in the following year but 2 males skipped a year before returning. Over 3 years, 7 of 43 males (16.3%) relocated 60-1,200 m from their former territories. Two had failed to fledge young the previous year on the territory that they abandoned; the breeding success of 1 male was unknown. One male had been successful the previous year. He returned to his original territory for 1 day then disappeared. Five additional males moved 200-1,200 m (average 460 m) within breeding seasons. Most returning females moved less than 200 m from their previous year's

nest. Three females moved longer distances of 0.6, 1, and 10 km (Mitra 1999). In Colorado, annual return rates were 60-62% for males and 32-44% for females (Knopf and Sedgwick 1992). In Montana, Cilimburg et al. (2002) established 7 study areas but searched for returning birds over a larger area that encompassed 85-90% of the available habitat. Overall, 46.3% of males and 29.5% of females returned in 1 or more subsequent years. In the first year of expanded searches, 17.0% of the resighted birds were found off the core study areas or in a different core area and that increased to 29.6% the following year. Only 4 of the birds found on extended searches were within 0.5 km of the original breeding sites. The distance that birds moved between subsequent years was 4-24,728 m, with a median of 86 m for males and 153 m for females. Seven percent of males and 12% of females dispersed further than 1.5 km. For males, the survival rate was estimated at 41.8% using core analyses and 49.5% using dispersal analyses. For females, these numbers were 35.0% and 41.3%. The authors concluded that emigration could have substantial effects on survival rate estimates for the Yellow Warbler.

Limiting Factors

Eggs have been reported in Ontario nests from mid-May until the third week of July, with most present in the first 3 weeks of June (Peck and James 1987). At North Point on the James Bay coast, clutch initiation averaged 21, 23, and 23 June over 3 years (range 15 June to 2 July). Fledging averaged 11, 12, and 12 July (range 5-27 July). Active nests were present from 6 June until 5 August (Rimmer 1988). In Algonquin Park, eggs were present from early June to late June, nestlings were present mid-June to mid-July, and dependent fledglings were observed from early July to early August (Tozer 2012).

Males have established territories by the time females arrive. Females may visit several territories before they finally select a territory and mate. It may be several days before pair bonds are stabilized. At Churchill, females began to build nests 1-2 days after arrival, but longer intervals may occur further south. Construction of first nests may take 4-10 days and averaged 6.2 days at Churchill. Replacement nests may be built in 1-3 days and a cowbird egg can be buried in 1 day. In Rhode Island, an average of 6.3 days (range 1-12 days) elapsed between nest construction and laying of the first egg. In more northern areas where the breeding season is shorter, it is likely that the interval between nest completion and egg laying is much less. In Iowa, egg laying began on the day after nest completion or even on the same day. In more northern areas, clutch initiation is much more synchronized than in southern locations. At Churchill, clutch initiation spanned 2 weeks, less than half the period at Delta Marsh. Nest initiation also occurred within a 2-week period at North Point. One egg is typically laid per day but occasionally a day may be skipped. In Manitoba, significantly more laying interruptions occurred between the first and second eggs compared with eggs 3 and 4 and eggs 4 and 5, and more interruptions occurred between the second and third eggs than between the fourth and fifth eggs. More than half of egg interruptions occurred during the week that coincided with the peak of clutch initiation and they were more likely to occur when May temperatures were warmer. Eggs not laid during interruptions were not replaced resulting in lower clutch sizes when laying was skipped. Partial or full incubation may occur with laying of the penultimate egg, but typically full incubation begins with laying of the final egg or even later. At North Point, the incubation period was invariably 11 days. The incubation period at other Ontario nests was 9-14 days, but mostly 11-13 days. Overall, incubation periods of 9-15 days have been

reported; most eggs hatch in 11 or 12 days. At Churchill, the average incubation period was 11.7 days, significantly longer than the average of 11.3 days at Delta Marsh. Northern birds compensated for the shorter breeding season and slightly longer incubation period by initiating nesting earlier than more southern birds, prior to leaf-out. Most eggs hatch within a day, with an average hatching spread of 1.3 days for 4-egg clutches and 1.2 days for 5-egg clutches at Churchill. Nestling periods of 8-15 days have been reported, with the time that young spend in the nest decreasing northward. In Mexico, the nestling period averaged 11 days (range 9-13 days); in Florida, the nestling period averaged 12 days (range 10-14 days); in Iowa, the nestling period was 9.5 days (range 8-11 days); and at Churchill, the nestling period was 8.5 days (range 8-10 days; Bent 1953; Bigglestone 1913; Briskie 1995; Campbell et al. 2001; Ficken and Ficken 1966; Goossen and Sealy 1982; Graber et al. 1983; Gullion 1988; Harrison 1984; Hébert and Sealy 1992; Jehl 2004; Lowther et al. 2020; McMaster et al. 1999; Mitra 1999; Mousley 1926; Peck and James 1998a; Prather and Cruz 1995; Rimmer 1988; Salgado-Ortiz et al. 2008; Schrantz 1943; Westphal and Sealy 2018).

The Yellow Warbler typically raises a single brood in a breeding season, but a few birds raise a second brood. Most studies found no evidence of double brooding but Sealy (2014) reported that 20 birds had double broods at Delta Marsh in 5 of 11 years. All pairs remained together through the second nesting attempt and both yearlings and adults raised second broods. Eighteen of the 20 double-brooded pairs initiated their first nest by 2 June. None of the first clutches of double-brooded pairs were parasitized but 4 of the 20 second clutches were parasitized. Eleven pairs used the same nest for both broods and 9 built new nests for the second brood; in 5 cases, the original nest had deteriorated. The mean time between the initiation of first and second clutches was 30.2 days. Double broods have also been reported from the Northwest Territories, British Columbia, Saskatchewan, Quebec, and Mexico. Although no double broods have been reported in Ontario, there is a good probability that a small percentage of pairs raise a second brood. Renesting occurs if a nest fails and as many as 5, but rarely more than 3, attempts may be made to raise a brood. In more northern areas such as Churchill and North Point, only 1 replacement clutch may be attempted. These may not be successful due to the shortness of the season. At North Point, only 3 pairs renested and only 1 replacement nest was successful. Clutches of 2-6 eggs have been reported in Ontario and there is a single record of an 8-egg clutch, with possibly more than 1 female contributing to this nest. Most clutches contained either 4 or 5 eggs; the average clutch size was 4.04 eggs. Clutch size increases with latitude, averaging 2.5-2.8 in the tropics and 3.8-5.1 in temperate areas, with largest clutch sizes reported in Alaska. Most Canadian clutches contain 4 or 5 eggs with averages of 4.65 at Churchill, 4.5 at Delta Marsh, and 4.24 for the Prairie Provinces. In Quebec, most nests started before 15 June had 5-egg clutches but later nests had mostly 4-egg clutches. The same occurred in Manitoba before and after 7 June. A similar decline in clutch size with season was documented in Rhode Island, with clutches decreasing at a rate of 1 egg per 36 days (Briskie 1995; Campbell et al. 2001; Chapman 1907; Goossen and Sealy 1982; Graber et al. 1983; Hobson and Sealy 1989b; Jehl 2004; Leighton et al. 2002; Lozano and Lemon 1995, 1999; Lowther et al. 2020; Peck and James 1987; Prather and Cruz 1995; Rimmer 1988; Salgado-Ortiz et al. 2008; Schrantz 1943; Sealy 2014; Sodhi 1995).

Both sexes are capable of breeding when they are 1 year old and breeding occurs every year thereafter. All Manitoba females that were captured had incubation patches suggesting that they

all nested. At North Point, the sex ratio was male biased and many of the nonbreeding males were yearlings. In this population, a high proportion of yearling males and possibly some older males did not breed. Presence of a floating population has been reported from other areas suggesting that some males are unsuccessful in defending a territory or attracting a mate. The mating system is typically monogamous, but a small proportion of males are bigamists. In British Columbia, 1 of 77 males (1.3%) was a bigamist. Polygynous males may either have larger than normal territories capable of supporting 2 females, or have 2 discrete territories. In Michigan, polygynists were first to settle on territories and they were selected first by females. A yearling male in Manitoba was polygynous and he had one of the lowest song rates and repertoires and fed nestlings at a much lower rate than other males. It appeared as though females were selecting the territory rather than the male. Females that nest on the same territory with a bigamous male are aggressive toward each other until the eggs hatch. The primary female is more aggressive suggesting that she is attempting to prevent polygyny in order to ensure the male's parental care. When females in a polygynous relationship nest asynchronously, the male provides more care to the first nest. When both members of a pair return the subsequent year, they may or may not reunite. Most studies have found no evidence of remating, but 3 of 14 returning pair members (21.4%) reunited in Rhode Island. In Massachusetts, most returning males and females nested on the same territory as the previous year and remated with a previous mate if available. Extra-pair copulations are an important component of the Yellow Warbler's mating system. Extra-pair paternity was found in 25% of 12 nests at Churchill and in 53.8% of 130 nests north of Kingston. At Churchill, 13% of 53 nestlings were extra-pair compared with 33.1% of 484 nestlings at Kingston. Lower incidence of extra-pair young at Churchill was probably related to the lower breeding density and the highly synchronous nesting. Broods comprised of only extra-pair young or completely lacking them were more abundant than expected. Broods with mixed paternity were under-represented. Most confirmed extra-pair sires were neighbours, but some males travelled considerable distances for extra-pair copulations: occasionally as far as 3 territories away and some extra-pair sires did not nest in the same field. Neighbours occasionally have extra-pair young in each other's nest. Intrusions into other territories were most frequent during the neighbouring female's prefertile and fertile periods and declined significantly during incubation. Males intruded into neighbouring territories before, during, and shortly after their own female's fertile period. In an attempt to avoid cuckoldry, males perch higher and remain closer to their female during her fertile period. Thus, populations with highly synchronized nesting have fewer opportunities for extra-pair copulations. Divorce of pairs has not been documented within a breeding season, even through several renesting attempts. Intraspecific parasitism has not been positively confirmed, but abnormally large clutches of 6, 7, and 8 eggs occur rarely. In 4 of 1,500 nests at Delta Marsh, more than 1 egg appeared per day, suggesting intraspecific parasitism. At Delta Marsh, Yellow Warbler eggs were added to other clutches by researchers. Of 17 eggs added to nests that were still unlined, 16 were buried and the other nest was abandoned. All 21 eggs added to lined nests were accepted. This suggested that egg burial resulted from continued building of an unfinished nest rather than a response to a parasitic egg (DellaSala 1986; Ford 1996; Goossen and Sealy 1982; Hobson and Sealy 1989a, 1989b; Lowther et al. 2020; Mitra 1999; Quinlan and Green 2012; Reid and Sealy 1986; Sealy et al. 1989; Rimmer 1988; Yezerinac et al. 1995, 1996, 1999).

Males forage at higher heights than females. Females tend to remain in shrubs near the nest level while males display and forage in taller trees. In Manitoba, the mean foraging height was 7.1 m for males and 4.4 m for females. Average foraging heights of females remained constant through the nestling period but males' foraging heights varied: 9.2 m from arrival until the first egg was laid, 6.1 m during egg laying and incubation, and 5.4 m during the nestling period. Both sexes increased their foraging height during the postfledging period: 8.0 m for males and 6.8 m for females. Overall, both sexes foraged from less than 3 m from the ground to 21 m. Foraging heights depend upon the available vegetation. In some areas, females may concentrate their foraging 0.5-1.5 m above ground. In Utah, Yellow Warblers foraged from 0.3 m to the top of the vegetation (16.8 m), but mostly at 6-8 m (mean 7.3 m). Mean foraging height in the Mackenzie District of the Northwest Territories was 5.1 m; in Wyoming and Mexico, mean foraging height was 2.6 m. In data combined from southern Ontario, Montana, and Colorado, Yellow Warblers foraged as high as 14.9 m at mean heights of 4.0-6.1 m at a proportional height of 71.8% of the canopy in areas of moderate foliage density (Busby and Sealy 1979; Greenberg et al. 1999; Hobson and Sealy 1989b; Hutto 1981; Lowther et al. 2020; Morse 1973; Weidenfeld 1992). During the breeding season in North Carolina, 92.9% of observations of the Yellow Warbler were in low trees and 7.1% were in shrubs. It was not observed in the canopy or on the ground. In low trees, 50.0% of foraging occurred at the top of the crown, 35.8% in the inner crown, 7.1% in the lower crown, and 0% on the bole. All observations in shrubs were in the inner crown. Singing males were observed at heights of 1.5-15 m, mostly at 3.7-6.1 m (average 4.9 m). Nonsinging birds were seen at heights of 0-15 m, mostly at 3-7.6 m (average 4.5 m; Parnell 1969). In Wyoming and Mexico, most foraging (39.2%) occurred in the top quartile of shrubs, 33.9% in the third quartile, 17.9% in the second quartile, and 8.9% in the bottom quartile. Most foraging occurred in lower vegetation densities: 37.5% in 0-15% vegetation density, 46.4% in 15-50%, 10.7% in 50-85%, and 5.4% in 85-100%. It foraged 71.4% of the time on outer vegetation, 12.5% in the middle of shrubs, and 16.1% in the interior. Foraging techniques included 68.2% gleaning, 25.8% sallying, and 5.9% hovering. Foraging substrates included 41.9% foliage, 30.1% bark, 25.8% air, and 2.2% ground. Once young fledged, the mean foraging height increased from 2.6 to 3.1 m (Hutto 1981). In Utah, 95.5% of prey was obtained by gleaning, 1.7% by sallying, and 2.8% by hovering (Lowther et al. 2020). In Ontario, Montana, and Colorado, the Yellow Warbler captured prey while standing on a perch (58-70% of the time) or by aerial actions such as hover-gleaning, outward-striking, and aerial hawking (29-43% of manoeuvres; Weidenfeld 1992). In Mackenzie District, 94.9% of foraging was in deciduous species, 80.0% in foliage, 46.4% by aerial attacks, 8.5% by hanging, 1.5% by hovering, and 5.1% by reaching (Greenberg et al. 1999). On small islands in Maine, it concentrated its foraging heavily upon small limbs. It used deciduous vegetation more frequently and dead limbs less frequently than the American Redstart (Morse 1973). In Manitoba, the sexes differed in the substrates they used for foraging. From arrival through egg laying, males foraged in the upper and outer sections of trees and shrubs. Females foraged in the lower and inner sections. Later in the season, there was more overlap in the portions of trees used, but the difference was still significant. In all periods, females gleaned less and hovered more than males. From arrival to initiation of egg laying, females foraged more in ashes and less in willows than males. Females foraged more in shrubs throughout the breeding season than males. Males frequently foraged in large willows with sparse foliage, thereby making them more conspicuous for displaying. Females preferred Manitoba.

maples, partially due to greater abundance of food, but possibly because they were less conspicuous among their leaves (Busby and Sealy 1979).

Near Kingston, more brightly coloured males provisioned less food to the young, but they held better territories and spent more time defending them such that the growth rate of nestlings and other reproductive parameters were not affected. In 1 experiment, weights were added to males that subsequently reduced their provisioning rates. Females did not compensate by delivering more food and nestlings of experimental birds had a lower growth rate. In another experiment, supplemental food was placed within 30 cm of the nest. This had no effect on the provisioning rates of males, but females with supplemental food spent more time brooding the young to age 6 days than control females but the reverse was true by age 8 days. It appears as though males and females provide for their brood independently of each other (Biermann and Sealy 1982; Bigglestone 1913; Briskie 1995; Graber et al. 1983; Hobson and Sealy 1989b; Lozano and Lemon 1995, 1996; Mousley 1926; Schrantz 1943; Studd and Robertson 1988, 1989). In Manitoba, young were fed midges, mosquitoes, geometer moth caterpillars, other larvae, other flies, and other insects. Females with 5 young provided more geometer moth caterpillars and fewer midges and mosquitoes than those with 4 young. Females feeding 4 or 5 young brought a larger proportion of midges and mosquitoes and a smaller proportion of geometer moth caterpillars to 8-day-old young than 2-day-old young, but proportions remained the same over time for broods of 3. Males with broods of 4 or 5 fed more midges and mosquitoes and fewer caterpillars to young than those with broods of 3, and the trends by age class were the same as for females. Overall, males brought more geometer moth caterpillars and females brought more midges and mosquitoes. Compared with availability, adults selected geometer moth caterpillars and avoided all other insects when feeding 2-day-old chicks. When feeding 8-day-olds, midges, mosquitoes, geometer moth caterpillars, and other larvae were selected and other flies were avoided. The main components of nestlings' diets were adult midges and mosquitoes and geometer moth caterpillars (Biermann and Sealy 1982). In Iowa, young were fed mostly insects and a few spiders. Insects provided to nestlings included flies, mayflies, moths, mosquitoes, grasshoppers, ants, beetle larvae and adults, damselflies, treehoppers, and bees. There are records of adults feeding nestlings green worms, but these probably refer to geometer moth caterpillars (Bigglestone 1913; Mousley 1926).

Busby and Sealy (1979) studied the feeding ecology of adult Yellow Warblers at Delta Marsh. Food consisted of midges, geometer moth caterpillars, mosquitoes, narrow-winged damselflies, long-horned caddisflies, other insects, and spiders. Adult midges were the dominant prey, comprising 58% and 56% of the diet over 2 years. The category of all other insects was second-most numerous in the diet, constituting about 30% of the diet. The diet of the sexes was almost identical, although females ate damselflies more frequently than males. Damselflies were the largest food items and mites were the smallest. Prey was taken in proportion to its availability, with the exception that lady beetles were avoided and mites and spiders were consistently taken less than their availability. In 1 year, midges were taken less than their availability and more than their availability in another. Geometer moth caterpillars were taken in proportion to their availability 1 year and were under-represented the other year. These apparent differences with respect to availability may have been due to sample sizes. Overall, 34 and 38 families of insects were included in the diet over 2 years and many groups were not identified to family. Other studies demonstrated that adult Yellow

Warblers eat mostly insects. They have been documented eating geometer moth caterpillars, adult moths, gypsy moth caterpillars, beetles (weevils, ground beetles, and soldier beetles), flies, aphids, grasshoppers, spiders, centipedes, locusts, true bugs, and hymenopterans. One bird in Saskatoon ate so many leafroller caterpillars that it was incapable of flight. It occasionally eats a few wild fruits such as raspberries. It does not respond numerically to infestations of forest tent caterpillars or other defoliating insects. In Maine, it avoided nesting on small islands where deciduous tree and shrub species had been defoliated by insects (Bent 1953; Goossen and Sealy 1982; Graber et al. 1983; Leighton et al. 2002; Lowther et al. 2020; McIlwraith 1894; Morse 1973).

The Yellow Warbler is a common host of the Brown-headed Cowbird. The warbler is capable of recognizing cowbird eggs by their larger size and artificial eggs with unusual colouration or patterns. Warblers may either accept or reject cowbird eggs. Cowbird eggs that are laid in nests containing 2 or more warbler eggs are usually accepted. By this point, warblers have a significant investment in their nest. Renesting at this stage may put the replacement nest out of synchronization with the rest of the population which may make it more vulnerable to predation. In addition, the peak abundance of insects may have passed by the time young hatch. Cowbirds begin laying approximately 3 weeks before Yellow Warblers and may lay eggs in incomplete nests. Most of these eggs are rejected and a high proportion of nests containing a single warbler egg and some containing 2 warbler eggs have the cowbird egg rejected. The percentage of nests near Kingston where cowbird eggs were rejected was 100% when there were 0 warbler eggs in the nest, 75% when there was 1 warbler egg, 33.3% when there were 2 warbler eggs, 50% when there were 3 warbler eggs, 20% when there were 4 warbler eggs, and 0% when there were 5 warbler eggs. The warbler's bill is too small to allow it to eject eggs and it does not pierce-eject eggs. The Yellow Warbler uses 2 strategies to reject cowbird eggs: by building another layer of the nest over them or by deserting the nest. At Delta Marsh, 66.7% of cowbird eggs were rejected by burial and 33.3% by desertion. In London, most cowbird eggs laid in empty nests were rejected through desertion. Occasionally only the cowbird egg is buried, but more frequently any warbler eggs that are present are also buried. When only the cowbird egg is buried, there is no interruption in the laying schedule of the female warbler. If a warbler egg is buried, the mean time from burial to the laying of the next warbler egg was 3.1 days near Kingston, with an additional 1-day delay for each additional egg that was buried. Kingston nests with buried cowbird eggs had a success rate of 78%, not significantly different from the 80% for unparasitized nests. The desertion rate was 41.7% of parasitized nests compared with 3.1% of unparasitized nests. During the laying but not the incubation period, the female cowbird may remove a warbler egg from the nest. In Manitoba, the number of warbler eggs in parasitized nests was 0.32 less than in unparasitized nests, suggesting that an egg was removed from about a third of nests. Near Kingston, mean clutch size of parasitized nests was 3.6 eggs compared with 4.1 eggs for unparasitized nests, suggesting that a warbler egg was removed from half of nests. At least 80% of egg removals occurred on day 1 or 2 of the warbler's laying cycle. All clutches reduced to a single cowbird egg were deserted, 31% of clutches reduced to 1 cowbird and 1 warbler egg were deserted and 0% of nests with 2 cowbird eggs were deserted. At Mer Bleue, 31% of nests were parasitized and 12% were depredated. Parasitism of replacement clutches was significantly higher in nests in new locations than in old re-lined nests in which the original clutch was buried. Of total egg losses, 41% were due to cowbird activity and 35% to predation. Of egg losses due to parasitism, 61% were

due to burial of the original clutch, 28% due to nest abandonment, and 11% due to warbler egg removal by cowbirds. At Delta Marsh, researchers artificially parasitized nests with real cowbird eggs and removed a single warbler egg from some nests. Hatching success of warblers varied significantly among treatments: 95% in control nests, 83% with 1 cowbird egg added and 1 warbler egg removed, and 73% with 1 cowbird egg added and no removal of warbler eggs. Results suggested that the ability of the warblers to incubate all eggs effectively was compromised by large clutches. Removal of warbler eggs by the female cowbird increases hatching success of cowbirds in some years and may increase the hatching rate of the remaining warbler eggs. The timing of hatching of the cowbird is a key determinant of warbler hatching success and survival. In 3 of 5 nests near Kingston where the cowbird hatched before the warblers, only a single warbler fledged. In 2 nests where the species hatched synchronously, 3 and 4 warblers fledged. In Michigan, parasitism had more significant effects on Yellow Warbler nesting success, with only 5.9% of parasitized nests fledging warblers compared with 55% of unparasitized nests. Clutch size was significantly lower in parasitized nests (2.16 compared with 3.53 eggs) and parasitized nests had smaller warbler broods (0.32 compared with 2.00 nestlings). Warblers nested at high density there and this may have facilitated parasitism. Light intensity at the nest was a good predictor of parasitism because well-concealed nests were less likely to be parasitized. Cowbirds did not fare well at this site either, with only 12.9% of eggs producing fledglings. All successful cowbird eggs were laid in synchrony with warbler eggs and were in nests containing a single cowbird egg. At Delta Marsh, 52% of parasitized nests failed, significantly more than the 37% of unparasitized nests. If nests are found by cowbirds, they may be more visible or have other attributes that make them more vulnerable to predators. Both predation and parasitism rates decrease with increasing nest height. Parasitism rates are highly variable and are related to the openness of the habitat and local abundance of the cowbird. Of 1,464 nests reported to the Ontario Nest Records Scheme (ONRS), 422 (28.8%) were parasitized. Of 256 nests reported to the ONRS south of the French River, Lake Nipissing, and Mattawa River, 110 (43.0%) were parasitized. Twenty-three percent of parasitized nests were deserted compared with 1% of unparasitized nests, significant at the 0.001 level. Clutches were buried in 50% of parasitized nests but egg burial was not recorded in 146 unparasitized nests. Considering both desertion and egg burial, cowbird eggs were rejected by the Yellow Warbler in 73% of parasitized nests. At London, 68% of nests were parasitized and 45 of 109 nests (41.2%) were parasitized north of Kingston. Parasitism rates are 0% in the Hudson Bay Lowland and probably close to 0% in most of the Boreal Forest Region. In Illinois, parasitism rates increased over time in response to continued deforestation and increases in the cowbird population. Prior to 1900, 6% of nests were parasitized compared with 40.5% after 1900. In 1 population, 87% of nests were parasitized. At Delta Marsh, the parasitism rate was 21%; in 3 Michigan study areas, 54%, 50%, and 0% of nests were parasitized; 1 of 94 nests (1.1%) was parasitized in Rhode Island, but Common Yellowthroat, Swamp Sparrow, Song Sparrow, and Red-winged Blackbird were commonly parasitized; 12 of 41 nests (29.3%) were parasitized in Iowa; 6 of 96 nests (6.25%) in New York were parasitized; 1 of 18 Minnesota nests (5.6%) was parasitized; 59 of 393 British Columbia nests (15.0%) were parasitized; and 29% of British Columbia nests were parasitized at 1 study area. In another British Columbia study area, 18% of nests were parasitized and females rejected 24% of these, mainly by deserting the nest. Parasitism reduced warbler clutch size by 0.8 egg and 1.3 fewer warblers fledged from parasitized nests. There was some evidence that parasitism reduced the productivity of older females less than it did for yearlings (Briskie et al. 1990;

Burgham and Picman 1989; Campbell et al. 2001; Clark and Robertson 1981; DellaSala 1985; Goossen and Sealy 1982; Graber et al. 1983; Graham 1988; Guigueno and Sealy 2010; Guigueno et al. 2014; Hahn and Hatfield 1995; Hanski et al. 1996; Hobson and Sealy 1989b; McLaren and Sealy 2000; McMaster and Sealy 1997; Mitra 1999; Peck and James 1998a; Quinlan and Green 2012; Rock et al. 2013; Rothstein 1975; Schrantz 1943; Scott and Lemon 1996; Sealy 1992; Sealy et al. 1987).

Habitat for the Yellow Warbler is probably declining south of the Canadian Shield. It formerly nested in residential yards and orchards, but these are now too manicured to provide suitable habitat. Many hedgerows between fields and along roads and ditches have either been removed or consist of narrow strips surrounded by unsuitable habitat. There are also fewer pastures than previously and most that persist are heavily grazed and support no shrubs. The shrubby fields it prefers are often considered suitable for development or a return to agricultural land and, if left undisturbed, develop into forest patches that are unsuitable nesting habitat. In Algonquin Park, forest maturation and succession in open areas have reduced the amount of suitable habitat (Tozer 2012).

In many areas, grazing by ungulates, particularly moose and elk, has affected the density and height of willows. In most of these sites, densities of the Yellow Warbler were significantly lower in ungrazed areas. Where cattle grazing has decreased or terminated, Yellow Warbler populations increased significantly (Anderson 2007; Celada 2004; Earnst et al. 2012; Knopf and Sedgwick 1992; Olechnowski and Debinski 2008; Taylor and Littlefield 1986). In southern Ontario, high densities of white-tailed deer may affect shrub density and consequently Yellow Warbler abundance. On the tundra near Churchill, heavy grazing by geese did not affect the abundance of the willow-nesting guild, which includes the Yellow Warbler (Sammler et al. 2008).

In northern populations, cold, windy, or wet weather can be a significant limiting factor. At North Point, the greatest cause of nest failure was exposure of eggs and nestlings due to severe northeast storms blowing in from James Bay (Rimmer 1988). At Churchill during a late spring, clutch initiation did not occur until 30 days after males arrived and most birds did not attempt to breed. Only 4 nesting attempts were observed that year, and 2 were abandoned before clutch initiation. In some years with late springs, birds may forego breeding altogether (Briskie 1995).

Leighton et al. (2002) concluded that domestic cats took a heavy toll of young in Saskatoon. This is probably true in the fragmented landscape of Ontario south of the Shield.

Presence of certain other warbler species may potentially inhibit usage by the Yellow Warbler. The Yellow Warbler uses earlier successional habitat than the Chestnut-sided Warbler. When the 2 species are present, there is frequently a rough zonation between the 2 species around edges of abandoned beaver ponds, forest edges, and other areas where succession is well underway. The songs of the 2 species are similar and they countersing at each other when they have adjacent territories. When the Chestnut-sided Warbler is absent, the Yellow Warbler may occupy more mature deciduous growth, although this is not preferred habitat (Morse 1989). In Maine, islands smaller than 1 ha supported either the Yellow Warbler or the American Redstart, but not both species. It is uncertain if this was because of interspecific competition or because the habitat on individual islands was much more suitable for one of the species (Morse 1973). In Illinois, upland shrubby areas that support Prairie Warblers support few, if any, Yellow Warblers (Graber et al. 1983).

In British Columbia, van Oort et al. (2015) examined the effects of fluctuating water levels at a reservoir. Typical of many Ontario reservoirs, water was stored in the spring and released later in the year. Yellow Warblers nested in shrubs around the margin of the reservoir at an average height of 2.2 m. Twenty-eight percent of warbler nests failed due to submergence. At that reservoir, peak water levels occurred in early July. Flooding of nests in riparian habitat at Ontario reservoirs is less likely to occur because reservoirs are typically full by the time it initiates nesting. Storms that occur after drawdown has been initiated have the potential to flood nests.

In New Jersey and Pennsylvania over a 15-year period, hemlock declined from representing 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The Yellow Warbler responded favourably to hemlock decline and increased, probably due to the increased prevalence of a deciduous understorey (Toenies et al. 2018).

Drake et al. (2013) studied the effects of winter habitat on breeding British Columbia Yellow Warblers. Winter habitat had a carry-over effect only on the productivity of yearling females. Birds originating in mesic winter habitat within a dry to seasonal climate region produced 0.8 more fledglings than those from wetter climate regions.

Chronic noise does not appear to affect the Yellow Warbler adversely during the breeding season. In Alberta, it was equally abundant near noisy compressor stations and quiet well pads. Near roads in Edmonton, it was not affected by road noise or any other variable tested (Bayne et al. 2008; Proppe et al. 2013).

In Alberta, the Yellow Warbler was equally abundant along seismic lines and pipelines as it was in adjacent forest interior, but was significantly more abundant near well pads than in adjacent forest (Bayne et al. 2016).

Price (2004) concluded that the Yellow Warbler might decline as a breeding species in southern Ontario if the average summer temperature increased by 2°C.

Status

The Yellow Warbler has always been common in Ontario and undoubtedly benefitted from forest clearing by European settlers. Baillie and Harrington (1937) stated that it nested from the southern boundaries of the province north to Hudson Bay and west to Lake of the Woods: essentially the entire province. They concluded that it was much more common in the south. The first atlas confirmed that its range included the entire province. It was found in almost every square south of the Canadian Shield but was absent from many squares in the Algonquin Highlands where there is almost continuous tree cover. It was most abundant in the agricultural south (Carpentier in Cadman et al. 1987). James (1991) considered the Yellow Warbler locally common throughout the province. Wilson and McRae (1993) stated that it was the most common and well-distributed warbler along the Hudson and James bay coasts.

The second atlas revealed no changes in the distribution of the Yellow Warbler, and it was found in every square south of the Shield. There was no difference in its probability of observation province-wide or in most regions, but a significant increase was documented in the Hudson Bay Lowland. The reasons for this increase, if it was real, were uncertain. It was most abundant south of the Shield and along the James Bay coast and portions of the Hudson Bay coast. In the south, it was

most abundant in a broad band south of the Shield from Lake Simcoe to the eastern boundary of the province, and in Niagara Region in a broad band westward along Lake Erie to Rondeau. Lowest densities occurred in heavily forested portions of the Shield, both in the Great Lakes–St. Lawrence and Boreal forest regions (McLaren in Cadman et al. 2007).

Breeding Bird Survey (BBS) data suggest that Yellow Warbler populations are stable or increasing. The data showed no significant trends for Canada and the United States for 1966-96, but there was a significant increase of 2.5% per year in southern Ontario (Lowther et al. 2020). Morse (1989) concluded that it appears to have increased throughout its range, perhaps due to the presence of hedgerows and suburban habitats. Results of the Marsh Monitoring Program indicate that the Yellow Warbler increased significantly in southern Ontario at a rate of 1.6% per year 1995-2004 (Timmermans et al. 2006). Gauthier (in Gauthier and Aubry 1996) concluded that it had probably increased over the past 20 years in the southern portion of Quebec, where it is most abundant. This was attributed to a decrease in cowbird populations and farmland abandonment. BBS data indicate that it decreased at annual rates of 0.296% in Canada and 1.03% in Ontario 1970-2021. Trends 2011-21 were annual decreases of 1.44% in Canada and 2.52% in Ontario. All results were highly reliable except that the long-term trend for Canada was of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

In Iowa, adults fed fledglings in the immediate vicinity of the nest for approximately 3 days. They became more dispersed after that, but could still be found in the general vicinity for 7-10 days (Schrantz 1943). On the James Bay coast north of Moosonee, both sexes cared for the brood, either by splitting the brood or by keeping it together and sharing duties. One male tended all 4 fledglings, frequently flying between his territory and areas as far as 100 m from the fledglings. At North Point, fledglings reached independence 2-3 weeks after leaving the nest (Rimmer 1988).

North of Moosonee, almost all adults initiated moult during the period of fledgling care. One female started her moult immediately after loss of a replacement brood. The moult occurred between early July and early September and was initiated from early July to early August. Moulting takes 35-42 days. Males initiate the moult before females and second-year birds are the first to moult. Moulting birds were incapable of sustained flight but those nearing completion of the moult were probably capable of flight (Rimmer 1988). In Alberta, moulting began while caring for fledglings. The moult was completed away from the breeding area (Flockhart 2010).

After the young reached independence at North Point, 7 males remained on or within 100 m of their territories and 4 migrated directly from their territories. Two males were on their territories late in the moult cycle, but may have temporarily moved off their territories following nesting. Two males were found considerable distances from their territories during the moult. Postbreeding females exhibited very little site attachment. Most dispersed from the study area while tending fledglings or after terminating parental duties. There was no evidence of pair mates associating after breeding. In addition to the departure of breeding females, there was a considerable influx of unbanded females in early and middle phases of the moult. These may have bred further north and some of these remained through all or most of their moult. It seemed unlikely that females initiated migration before or during the peak moult period (Rimmer 1988).

In British Columbia, Hepp et al. (2018) studied the effects of territory inundation by a reservoir on fledgling survival rates for 21 days following fledging. Water levels generally began to rise after Yellow Warblers had initiated nesting. Fledglings in areas that were flooded had significantly lower survival rates than those in territories that were not inundated. Reservoirs with fluctuating water levels have the potential to lower survival rates of fledglings.

MIGRATION

The Yellow Warbler is predominantly a nocturnal migrant but it may move diurnally to a greater extent than other warblers, particularly in autumn (Lowther et al. 2020). One juvenile travelled from Long Point to Georgia in 16 days, averaging 72 km per day. A second-year bird banded near Moosonee was recovered 3 months later in Milwaukee, 1,086 km from the banding location (Brewer et al. 2018).

Males arrive on the breeding grounds before females and adults arrive before yearlings. There may be a trend for the interval between arrivals of the sexes to be less in more northern areas, but results are variable. It is likely that the interval varies annually at each given location depending upon weather conditions. Males are likely to arrive earlier during favourable springs with a resultant longer interval between arrival dates of the sexes. At Prince Edward Point, the mean date of arrival was 1.7 days earlier for males than females. Although this was the shortest interval between the sexes of all the species that Francis and Cooke (1986) studied, the differences were still significant. At Churchill, females were first seen on the same day as males or within 2 days (Briskie 1995). At Lesser Slave Lake in Alberta, males arrived about 3 days earlier than females (Flockhart 2010). In Rhode Island, first arrival dates for males were 18-29 April compared with 25 April to 2 May for females (Mitra 1999). In Massachusetts, females arrived as early as males in 1 of 5 years. Elsewhere, intervals between the arrival of males and females has been reported as 10 days in Michigan, 9-10 days at James Bay, and 4-5 days in central Alberta (Lowther et al. 2020). In British Columbia, older males established territories an average of 8.1 days before yearling males. Older females initiated nests an average of 5.3 days before yearling females (Drake et al. 2013).

In southern Ontario, the Yellow Warbler arrives in late April or the first week of May. The main influx is during a 3-week period in May. In the southern Shield, average arrival is mid-May and the earliest records are in the first week of May. At North Point, birds arrive in late May with the main influx in the first 10 days of June. Birds at northern latitudes arrive earlier in relation to spring phenology than more southern birds. Southern birds arrive during or shortly before leaf-out but northern birds arrive to snow-covered ground long before leaves are out (Black and Roy 2010; Briskie 1995; Curry 2006; LaForest 1993; Keast 1990; Lancaster et al. 2004; Lowther et al. 2020; Mills 1981, 2005a; Tozer 2012; Weir 2008).

The Yellow Warbler is one of the earlier passerines to initiate autumn migration. Migration may begin in early to mid-July as soon as the juveniles are independent. Migrants have been observed in Florida as early as 20 July and in South Carolina on 4 July. Southern populations appear to leave earlier than northern birds, probably due to earlier completion of breeding and the prebasic moult. In Ontario, juveniles move south before females but at more southern latitudes there may be no difference in the timing of migration by the age classes. At Lesser Slave Lake in Alberta, there was no differential timing in migration of the sexes. At North Point, migration of juveniles peaked during

mid-August and adult numbers peaked in late August and early September. Latest dates were mid-September for juveniles and late September for adults. In the southern Shield, most autumn migrants are seen in August. Some probably leave in late July, most have left by early September, and the latest records are in late September. In the south, autumn migrants are moving through by mid-July with heavy flights later that month. Peak numbers occur in the first half of August and most are gone by the end of August. Some remain into the first or second week of September with rare records into November and December. At Prince Edward Point, local breeders leave their territories in the first 2 weeks of July and most have passed through by the end of August. Juveniles are present at the banding station from mid-July until the end of August with the peak near the end of July and early August. Adults are much less abundant and are present from mid-July to early August. The midpoint of autumn migration at Long Point is 7 August (Bent 1953; Black and Roy 2010; Campbell et al. 2001; Chapman 1907; Curry 2006; Flockhart 2010; Keast 1980, 1990; LaForest 1993; Lancaster et al. 2004; Lozano and Lemon 1999; Lowther et al. 2020; Mills 1981, 2005a; Rimmer 1988; Tozer 2012; Weir 2008).

Habitat used by the Yellow Warbler during migration is very similar to its breeding habitat. It occurs predominantly in deciduous shrub areas and woodland edges. It continues to favour areas of willow shrubs in wetlands and riparian areas. To a lesser extent, it may occur in second-growth forests that are either open or have considerable edge habitat. It frequents suburban and rural residential areas more often during migration than during the breeding season. During spring migration in North Carolina, the numbers of birds seen per hour were 3.54 in wet thickets, 0.07 in floodplain thickets, and 0 in pine forests, pine-hardwood forests, oak-hickory forests, dry thickets, and beech forests. During spring migration in Pennsylvania, detections per 100-m transect were 0.002 in forest and 0.370 in shrubs; captures per 1,000 net-hours were 0 in forest and 6.0 in shrubs. In Ohio during spring migration, it was equally abundant in mature upland and mature riparian forests. The Yellow Warbler was the least abundant of species for which data were presented, indicating that these habitats are marginal. In Minnesota and Michigan, it showed a nonsignificant affinity for floodplain forests rather than upland forests, but numbers in both forest types were low (Campbell et al. 2001; Graber et al. 1983; Kelly et al. 2000; Kirsch et al. 2013; LaForest 1993; Lowther et al. 2020; Parnell 1969; Rodewald and Matthews 2005; Smith and Hatch 2008; Tozer 2012).

During autumn migration at Prince Edward Point, the Yellow Warbler fed mostly at middle heights. Two percent of foraging occurred in the air, 53% on outer leaves, 7% on twigs and inner leaves, 2% on outer leaves, 27% on sapling foliage, 4% on sapling branches, and 5% in low shrubs. Foraging was not observed on inner branches, trunks, or the ground. Of 17 grounded at Point Pelee 28-30 April, 20% of foraging occurred on sapling twigs, 5% on sapling trunks, and 75% in low shrubs; aerial foraging occurred but was rare. No foraging was observed on outer foliage, bare twigs, branches, trunks, the ground, or in marshes. Foraging heights were 75% at 0.6-1.8 m, 15% at 3 m, 10% at 5 m, and 0% on the ground or above 5 m (Keast 1980). During spring migration in North Carolina, 10.5% of foraging occurred in the canopy, 77.3% in low trees, 13.1% in shrubs, and 0% on the ground. In the canopy, 7.9% of foraging occurred at the top of the crown, 2.6% in the inner crown, and 0% in the lower crown and on the bole. In low trees, 59.1% of foraging occurred in the inner crown, 18.2% in the lower crown, and 0% at the top of the crown and on the bole. In shrubs, 2.6% of foraging occurred at the top of the crown, 10.5% in the inner crown, and 0% in the lower

crown, dense thickets, brush piles, or grasses (Parnell 1969). During unusually inclement spring weather in Manitoba, Yellow Warblers were observed foraging on the ice of Lake Manitoba. Beetles, midges, other flies, and spiders were on the ice at that time (McNicholl and Goossen 1980). During autumn migration in New York, Yellow Warblers sallied for insects at night from the top of a conifer illuminated by lights from a football field (Lebbin et al. 2007).

During migration, the Yellow Warbler occasionally collides with television towers and other tall structures. Relatively few are killed, especially when the abundance of the species is taken into account. Ninety were killed at the Lennox generating station chimneys over a decade (Graber et al. 1983; Leighton et al. 2002; Lowther et al. 2020; Raveling and Warner 1978; Weir 2008).

DeGroote and Rodewald (2010) examined Ohio spring migrants for blood parasites and 12.7% of warblers were infected. They concluded that this was unlikely to have a negative effect on migration timing or energetic condition during spring migration.

During autumn migration in Idaho, McClure et al. (2013b) constructed a phantom road by broadcasting road traffic noise within a woodland. The Yellow Warbler was negatively affected by noise with an average of 4.5 birds present under quiet conditions and 0-0.25 at noise levels of 55-57 db(A). The results of this study contrast with those undertaken during the breeding season that found noise to have no effects on Yellow Warblers.

The effects that climate change have had and may have in future on migration of the Yellow Warbler are uncertain. Mills (2005a) examined spring arrival and autumn departure dates at Long Point 1976-2000. In spring, it could be considered as arriving earlier when the first arrival date is considered. Vanguard individuals may be responding disproportionately to climate change. When spring quartiles of the migration period were compared, there was no difference in arrival times over the study period. Instead of leaving later in autumn as would be predicted, warblers left earlier by 3.7 days per decade. It is possible that birds are completing breeding and their moult earlier than they did historically. Near Boston, it arrived significantly earlier 1988-2007 than in 1851-1973. All species of birds arrived in that area approximately 0.77 days earlier per 1°C increase in temperature (Ellwood et al. 2010). Boulet et al. (2006) identified other potential effects of climate change. It is anticipated that the frequency and severity of tropical storms and hurricanes will increase in the Gulf of Mexico. When weather conditions are unfavourable (strong rain, adverse wind directions, or storms), some birds barely make it to the first available land or oil rig and many probably die en route or at stopover sites.

James (1991) considered the Yellow Warbler a common migrant in the province. Hussell et al. (1992) reported a nonsignificant increase of migrant Yellow Warblers of 1.2% at Long Point 1961-88. Trends by periods were: 1961-70, –3.6%; 1970-79, +9.1%; and 1979-88, –6.3%. At the Port Weller piers in Niagara Region, counts of the Yellow Warbler 1993-2017 indicated a significant increase in numbers (Black 2017).

Chestnut-sided Warbler

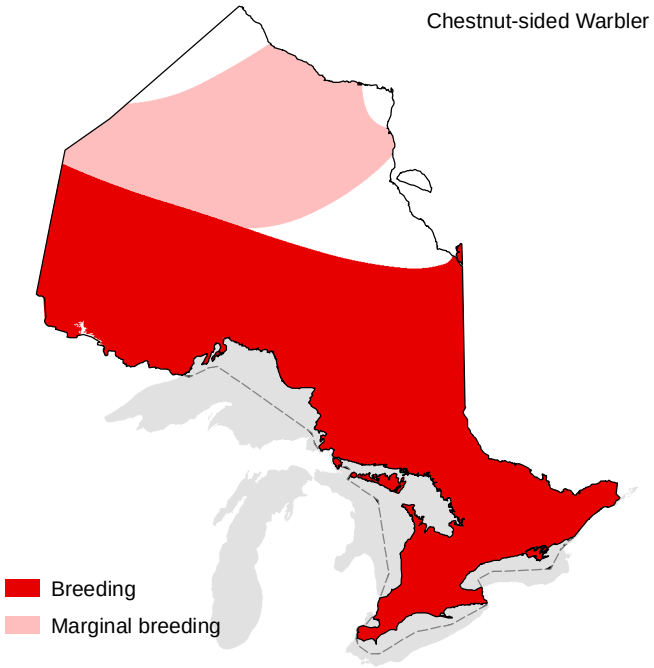
Setophaga pensylvanica

BREEDING SEASON

Habitat Requirements

Ontario Chestnut-sided Warbler nests were most often in the understorey and at edges of deciduous and mixed woods, occasionally in coniferous woods; in semi-open and logged woodlands; in overgrown fields; in brushy woodland borders; in swampy areas and beaver meadows; along shrubby hydro corridors; and in sphagnum bogs. Nests were commonly near roads and water, indicating its preferences for open and edge areas (Peck and James 1987).

In the Boreal Forest Region, the Chestnut-sided Warbler was associated with younger, more open deciduous forests that were highly disturbed. It was also associated with high levels of edge between young and old forests (Rempel 2007; Rempel et al. 2007). Welsh (1993) considered the Chestnut-sided Warbler an early successional species. It occurred only in stands 21 years old and younger. Near Pickle Lake, McLaren and McLaren (1981) observed it in low density in deciduous scrub and mixed forest. Also near Pickle Lake, James (1980) observed it in scrub vegetation near towns and in the Lysander Lake area. Near Lake Nipigon, it nested in low densities in trembling



aspen and spruce–balsam fir stands (Sanders 1970). At Quetico Park, it was most abundant in stands 1-23 years old, uncommon in stands 112-176 years old, and absent in stands 67-73 and 367-370 years old (Apfelbaum and Haney 1985). Near Hearst, it nested in upland and lower-slope clear-cuts in mixed forests 3-24 years old and in lowland coniferous clear-cuts 5-9 years old. It did not occur in unharvested upland mixed or lowland coniferous stands. It was often the dominant species in upland clear-cuts 3-11 years old (Welsh and Fillman 1980). Near Manitouwadge, it was common in stands 1-21 years old, uncommon in 24-36-year-old stands, and rare in stands 60-223 years old (Venier et al. 2009). On the northeast shore of Lake Superior, it inhabited older thickets and small second growth (Baillie and Hope 1943). In the Clay Belt, it was most abundant in stands dominated by balsam poplar and trembling aspen followed by those dominated by white spruce–white birch. It was associated with wet, nutrient-rich sites (Welsh and Lougheed 1996).

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Chestnut-sided Warbler occurred in both mature and old-growth white pine stands where it was more common in mature stands (Kirk et al. 2012). In jack pine stands near Gogama, it was associated with deciduous shrubs in mixed regeneration. It first appeared when growth was approximately 3 m tall, became abundant in growth 6-7 m tall with numerous small shrubs, and persisted in diminishing numbers until tree crowns formed a canopy. Few remained once trees reached a height of 10 m in these dense pine plantations (James and Peck 1995a). At Pimisi Bay, a nest was at the edge of an opening in the woods in an area that became overgrown with bracken fern later in the season. The opening was surrounded by mature second growth and supported deciduous saplings and beaked hazel (Lawrence 1948). In Algonquin Park, it was most abundant in plots at edges of forests. In one of these plots, it was the second-most abundant species. It was also common in poplar–white birch stands where it was fourth in abundance. It was common in balsam fir–spruce stands and these types of stands mixed with hardwoods, and uncommon in black spruce–white cedar stands. It was not recorded in bogs, immature white pine stands, pure hardwoods, or hemlock stands. In poplar-birch stands, it ranged 1.8-8.8 m from the ground which corresponded to the middle of the shrub layer to 2 m below the top of the canopy. In balsam fir–spruce stands, it occupied the central canopy. Martin (1960) considered it characteristic of pioneer deciduous forest. MacLulich (1938) considered it fairly common in Algonquin Park in logged forests and thickets; it appeared to favour white birch trees. In white pine stands in Algonquin Park, it was significantly less abundant in stands with no recent history of harvesting than it was in more recently cut stands. It occurred in 26.7-28.6% of

stands with no recent cutting, 72.7-90.0% of stands cut 10-16 years previously, and 83.3% of stands cut 2-9 years previously. Density was highest in the most recent cuts (Kingsley and Nol 1999). In Parry Sound District, the Chestnut-sided Warbler was absent in pure jack pine stands but occurred in open jack pine stands mixed with a variety of deciduous species (James 1979a). It nested in all sorts of semi-open areas in Parry Sound and Muskoka districts, including open woods, margins of ponds and streams, hydro corridors, and roadsides (Mills 1981).

In Durham Region in the off-Shield portion of the Great Lakes–St. Lawrence Forest Region, Speirs and Orenstein (1975) reported the Chestnut-sided Warbler in a pure pine plantation with no understorey. Included in their plot was a small relict of sugar maple–oak forest with an understorey of hophornbeam. Given its requirement for shrubs, it is most likely that it nested in the deciduous forest.

In the Carolinian Forest Region, the Chestnut-sided Warbler benefitted from forest thinning in Elgin County. It nests there in dense tangles of raspberry shrubs that grow up on logging trails throughout woodlots (Lancaster et al. 2004). McIlwraith (1894) commented that it was very partial to raspberry patches in the Hamilton area. In southern Ontario, its abundance was positively correlated with the amount of forest cover within 2 km and negatively correlated with the amount of forest cover more than 100 m from edge, woodlot size, and the amount of regional forest cover. These relationships were not significant (Austen et al. 2001).

Throughout its range, the Chestnut-sided Warbler is associated with early successional deciduous growth. This may include shrubby meadows and pastures, regenerating clear-cuts and burns, utility rights-of-way, forest edges, and open-canopied forests of almost any type that have deciduous undergrowth. It nests in both wet and dry areas, but has a tendency to inhabit drier areas than the Yellow Warbler. It responds favourably to small openings in mature forests such as anthropogenic clearings, those resulting from windthrow, beaver ponds, hydro or pipeline corridors, roads, and strip-cuts as narrow as 20 m. It typically avoids the immediately adjacent mature forest along rights-of-way and strip-cuts. Where there are only small gaps, it may forage in forested habitat but nests within the gaps. Less frequently used habitats include coniferous plantations with a deciduous understorey, black spruce stands, and bogs and fens. In young clear-cuts and shrubby rights-of-way through forested habitat, the Chestnut-sided Warbler is often one of the most common species. In forested areas, it shows a preference for areas dominated by white birch or poplars. In forested landscapes, it may be a fugitive species that must be constantly moving in response to the shifting mosaic of open habitat patches embedded within extensive woodlands (Back 1979; Beals 1960; Bent 1953; Bielefeldt and Rosenfield 1994; Brooks 1940, 1947b; Byers et al. 2004, 2020; Chapman 1907; Dawson 1979; DeGraaf et al. 1998; Dessecker and Yahner 1987; Erskine 1977; Faanes and Andrew 1983; Falardeau et al. 1999; Ferris 1979; Freedman and Johnson 1999; Freedman et al. 1981; Graber et al. 1983; Hanski et al. 1996; Hobson and Bayne 2000; Kendeigh 1945; King and DeGraaf 2004; Kirk et al. 1996; Klaus et al. 2010; Lemieux and Choinière in Gauthier and Aubry 1996; Lent and Capen 1995; Litwin and Smith 1992; Moorman et al. 2012; Morgan and Freedman 1986; Mossman and Hoffman 1989; Mossman et al. 1991; Mousley 1916a; Niemi and Hanowski 1984b; Noon et al. 1979; Pitts 1990; Schill and Yahner 2009; Siebenheller and Siebenheller

1990; Sodhi and Paszkowski 1995; Streby et al. 2011b; Suthers 1988; Taylor and Taylor 1979; Titterington et al. 1979; Yahner 1993, 2003; Yahner et al. 2002).

Chestnut-sided Warbler abundance may be related to the amount of forest cover in the landscape, but results are contradictory. In southern Ontario, Austen et al. (2001) found that it had a tendency to be more common where there were greater amounts of forest within 2 km, although this relationship was not significant. Byers et al. (2020) noted that it was largely absent in intensive agricultural areas of Ontario and Wisconsin. This may be a result of the paucity of shrublands in these areas rather than an influence related to the amount of forest cover. In Saskatchewan, its abundance was significantly correlated with the amount of forest cover within 5 km, although it occurred in both forested and fragmented landscapes (Hobson and Bayne 2000). In the mid-Atlantic states, it was positively correlated with the amount of forest within 2 km (Robbins et al. 1989). More forest equates to more forest edge which may potentially provide suitable habitat. Near Quebec City, the Chestnut-sided Warbler was the species least likely to be found in forest habitat of all species studied by Bourque and Desrochers (2006). This area is heavily forested, usually with 50-60% or more forest cover; consequently, much of this area was unsuitable habitat. It is likely that increasing forest cover is beneficial in fragmented landscapes, particularly those that are agricultural or urban in nature, but detrimental in areas that are heavily forested. In North Dakota, it was positively correlated with elevation at the 200-m scale. This indicated that it was capable of occupying high-elevation landscapes that have experienced limited disturbances, where there are only small gaps in forest cover (Gilbert and Ferguson 2019).

Numerous studies examined the age or tree-size classes of forests that the Chestnut-sided Warbler inhabits. These almost unanimously concluded that it prefers young stands and those dominated by smaller trees. It occurs sparingly in more mature stands where it is associated with deciduous shrubs and saplings in the understorey. In Maine spruce–balsam fir stands, it was absent in both mature forests and recent clear-cuts characterized by much bare soil and dense slash. It reached its greatest abundance in clear-cuts with dense coverage by raspberry bushes and regenerating hardwoods less than 2 m tall. It was one of the dominant species in this stage of succession. It continued to be common in the next stage of succession when hardwood regeneration was taller than 2 m and there was a well developed but slower growing coniferous stratum. It declined considerably once hardwood regeneration was taller than 4.5 m with trees 10-15 cm diameter at breast height (DBH; Titterington et al. 1979). In Vermont, it was associated with low successional age, few conifers, more snags, moderate amounts of poplar and white pine, more red maple, and limited amounts of hophornbeam, red oak, beech, and sugar maple (Lent and Capen 1995). In Pennsylvania, it occurred in 9.1% of old-growth forests, 40.7% of forests statewide, and 68.6% of forests on the Appalachian Plateau. Its abundance was significantly negatively correlated with old-growth forest (Haney 1999). In northern mesic forests in Wisconsin, it was associated with young and often dense forests and sapling deciduous forests (Hoffman 1989a). In Alberta and Saskatchewan, it was situated at the younger end of the forest-age scale (Kirk et al. 1996). In northeastern mixed forests, Temple et al. (1979) considered it a mid-seral stage species associated with increasing density of yellow birch, sugar maple, and pine. In New Jersey, the Chestnut-sided Warbler nested in old fields that were 10 and 20 years old, but not in a 40-year-old field. The older field was too overgrown with dense shrubs and trees to provide suitable habitat (Suthers 1988). In

New Hampshire and Maine, it demonstrated a significant preference for tree-size classes within forests. It was most abundant in the sapling stage (trees 2-12.5 cm DBH), approximately equally abundant in pole-sized (12.5-22.5 cm DBH) and sawtimber-sized trees (larger than 22.5 cm DBH), and least abundant in trees larger than 60 cm DBH. It was 1 of 4 species exhibiting the strongest association with sapling-sized stands (DeGraaf et al. 1998). In Wisconsin, it tended to increase where the trees were small or the total basal area (BA) was low (Beals 1960). In northern hardwoods in Nova Scotia, the Chestnut-sided Warbler is the most characteristic and abundant species of young stands (Morgan and Freedman 1986).

Microhabitat preferences of the Chestnut-sided Warbler were described in several studies. Its average habitat characteristics in Minnesota were 92.8% ground cover, 66.9% shrub cover, 46.3% canopy cover, 13.1 m canopy height, 9.1% coniferous cover, 3.4 tree species per 0.04-ha circle, 7.1 trees 7.5-15 cm DBH, 6.7 trees 15.1-23 cm DBH, 3.2 trees 23.1-30 cm DBH, 1.1 tree 30.1-38 cm DBH, 0.3 tree 38.1-53 cm DBH, 0.4 tree 53.1-68 cm DBH, and 0.2 tree larger than 68 cm DBH. Its habitat was most similar to that of the Golden-winged and Mourning warblers and also the Common Yellowthroat and Yellow Warbler. These 5 species prefer open habitats with dense ground cover and moderate shrub cover. The habitat of this guild ranged from open marshland with few or no trees (Common Yellowthroat and Yellow Warbler) to areas of dense aspen coppice (Mourning Warbler) and deciduous edge vegetation (Chestnut-sided and Golden-winged warblers). The Chestnut-sided Warbler was associated with more ground cover and more medium-sized trees and was found in deciduous second growth (Collins et al. 1982). In Maine, it was significantly associated with raspberry bushes and the number of deciduous woody stems smaller than 10 cm DBH, 2.1-4.5 m tall (Titterington et al. 1979). In Vermont, mean habitat characteristics were 84.0% green ground cover, 7.9% ground slash, 35.8% canopy closure, 9.5 m canopy height, 6.1 m canopy depth, 3.6 m^2 per ha BA deciduous plants, 0.5 m^2 per ha BA conifers, mean DBH 5.5 cm for deciduous species, and 4.6 cm DBH for conifers. It was associated with dense understorey, open habitats, and deciduous cover (Thompson and Capen 1988). In the Prairie Provinces, the Chestnut-sided Warbler was on the midpoint of the scales for moisture and nutrient richness (Kirk et al. 1996). In the mid-Atlantic states, its abundance was negatively correlated with BA and snags larger than 3 cm DBH (Robbins et al. 1989). In North Carolina, its abundance was significantly negatively correlated with canopy coverage (Lumpkin and Pearson 2012). In Minnesota clear-cuts, it was positively correlated with increasing foliage complexity: BA of dead trees, shrub density, shrub BA, and shrub height (Niemi and Hanowski 1984a). In New Hampshire and Maine, it was significantly correlated with the number of coniferous and deciduous trees larger than 10 cm DBH and the number of woody stems per ha. It was negatively correlated with foliage volume of both deciduous and coniferous trees larger than 10 cm DBH and the foliage volume of deciduous trees smaller than 2 cm DBH (DeGraaf et al. 1998).

Collins (1983a) compared the habitat characteristics of the Chestnut-sided Warbler in Minnesota and Maine. The percent ground cover and number of trees 7.5-15 cm DBH in territories differed significantly between the 2 states. In Minnesota, it was associated with moderate ground cover and intermediate numbers of medium-sized deciduous trees. In Maine, it inhabited areas with slightly more ground cover and more medium-sized trees.

Territories in shrubby areas typically have some taller shrubs, saplings, or trees that function as song perches. Collins (1981) compared the vegetation at nest sites and song perches and found that they were significantly different. Perch sites had a greater number of trees than nest sites, which increased the values for percent canopy cover, average tree height, and percent conifers.

Freemark and Collins (1992) considered the Chestnut-sided Warbler an area-sensitive species but noted that various studies classified it differently. In addition, many studies were examining forested habitat when determining its area sensitivity but few studies examined area sensitivity in the shrubby habitats that it prefers. In forested habitat, Byers et al. (2020) concluded that patch size did not affect any breeding parameters. It was not area sensitive in Saskatchewan (Hobson and Bayne 2000). In Wisconsin, Mossman and Hoffman (1989) stated that it preferred large tracts of upland forests but provided no additional information. In Rhode Island, it was not observed in swamps smaller than 5 ha and occurred in low density in swamps 6-20 ha. Larger swamps had longer and often more irregular perimeters with a greater diversity of upland habitats along the edge. All edge species increased with increasing swamp edge (Golet et al. 2001), and this was likely also true for upland forests. King and DeGraaf (2004) examined Chestnut-sided Warbler usage of clear-cut patches 0.15-0.69 ha (average 0.39 ha) imbedded in extensive upland deciduous forests in New Hampshire. Every patch was occupied by 1-3 territorial males indicating that it was not exhibiting area sensitivity. Density was highest in small patches and decreased with increasing patch size. Despite the fact that it was more abundant in smaller patches, larger patches appeared to be of higher quality. Larger patches were occupied first, nests were initiated earlier in large patches, and large patches were occupied by birds with larger and brighter patches of colour in their plumage. Younger birds may be relegated to inferior habitat (smaller patches) where they are confined to smaller territories. Birds in this area appeared to nest away from edges of habitat patches, although the authors acknowledged that patches might be entirely edge. There was no relationship between patch size and shape and rate of predation. Roberts and King (2019) conducted similar studies in Massachusetts in forest canopy openings created by group-selection harvesting. The chestnut-coloured flank appeared to function as a status badge signalling older and larger birds. Probability of occurrence did not reach 90% until patch size was 0.48 ha in 1 year and 0.72 ha in another, suggesting that larger openings conferred advantages with respect to nesting success. Birds in larger openings nested earlier, giving them time to renest in the event of a failure. Birds with larger badges were negatively correlated with the presence of forbs, ferns, and grasses, confirming that these represent inferior habitat. Larger-patched birds were positively correlated with irregularly shaped openings.

The habitat requirements of Chestnut-sided and Yellow warblers are similar and the 2 species occasionally nest in the same area. The 2 species countersing when they have adjoining territories. The Chestnut-sided Warbler prefers drier areas with slightly more advanced succession than the Yellow Warbler. The Chestnut-sided Warbler is much less likely to be found in the willow and alder thickets that the Yellow Warbler prefers. The Yellow Warbler seldom occurs in sapling-stage forests that are suitable habitat for the Chestnut-sided Warbler. In successional gradients around beaver ponds, the Yellow Warbler nests in the inner edge that is wetter and supports few trees. The Chestnut-sided Warbler inhabits the outer drier band with more deciduous shrubs and saplings. The

Yellow Warbler may nest in suburban areas but the Chestnut-sided Warbler avoids these areas (Byers et al. 2020; Chapman 1907; Lemieux and Choinière in Gauthier and Aubry 1996; Morse 1989).

Ontario nests were elevated over ground or occasionally over water (1.3% of nests). They were most often in shrubs or small trees but sometimes in ferns and herbaceous plants. Deciduous trees and shrubs (18 species, 91.4% of nests) were greatly preferred to conifers (5 species, 8.6% of nests). The most commonly selected species were hazel, raspberries, maples, and alder. Most nests were in crotches of trees or shrubs but some were at the junction of 2 adjacent plants. Occasionally nests were saddled on 1 or 2 branches. Nest positions varied from the outer periphery of a shrub to against the main trunk of a small tree. Nests were 0.2-1.8 m from the ground, with most 0.5-0.9 m up (Peck and James 1987). Lawrence (1948) reported a nest near Pimisi Bay 45 cm from the ground in a raspberry bush. In Algonquin Park, nests are typically in deciduous shrubs, particularly beaked hazel, 1-2 m from the ground (Tozer 2012). A nest in Elgin County was 1.3 m up in a red elderberry in a woodlot that had been logged 5 years previously (Lancaster et al. 2004).

In Pennsylvania, nest sites had a higher woody stem density than randomly selected sites. Schill and Yahner (2009) concluded that abundance of the Chestnut-sided Warbler may be limited by availability of suitable nest sites represented by sites with high foliage density. Throughout its range, it nests predominantly in deciduous shrubs and saplings close to the ground. Beaked and American hazel are highly preferred for nesting where they occur. Other species it has nested in include raspberries and blackberries, huckleberry, mountain laurel, barberry, viburnums, spiraeas, alder, red-osier and gray dogwood, and bracken fern. In Massachusetts, it nested in equal numbers in native and nonnative shrubs such as multiflora rose and Russian olive. It may nest in saplings of oak, maple, birch, beech, and hophornbeam. Nests may be 0.2-2.0 m from the ground, but most are 0.5-0.8 m up; in New Hampshire, 2% of 217 nests were on the ground. Most nests are well concealed but a few are exposed. In dense shrubs, nests may be attached to as many as 4 stems but most are in a fork in a single shrub or sapling (Bent 1953; Byers et al. 2020; Chapman 1907; Graber et al. 1983; Harrison 1984; Kendeigh 1945; King et al. 2001; Mousley 1916a, 1924; Pitts 1990).

The Chestnut-sided Warbler is territorial and males may chase each other when their territories are close to each other. It may also chase male Yellow Warblers and the 2 species commonly countersing when they have neighbouring territories. Near Quebec City, territories were significantly clumped at scales of 250 and 350 m, but not at 450 or 550 m. A similar study found no evidence of autocorrelation of territories at any scale. Near Pimisi Bay, 1 territory was 0.30 ha with the nest near its centre. In Algonquin Park, territories averaged 0.15 ha (range 0.04-0.51 ha). In New York, 4 territories averaged 0.64 ha (range 0.49-1.02 ha). During the incubation period, males greatly increased the area that they used, wandering 60-215 m outside the territory and covering an area of 0.8-4.9 ha or more. These additional areas, which may be considered the home range, always extended into unoccupied areas and in no cases did the home ranges of 2 males overlap. In small forest gaps in New Hampshire, birds frequently foraged in adjacent mature forest. It was not determined if these foraging areas were defended as part of the territory or if foraging home ranges overlapped. Gap sizes were 0.15-0.69 ha and all were occupied, suggesting that some territories were as small as 0.15 ha provided that adjacent forest was not part of the territory. Elsewhere,

territories as large as 0.405-1.10 ha have been reported (Bourque and Desrochers 2006; Byers et al. 2020; Kendeigh 1945; King and DeGraaf 2004; Lawrence 1948; Martin 1960).

No information is available on natal philopatry, but it is probably very low. The only information on adult site fidelity is from old-field habitat in New Jersey where 9 of 46 adults (19.6%) returned in a subsequent year (Byers et al. 2020; Suthers 1988). Because suitable habitat is transitory due to natural succession, adult return rates for adult Chestnut-sided Warblers may be lower than for many other species.

Limiting Factors

Eggs have been reported in Ontario nests from the last week of May until the end of July, with most present in the second and third weeks of June (Peck and James 1987). In Algonquin Park, nests are under construction late May to late June, eggs are present late May to late July, nestlings are present mid-June to late July, and dependent fledglings have been observed from late June to mid-August (Tozer 2012).

The female occasionally selects a nest site outside the territory so that territorial boundaries must be adjusted. Limited information is available on how long it takes to build the nest; 2 took 4 and 5 days to complete. In 1 nest at Pimisi Bay, the first egg was laid 4 days after the nest was complete. In Michigan, the first egg was laid 1-6 days after the nest was completed, but typically 3 days after completion. In Massachusetts, males are present and defending territories for several weeks before any females lay eggs. This is unlikely to be the case in Ontario and other more northerly areas. One egg is laid per day. Incubation begins with the laying of the last egg or in the afternoon the day before the last egg is laid. The incubation period of 26 Ontario clutches was 10-13 days with most eggs hatching in 10 or 11 days. Other studies confirmed the same range of incubation periods. Eggs often hatch asynchronously, with the last chick to hatch frequently a day younger than its siblings. Young may fledge when they are 8 days old, but usually only if they are disturbed. They are capable of flight at age 9 days but may remain in the nest 10-11 days if undisturbed (Bent 1953; Byers et al. 2004, 2020; Harrison 1984; Kendeigh 1945; Lawrence 1948; Mousley 1924; Peck and James 1998a).

There are anecdotal records of the Chestnut-sided Warbler raising 2 broods, but this does not appear to have been confirmed with banded birds. McIlwraith (1894) stated that it raised 2 broods in Ontario and Andrle and Carroll (1988) concluded that it occasionally raised 2 broods in New York. In Massachusetts, Kroodsma et al. (1989) concluded that it raised 2 broods and noted that there was a resurgence in singing after the first brood fledged that may have been associated with initiation of a second brood. Renesting commonly occurs if the first nest is lost. A new nest is built for the replacement clutch. Clutches of 1-5 eggs have been reported in Ontario. A fledgling was successfully reared from the nest in which a single egg was laid. The most frequent clutch size was 4 eggs (61.8% of clutches); clutches of 1, 2, and 5 eggs were rare. The average clutch size for Ontario nests was 3.49 eggs. Elsewhere, the clutch size was reported as 3-5 eggs. Four-egg clutches are typical; those containing 3 eggs are occasional and 5-egg clutches are rare (Bent 1953; Byers et al. 2020; Chapman 1907; Kendeigh 1945; Lawrence 1948; Mousley 1916a; Peck and James 1998a).

Both sexes are capable of breeding at age 1, although the proportion of birds that do so is unknown. Some populations contain floating unmated males or males that are successful in

defending a territory but unsuccessful in attracting a mate. The mating system is social monogamy, although 2 cases of bigamy have been reported. In Quebec, a female was killed after working on a nest for 2 days and the male continued to sing for several days before deserting it. He later moved about 75 m and was successful in securing another mate. Members of a pair that return in subsequent years are not known to remate, but sample sizes are very low (Byers et al. 2004, 2020; Mousley 1924). Only 1 study, in Massachusetts, has been undertaken on extra-pair paternity in the Chestnut-sided Warbler. Both sexes made regular forays into neighbouring territories. Twenty of 33 nests (60.6%) contained 1 or more extra-pair young and 47.4% of all young were extra-pair. For all brood sizes, the number of nests with 0 or many extra-pair young was greater than expected. Most extra-pair young were fathered by a nearby resident male (28% by a neighbour and 62% by males 2 or 3 territories distant). A few extra-pair young were sired by males 10 territories away, but territories averaged only 45 m in width such that the most distant extra-pair male resided within 400 m. Single nestlings in 2 nearby nests were fathered by a male that was not a resident within the study area. He may have been a nonterritorial floater or a more distant resident. Fifty-six percent of extra-pair males had nests that contained extra-pair young. A male's success at ensuring paternity in his own nest was not closely related to his success in obtaining extra-pair fertilizations. In 77% of extra-pair fertilizations, the first egg in the nest containing a male's extra-pair young was laid within 4 days before (54%) or after (23%) the first egg was laid in the male's own nest. The remainder were secured either later during the incubation period of his social mate (15%) or after his young had fledged (8%). All males but one were paired when they sired extra-pair young. Most extra-pair fertilizations were obtained during their own mate's fertile period, thus making them vulnerable to cuckoldry (Byers et al. 2004).

The Chestnut-sided Warbler tends to forage at low levels in shrubs and saplings or in the lower canopy, but may forage from the ground (rarely) to the canopy. It makes extensive use of shrubby patches when foraging, especially those dominated by raspberries. In Parry Sound District, foraging during early and midsummer was associated with early successional deciduous species such as willow, trembling aspen, alder, elm, black cherry, chokecherry, silver maple, and black ash. In autumn, it used areas with a higher component of white birch. Foraging height was 2-11 m during the breeding season and 2-10 m in autumn. In Wisconsin, it foraged in young disturbed forests with high light penetration and a well developed layer of shrubs and herbaceous species. Males foraged 55% of the time in hardwoods, 28% in aspen, 10% in conifers, and 7% in shrubs. Females foraged 36% of the time in aspen, 34% in hardwoods, 22% in shrubs, and 8% in conifers. Mean heights of activities were 5.47 m for males and 4.06 m for females. In the Clay Belt of Ontario, 96% of foraging occurred in deciduous species at an average height of 8.4 m. Seventy percent of foraging occurred in foliage and was 47.1% by aerial attacks, 2.8% by hanging, 15.8% by hovering, and 17.1% by reaching. This warbler relies heavily on searching the undersides of leaves for prey: 70% of searching occurs on the undersides of leaves, 11% on the upper surfaces of leaves, and 13% on twigs. Foraging techniques were 62% by gleaning, 17% by hovering, and 10% by leaping in 1 study. In Vermont, 70% of prey was captured in foliage, 18% in the air, 5% each on branches and twigs, and 2% on trunks. Forty-two percent of prey was captured by gleaning, 5.6% by aerial manoeuvres, and 2% by hanging. In Wisconsin, foraging substrates of males consisted of 54% branches, 25% twigs and leaves, 17% air, and 4% limbs and trunks. Female foraging substrates consisted of 55% branches,

24% twigs and leaves, 20% air, and 1% limbs and trunks. Males foraged 51% of the time by gleaning, 20% by hovering, 15% by sallying, and 14% by pouncing. Females foraged 42% of the time by gleaning, 33% by hovering, 20% by pouncing, and 5% by sallying (Bent 1953; Byers et al. 2020; Greenberg et al. 1999; Lent and Capen 1995; Mills 2007; Sodhi and Paszkowski 1995).

Nestlings are fed mosquitoes, small moths, and small flying insects when they are young and caterpillars, crane flies, small grasshoppers, large moths, dragonflies, and a variety of flying insects when they are older. During the breeding season, adult Chestnut-sided Warblers are almost entirely insectivorous, although they also eat spiders. It was the only old-field species that showed no evidence of eating plant food in New Jersey. In Illinois, 2 had eaten 77% caterpillars, 11% beetles, and 5% aphids. One bird had consumed 17 locusts and 21 other insects. Its primary prey includes caterpillars, fly larvae and some adults, and beetles. It consumes small tent caterpillars but not larger ones, spiders, metallic wood-boring beetles, ants, aphids, and leafhoppers. Near Manitouwadge, it increased in response to increasing spruce budworm populations, but not significantly. One stomach collected in Maine when spruce budworm populations were low contained 65% budworm larvae and pupae by volume (Bent 1953; Byers et al. 2020; Graber et al. 1983; Kendeigh 1945; Lawrence 1953; Mitchell 1952; Mousley 1924; Pitts 1990; Suthers 1988; Venier et al. 2009).

The Chestnut-sided Warbler is a common host of the Brown-headed Cowbird. The warbler rarely buries the cowbird egg in the nest. This most likely occurs only when the cowbird lays an egg in a nest that is still incomplete. In Ontario, 51 of 235 nests (21.7%) were parasitized and 29% of Quebec nests were parasitized. In Pennsylvania, 0 of 12 nests were parasitized but a high proportion of Hooded Warbler nests were parasitized. In Illinois, 5 of 7 nests (71.4%) were parasitized and 3 of 16 Minnesota nests (18.8%) were parasitized. Of 194 clutches reported in the late 19th and early 20th centuries, 18 (9.3%) were parasitized, suggesting that parasitism rates have increased (Bent 1953; Byers et al. 2020; Graber et al. 1983; Hanski et al. 1996; Lemieux and Choinière in Gauthier and Aubry 1996; Peck and James 1998a).

Habitat for the Chestnut-sided Warbler is probably declining south of the Canadian Shield. Shrubby and other early successional habitats are being lost to agricultural and urban land uses or to natural succession. Further north, early successional habitat continues to be provided regularly by forest management.

The Chestnut-sided Warbler responds favourably to forest harvesting and increases at all levels of harvesting intensity from single-tree selection to strip-cutting and clear-cutting. It increases with increased intensity of harvest. In the Boreal Forest Region of Ontario, models indicated that it would increase with forest management in comparison with natural disturbance regimes for all silvicultural options. A study in Algonquin Park determined that it was significantly more abundant in stands harvested within 1-5 years than in reference stands or in stands harvested 15-20 years previously. The logged stands were selectively cut with approximately 25% of BA removed. It was positively correlated with the percent coverage by slash and amount of shrubs 0.5 m or less tall. Another study in Algonquin Park confirmed that it responded positively to typical and intensive group selection, increasing 1 or 2 years postharvest. In northern hardwoods near Sault Ste. Marie, the Chestnut-sided Warbler increased in all areas where selection harvesting occurred. It increased 2-3 years postharvest. Its population in unharvested stands decreased during the same time period. It was

positively correlated with grass and sedge cover and the density of tall shrubs. In the Carolinian Forest Region of Ontario, it was a significant indicator of heavy or diameter-limit cuts. It was negatively correlated with the amount of retained BA. Similar positive responses to forest thinning or clearing have been documented throughout its range. In New York, it increased with increasing intensity of harvest. Populations peaked 1-6 years after harvest, declined to about 70% of the peak by year 7, declined to 50% in years 8 and 9, and were 40% of the peak 10 years postharvest. In Pennsylvania, it was absent in uncut aspen and oak stands but became abundant once these stands were cut. In the same state, it was more abundant where snags had been retained when stand improvements were made. Snag retention resulted in more woody plant growth as tall as 1.5 m. In New Brunswick, the Chestnut-sided Warbler exhibited a significant positive response to selection harvesting. It was absent prior to cutting, first appeared 1 year after harvesting and increased each year until 5 years postharvest when the study was terminated. In New York, it increased 10-fold 2-6 years postharvest, attaining its peak population 6 years after harvest and declining thereafter and becoming absent by 24 years postharvest. In 3 Minnesota areas, it responded positively to clear-cutting and to any amount of tree removal. In partially harvested areas, it was either the species that responded most favourably or was second in intensity of response to the White-throated Sparrow. In Nova Scotia clear-cuts, the Chestnut-sided Warbler was present in cuts 1-18 years old. Numbers increased to a peak 6-10 years after cutting and declined rapidly thereafter with few documented in stands 13 years or older. Timber harvesting in extensively forested landscapes provides habitat for it where it would typically be rare or absent (Byers et al. 2020; Haché et al. 2013; Hanowski et al. 2003; Holmes and Pitt 2007; Holmes et al. 2004; Jobes et al. 2004; Keller et al. 2003; Morgan and Freedman 1986; Niemi and Hanowski 1984a; Rempel et al. 2007; Stribling et al. 1990; Tozer et al. 2010; Webb et al. 1977; Yahner 2003). In the Canadian Shield of Ontario, there was no difference in its abundance in early successional and mid-successional clear-cuts and burns in the same seral stage. It was equally abundant in early successional and mature stands, but significantly less abundant in mid-successional than mature stands (Zimmerling et al. 2017).

In Minnesota, Hanski et al. (1996) studied the effects of clear-cuts on nest survival. The Chestnut-sided Warbler had the second-highest nest success rate (59%) of all species in trembling aspen–white birch stands interspersed with clear-cuts. In trembling aspen–jack pine stands, it had the lowest nest success rate (46%). Predation rates of all nests were lowest in open areas and regenerating clear-cuts and highest in forests. In New Hampshire, nest survival rates did not differ between clear-cuts and group-selection cuts or between cut edges and cut interiors. Survival was not lower in small patches (King et al. 2001).

In Michigan, Valentine et al. (2019) compared predation rates on artificial Chestnut-sided Warbler nests placed near forest openings and in forest interior. Openings were less than 100 m^2 and were cut as drilling pads for oil and gas extraction. Nests near edges were depredated more quickly and at higher rates. Birds appeared to be the primary predators and nests in shrubs may be more vulnerable to them than those on the ground.

Byers et al. (2020) documented some potential adverse effects of certain forest management practices. Control of caterpillars with pesticides or Bt may cause decreased productivity or abandonment of areas. The early successional areas inhabited by the Chestnut-sided Warbler are

less likely to be infested with caterpillars and treated, however. In 1 area, it continued to feed after spraying with fenithrothion but returned in smaller numbers in subsequent years.

The Chestnut-sided Warbler responds well to forest fires and prescribed burns. Forest fires create large areas of early successional habitat similar to clear-cuts. Regeneration may be more retarded on burns than cuts because the litter area is removed in burns and organic soils may be damaged or burned. In Georgia, it responded favourably to severe-intensity prescribed burns which resulted in significantly less canopy coverage than control areas. Warbler densities were low in severe burns for the first 1-2 years and increased significantly 3-6 years postburn; shrub density was significantly lower 1-2 years after fire. It was positively correlated with shrub density and negatively correlated with canopy cover and BA (Klaus et al. 2010). Effects of prescribed burns are likely to vary considerably depending upon soil types and species of trees and shrubs present. Fires that eliminate or significantly reduce shrub coverage for extended periods of time could be detrimental.

Mahoney et al. (1997) studied the effects of acid rain on the Chestnut-sided Warbler. Their study areas were near North Bay, which is downwind of Sudbury and subjected to acid rain, and Loring, which is unaffected by air pollution. They predicted that it was less likely to be affected than a forest-dwelling species (Black-capped Chickadee), and this was correct. At the area of declining forest (North Bay), there were significantly lower calcium levels in geometer moth caterpillars, lower magnesium levels in beetles, and higher aluminum and magnesium concentrations in geometer moth caterpillars. There was no significant difference in Chestnut-sided Warbler clutch or brood size and hatching success at the 2 sites. It appeared to obtain sufficient calcium for eggshell formation despite a scarcity of snails at both sites.

In Pennsylvania, daily nest survival rates increased with woody stem density but decreased with the amount of coverage by Allegheny blackberry. Better concealed nests had lower survival rates (Schill and Yahner 2009).

Blake et al. (1992) determined that abundance of the Chestnut-sided Warbler was significantly negatively correlated with drought and moisture anomaly indices in Michigan but not in Wisconsin. During the study period, drought was more severe in Wisconsin than it was in Michigan. It is uncertain if drought has a significant effect on the Chestnut-sided Warbler.

In the Appalachian Mountains in North Carolina, abundance of the Chestnut-sided Warbler was significantly negatively correlated with the number of houses and other buildings within 200 m. It appears to avoid houses even if there is suitable habitat around them (Lumpkin and Pearson 2012).

Price (2004) predicted that the breeding range of the Chestnut-sided Warbler might contract in southern Ontario if the average summer temperature increased by 2°C. In North Carolina, its abundance was negatively correlated with temperature, suggesting that it may be vulnerable to climate change there (Lumpkin and Pearson 2012).

Status

The Chestnut-sided Warbler is one of the species that benefitted most from deforestation by European settlers. In the mid-19th century, it was extremely rare and Audubon saw it on only 1 occasion, although he saw 5 at the same time. Its highly specialized requirements for early successional habitat probably confined it mostly to shrubby riparian areas, successional growth

around beaver ponds, areas cleared or burned for agricultural purposes by First Nations, and areas regenerating after forest fires. By 1900-20, it had become one of the most common species in areas disturbed by settlers (Bent 1953; Byers et al. 2020; Chapman 1907; Lemieux and Choinière in Gauthier and Aubry 1996; Morse 1989).

McIlwraith (1894) considered the Chestnut-sided Warbler a common breeder in the Hamilton area but Fleming (1907) considered it a rare summer resident that probably bred in the Toronto area. In 1859 in the Kingston area, it was a rare spring migrant. Its status began to change there around the end of the 19th century and the first nest was found in 1896. It became common and remained so in the late 20th and early 21st centuries (Weir 2008). Its status followed a different path in Elgin County where it was a common breeder in 1891, rare breeder in 1954, and an uncommon and local breeder in 2000 (Lancaster et al. 2004). Baillie and Harrington (1937) considered it a common summer resident north to latitude 55°N on the Ontario-Manitoba border east to northern Algoma District and Lake Abitibi. The first atlas refined the breeding range of the Chestnut-sided Warbler. The northern extent of its range in the west was approximately latitude 51°N eastward to the Moosonee area, with 1 extralimital record from the Fawn River in the northern portion of the Hudson Bay Lowland. It was most common in the Shield portion of the Great Lakes–St. Lawrence Forest Region. Its distribution south of the Shield was somewhat spotty from east of Toronto and Lake Simcoe through the extreme southwest. There were few records from Essex County or Niagara Region (Martin in Cadman et al. 1987). James (1991) considered the Chestnut-sided Warbler a common summer resident in the Canadian Shield north to Kenora and Kapuskasing; occasional and rare north to Ney Lake and Moosonee; and rare to absent in southern agricultural areas.

The second atlas indicated that only minor changes in the breeding distribution of the Chestnut-sided Warbler had occurred since the first atlas. It was observed in scattered locations further north in the Hudson Bay Lowland and even the Tundra Region. Nonetheless, it is likely absent or very thinly distributed in these ecoregions due to the scarcity of preferred habitat. It was observed in almost every square in the Shield portion of the Great Lakes–St. Lawrence Forest Region. Considerable infilling occurred in its range south of the Shield, including in Essex County and Niagara Region, but losses were experienced in Lambton County. Its probability of observation was unchanged province-wide, although the trend was positive. Significant increases occurred in the Hudson Bay Lowland and the Great Lakes–St. Lawrence Forest Region south of the Shield. Trends in all other areas were positive but nonsignificant. It was most abundant in the Shield portion of the Great Lakes–St. Lawrence Forest Region. Moderate density occurred in the southern portion of the Boreal Forest Region with low density further north and south of the Shield (McLaren in Cadman et al. 2007). Numbers declined in Algonquin Park due to a greater prevalence of more mature forest than previously (Tozer 2012).

Byers et al. (2020) stated that the Chestnut-sided Warbler had been declining slowly since the 1960s, but that the population still remained healthy and that management did not appear to be warranted. Breeding Bird Survey data indicate that it decreased at annual rates of 0.57% in Canada and 1.36% in Ontario 1970-2021 and increased at annual rates of 0.996% in Canada and 0.584% in Ontario 2011-21. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

At 1 Ontario nest, brood division occurred once the young left the nest. Fledglings remain in dense shrubbery after leaving the nest. In Ontario, a fledgling accompanied by a female was last seen 91 m from the nest 28 days after fledging. One fledgling was observed begging for food 28 days after leaving the nest suggesting that young may be still partially dependent upon the adults 4 weeks after fledging. Young males may form small groups that wander widely during the period between independence and autumn migration (Byers et al. 2020; Lawrence 1948; Pitts 1990; Siebenheller and Siebenheller 1990).

During the postfledging period, the Chestnut-sided Warbler may be very common in young clear-cuts and is occasionally the most abundant early successional species in this habitat. Family groups may occur in other shrubby habitats such as power line rights-of-way. It seldom uses forested habitats during this period. In Pennsylvania, 126 adults and 78 juveniles were captured in clear-cuts compared with 1 adult and 0 juvenile in adjacent mature forest. Forests had greater canopy closure but there was no difference in shrub density in clear-cuts and forests. Shrub composition varied with raspberry canes and cherry saplings predominating in clear-cuts and beech and red maple saplings predominating in forests. In Michigan forested habitat, capture rates per 100 net-hours were 0.3 in upland habitat and 3.3 in riparian habitat. Upland habitat consisted of 100-year-old trembling and large-toothed aspens. Riparian areas had a mixture of alder, honeysuckle, and trembling aspen; 73% of juveniles were captured in riparian habitat. In this study area, it selected habitats with higher shrub coverage (Akresh et al. 2009; Major and Desrochers 2012; Marshall et al. 2003; McDermott and Wood 2010; Stoleson 2013; Streby et al. 2011b; Vitz and Rodewald 2006; Yahner et al. 2002).

In 4-7-year-old clear-cuts in West Virginia, adult Chestnut-sided Warbler abundance was positively associated with total arthropod biomass, BA, and understorey stem density and negatively correlated with caterpillar biomass and vertical vegetation complexity. Adults had higher capture rates at nets with more understorey stems which could serve as protective areas (McDermott and Wood 2010).

MIGRATION

The Chestnut-sided Warbler is a nocturnal migrant but some dispersal from the landing site may occur after dawn. During migration, it may join flocks and forage with other species, particularly the Black-capped Chickadee (Byers et al. 2020). One bird banded at Long Point was recovered in Cuba in autumn (Brewer et al. 2018).

In spring, after-second-year birds arrive before second-year birds, and males arrive before females. At Long Point, the mean capture dates for males were 16.0 May for after-second-year birds, 20.1 May for second-year birds, and 16.4 for males of undetermined age. Mean capture dates for females were 20.4 May for after-second-year birds, 22.8 May for second-year birds, and 20.7 May for females of undetermined age (Stewart et al. 2002). At Prince Edward Point, the mean date of arrival of males was 5.1 days earlier than for females: 20.3 May for males and 25.4 May for females. The average date of arrival was 10 May (peak 19-31 May; Francis and Cooke 1986; Keast 1980). In New York, males arrived 8 days earlier than females; males were 7 days earlier than females in Massachusetts (Kendeigh 1945; Kroodsma et al. 1989).

In southern Ontario, average arrival is in early May and migrants are common throughout May. Migrants may arrive in mid- to late April and remain into early June (Black and Roy 2010; Curry 2010; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Weir 2008). Average arrival in the southern Shield is mid-May with the earliest records at the beginning of May (Mills 1981; Tozer 2012).

In the southern Shield, flocks of autumn migrant warblers contain good numbers of Chestnut-sided Warblers from mid-July through early September, and most are gone by the end of September (Mills 1981; Tozer 2012). In the Kingston area, approximately 30% have passed through by 31 August and 75% are gone by 15 September (Weir 2008). In the south, average arrival is mid-August and average departure is late September or early October. Migrants may be present from late July to early November (Black and Roy 2010; Curry 2006; Keast 1980; LaForest 1993; Lancaster et al. 2004).

During migration, the Chestnut-sided Warbler may be associated with shrubby and treed vegetation of almost any type. It may occur in areas seldom used for breeding, such as forest interior or pine woods, but these habitats are still used much less than typical breeding habitat (Byers et al. 2020; Campbell et al. 2001; Chapman 1907; Graber et al. 1983). During spring migration in Pennsylvania, it was significantly more abundant in shrubby areas than forests. Detections per 100 m of transect were 0.190 in shrubs and 0.007 in forests. Captures per 1,000 net-hours were 8.6 in shrubs and 0.6 in forests; 131 were captured in shrubs compared with 6 in forests (Smith and Hatch 2008). In Ohio during spring migration, it was more abundant in mature upland forests than mature riparian forests. The 2 forest types differed significantly for 2 vegetation parameters. Upland forests had less canopy cover (74% compared with 83%) and more shrub coverage (39% compared with 19%; Rodewald and Matthews 2005). In Pennsylvania, it occurred in all habitat types studied during autumn migration. It was significantly more abundant in forest edge and shrub-sapling-stage forest than in pole-stage forest. In 1 of 2 years, it was also significantly more abundant in these habitats than in forest interior. Intermediate usage was made of suburban forests and forest-agricultural edges (Rodewald and Brittingham 2002, 2005).

At Prince Edward Point during autumn migration, the Chestnut-sided Warbler foraged at heights of 1.5-12 m, but mostly at 5-10 m. Sixty-seven percent of foraging occurred on outer leaves, 6% on twigs and inner leaves, 6% on outer branches, 17% on sapling foliage, 3% on sapling branches, and 3% in low shrubs. No foraging occurred in the air, on inner branches, trunks, or the ground (Keast 1980). Graber et al. (1983) noted that it often foraged within 3 m of the ground during migration. During adverse weather conditions, the Chestnut-sided Warbler may alter its foraging techniques and consume atypical food items. During a spring grounding at Point Pelee during inclement weather, aerial foraging was the predominant foraging technique. Foraging on other substrates consisted of 20% on branches, 20% on sapling trunks, 10% on low shrubs, 10% on the ground in thickets, and 40% on bare ground. No foraging occurred on outer foliage or bare twigs or in marsh habitat. The proportion of foraging done at different heights was 50% on the ground, 10% 0.6-1.8 m from the ground, 10% at 3 m, 10% at 5 m, 10% at 7 m, 10% at 10 m, and 0% at 13 m and 17 m or higher (Keast 1980). Five birds collected by Audubon during a light snow in May had eaten nothing but grass seeds and spiders (Byers et al. 2020). During inclement weather during autumn migration in Ohio, 2 juveniles investigated yews and honeysuckles, but were not observed eating any berries (Tramer and Tramer 1977). During autumn migration, Lebbin et al. (2007) suspected that

it was foraging at night in trees illuminated by lights from a stadium, but could not positively confirm this behaviour.

The Chestnut-sided Warbler occasionally collides with tall structures during migration. A total of 349 were killed at the Lennox generating station chimneys. Of 2,552 birds killed in a single autumn night in Georgia, 320 (12.5%) were Chestnut-sided Warblers. Kills have also occurred in mid-May at television towers in Illinois (Byers et al. 2020; Graber et al. 1983; Weir 2008).

James (1991) considered the Chestnut-sided Warbler a common migrant in Ontario. At Long Point, the numbers banded decreased at a rate of 0.8% per year 1961-88. Trends by periods were all nonsignificant: 1961-70, –6.3%; 1970-79, +5.1%; and 1979-88, +3.0% (Hussell et al. 1992).

Blackpoll Warbler

Setophaga striata

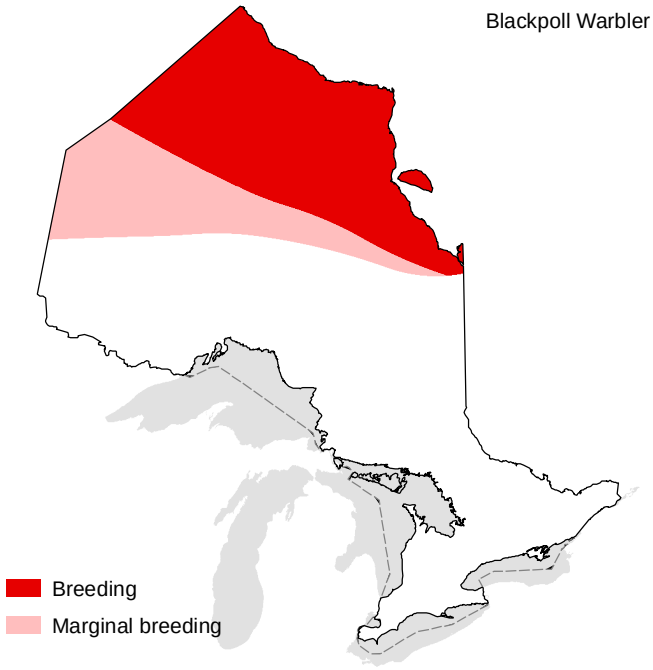
BREEDING SEASON

Habitat Requirements

Blackpoll Warbler nests in Ontario were in wet spruce-tamarack muskeg; a cutover spruce stand on mossy ground with growths of willow, poplar, and Labrador tea; and a willow-poplar stand on a high river bank. All nests were found in the 3 northernmost ecoregions in the province: the Tundra Region, the Hudson Bay Lowland, and the most northerly portion of the Boreal Forest Region (Peck and James 1987).

Little has been written about the Blackpoll Warbler's habitat preferences in Ontario and most data were collected in the Boreal Forest Region. Sutherland (in Cadman et al. 2007) identified its preferred nesting habitat as open spruce-lichen woodlands in wet spruce-tamarack taiga and burns. These habitats are dominated by black spruce with a variable low understorey of spruce saplings, alder, willow, birch, and Labrador tea. It also occurs in isolated groves of stunted spruce in open tundra, around small lakes and ponds, and along drainage courses in tundra. Less commonly, it occupies willow-aspen riparian woodlands. From Pickle Lake northward to the Manitoba border, it was most common in coniferous scrub followed by deciduous scrub, mixed scrub, coniferous forests

with an understorey, heath and tundra habitats, coniferous forests without an understorey, and mixed forests. It was absent in deciduous forests (McLaren and McLaren 1981). Near Hearst at the extreme southern limits of its range, it occurred in unharvested upland mixed forest dominated by white spruce. The site was moderately wet and slightly above average on the nutrient richness scale (Welsh and Fillman 1980; Welsh and Lougheed 1996).



The Blackpoll Warbler nests in 4 general habitats throughout its range. It has the most northern breeding range of the North American warblers. North of the treeline, it nests in deciduous shrub thickets dominated by alders or willows. These habitats are often at margins of wetlands, ponds, lakes, and watercourses. Usage of these habitats is widespread in Alaska, the Yukon, the Northwest Territories, Manitoba, and Quebec (DeLuca et al. 2020; Jehl 2004; Nadeau in Gauthier and Aubry 1996; Porsild 1943; Sinclair et al. 2003). It has not been documented breeding in willow or alder thickets in Ontario's Tundra Region (Sutherland in Cadman et al. 2007), although it has nested among willows and aspens in the Hudson Bay Lowland (Schueler et al. 1974).

Most of the Blackpoll Warbler population breeds in the northern portion of the Boreal Forest Region, from Alaska and the Yukon eastward to Newfoundland and Labrador. It is associated with spruce forests in this region and is most abundant in the taiga interface between the denser spruce forests to the south and the northern tundra. It prefers areas of young or stunted spruce and semiopen stands. It may nest in regenerating clear-cuts and where the canopy has been opened due to wind damage or spruce beetles. In most cases, it is associated with moist, nutrient-poor sites. Typical sites consist of open spruce woodlands, often with beard lichen growing on the trees, and a ground cover of sphagnum moss. It may occur in scattered locations far south of its normal breeding range. In these cases, it is confined to black spruce bogs and spruce swamps at high elevations. It is rare to uncommon in white cedar and tamarack stands (Dawson 1979; DeLuca et al. 2020; Erskine 1977; Gross in Bent 1953; Imbeau et al. 1999; Jehl 2004; Jehl and Smith 1970; Kirk et al. 1996; Matsuoka et al. 2001; Nadeau in Gauthier and Aubry 1996; Walley 1989a).

The third habitat type used by the Blackpoll Warbler is subalpine spruce forests. These high-elevation habitats allow it to nest south of the Boreal Forest Region in southern Alberta, southern Quebec, New York, New Hampshire, and Maine. Although it is found predominantly in spruce habitats in subalpine areas, it may also inhabit balsam fir stands. It may occur in mixed forests that include yellow and white birch and pin cherry. It inhabits forests that are 3-12 m in height with 60% canopy closure or less. It increases with elevation and is usually the dominant species in the upper

treed levels among dwarf spruce. In a high-elevation, 10-year-old clear-cut in New Hampshire occupied by the Blackpoll Warbler, the dominant trees were white birch, pin cherry, red maple, mountain maple, and balsam fir. Most trees were less than 7 cm diameter at breast height (DBH) and less than 4 m tall. Densities of stems per 10 m^2 were 5.8 for those 3 cm DBH and larger and 23.6 for those smaller than 3 cm (Campbell et al. 2001; DeLuca et al. 2020; Morse 1979; Nadeau in Gauthier and Aubry 1996; Sabo 1980).

The fourth habitat used by the Blackpoll Warbler consists of coniferous and mixed forests along the Pacific and Atlantic coasts. These forests may have a mix of spruce species and balsam fir as the dominant species. On an island in New Brunswick, tree-species composition in territories averaged 62.9% balsam fir, 28.3% red spruce, and 8.8% white spruce. It occurred in 2 distinct habitats based on the density per 100 m^2 of trees taller than 2 m and with a minimum DBH of 8 cm: areas dominated by white spruce with a modal density of 11-20 large trees; and areas dominated by balsam fir and red spruce with a modal density of 51-60 large trees. In British Columbia, it breeds at edges of spruce forests, often near water where deciduous shrubs such as willow are abundant. It also nests in forests dominated by fir (Campbell et al. 2001; DeLuca et al. 2020; Eliason 1986).

Near Quebec City, abundance of the Blackpoll Warbler was positively correlated with the amount of forest cover, edge, and core area combined within the landscape. Although it was associated with these landscape measures combined it did not appear to respond to these parameters individually (Drolet et al. 1999). Three landscape-type studies were completed in Newfoundland. Whitaker et al. (2008) captured 52% of birds in clear-cut landscapes and 48% in natural landscapes. In natural landscapes, forest openings consisted of peatlands and water bodies. Clear-cuts were the dominant openings in the modified landscape, which also contained natural openings. These authors were unable to identify a suitable habitat model for the Blackpoll Warbler. Taylor and Krawchuk (2006) observed no difference in its abundance in cut or uncut landscapes, with the landscape scale defined as a radius of 1,250 m around a territory. Its overall rate of occurrence was 50%: 49% in cut landscapes and 51% in uncut landscapes. At the neighbourhood scale of 150 m and the local scale of 12.5 m, it was associated with the amount of forest cover. Despite the almost equal occurrence rates in the 2 landscape types, more individuals were detected in natural landscapes. This suggested that it is less able to use regenerating clear-cuts despite its preference for partially forested landscapes. Competition with other early successional forest specialists would potentially contribute to this response. In natural landscapes, its probability of occurrence was 80% with 10-60% forest cover, 60% at 80% forest cover, and 30% at 100% forest cover. In cut landscapes, its probability of occurrence was 50% at 10% forest cover and 60% at 50% forest cover, declining to 20% at 100% forest cover. Leonard et al. (2008) completed a similar study in Newfoundland and obtained different results. They used the same landscape scale but their neighbourhood scale was 115 m. They captured fewer Blackpoll Warblers in naturally patchy neighbourhoods than in harvested neighbourhoods. The number of birds detected at the neighbourhood scale was 10 when 0% of the land was harvested, 0 when 10-90% of the area was harvested, and 17 when 100% was harvested. At the landscape scale, 0 were seen when 0% of the land was harvested, 3 when 10% was harvested, 2 when 20% or 30% was harvested, 8 when 40% was harvested, 4 when 50% was harvested, 5 when 60% was harvested, 1 when 70% was harvested, 2 when 80% was harvested, and 0 when 90-100% was harvested. Of 17 pairs that settled in

neighbourhoods where gaps in forests were created only by harvesting, only 2 occupied territories that were completely harvested. The remainder settled where all woodland gaps in the neighbourhood were created by harvesting, but where some woodland cover was available. Most Blackpoll Warblers occupied territories in harvested landscapes. Nesting also occurred in 5-6-year-old regenerating clear-cuts, and these birds were successful in fledging young. The authors concluded that clear-cuts created habitat for the Blackpoll Warbler, possibly by providing a richer food resource and an abundance of potential extra-pair mates in a more densely populated landscape.

Ralston et al. (2019) surveyed for the Blackpoll Warbler in 20 plots in boreal forest habitat in New York, Vermont, Maine, Nova Scotia, and Newfoundland. It occurred at 15 of the sites, but was restricted to colder sites at higher elevations or latitudes. This suggested that it might be adversely affected by warming due to climate change.

In the western portion of its range, the Blackpoll Warbler is predominantly a forest edge species. It nests in deciduous shrubs and scattered deciduous trees at edges of spruce forests. Suitable edge habitat is provided by river valleys, lakeshores, beaver ponds, avalanche tracks, sloughs, slow-moving streams, and patches of black spruce muskeg, a particularly favoured breeding habitat. In Alaskan spruce forests, it occurred only where heavy mortality of white spruce had occurred. This opened the canopy and promoted growth of alder and crowberry in the understorey. In Newfoundland, it was equally abundant in riparian stands, forest interior, and forest edges bordering on clear-cuts or non-forested openings. In the east, presence of deciduous shrubs is less important and young conifers are more important for nesting. It is less reliant on forest edge in the east, but prefers stands with a semiopen canopy. In Newfoundland, it nests in scrub and edge habitat as well as wooded and open areas (Campbell et al. 2001; Dalley et al. 2009; Matsuoka et al. 2001; Sinclair et al. 2003; Thompson et al. 1999; Whitaker and Montevecchi 1997, 1999).

Several studies examined microhabitat preferences of the Blackpoll Warbler. In deciduous shrub habitat in Alaska, the average height of shrubs in occupied plots was 2.6 m with 69% of occurrence in shrubs 1.3-2.8 m tall. It preferred nest sites with dense coverage below 1 m (DeLuca et al. 2020). Near Quebec City, it occurred only in sapling-stage and young forests and was not detected in forests 120 and 200 years old (Imbeau et al. 1999). In Vermont, nest sites had significantly more red spruce and leaf litter within 5 m and less green ground cover than unused random sites (DeLuca et al. 2020). In subalpine areas of New Hampshire, territories contained no surface water, mean canopy height was 6.4 m, canopy coverage averaged 57%, there was 69% coniferous foliage volume, 39% coniferous foliage volume 0-2 m from the ground, 25% deciduous foliage volume above 5 m, and live trees had an average DBH of 9 cm. It occupied mid- and upper slopes. In Maine, it was in a guild of forest and edge species occupying habitats with a high percentage of ground cover (70%) and moderate canopy cover. The Blackpoll Warbler was associated with high percent conifer cover (the highest of all warblers) and large trees (Collins 1983a). In Newfoundland, there was more coarse woody debris, more stems 1-2 m tall and taller than 2 m, and less high ground cover within 1 m of the nest compared with unused sites. Nest sites had more stems 1-2 m tall within 5 m than unused sites. Nest sites averaged 11% coverage by high vegetation compared with 13% for random sites, 0.5 stems 1-2 m tall within 1 m compared with 0 at random sites, 0 stems taller than 2 m at the nest

compared with 9 at random sites, and 5 stems 1-2 m tall at the nest site compared with 3 at random sites. Canopy cover was not an important variable differentiating nest sites from random sites. Variables within 1 m were more important than those within 5 m, and these were indicative of habitat that is both open (more coarse woody debris and less vegetation taller than 10 cm) and forested, with more stems 1-2 m and taller than 2 m. Structural objects, such as small and large downed wood and coarse woody debris, were more common at nest sites than random sites. Tall vegetation was denser at random than nest sites. Tall vegetation was found within the territory and was characteristic of the nest site at a larger scale but was not specifically selected for at the nest microsite (Dalley et al. 2008).

Four of the 5 nests reported in Ontario were on the ground at the base of willows, tamarack, and black spruce in lichens. The other nest was 15 cm from the ground in a 60-cm-tall spruce (Peck and James 1987).

Most nests reported elsewhere were in shrubs, saplings, or trees with lesser numbers on the ground. Nests have been reported 0-10.1 m from the ground, but most are 1 m or less from the ground. Mean nest heights included 0.4 m in Newfoundland (96.9% 1 m or less from the ground), 0.5 m in New Hampshire (range 0.3-0.8 m), 62% below 0.6 m and 42% below 0.3 m in Alaska, 3-3.5 m in British Columbia, 1.5 m on Grand Manon Island (range 0.3-3 m), 1.2 m in the Magdalen Islands, and 0.6-2.1 m on Kent Island in New Brunswick. In New Brunswick, second nests were higher than first nests, averaging 3.4 m from the ground (range 1.3-5.3 m) compared with an average of 2.5 m (range 0.6-5.3 m). Ground nests are frequently at the base of a tree and one was in a clump of grasses underneath a small fallen spruce. In the west, both deciduous and coniferous species are used for nesting, with alder, willow, and spruce favoured. Conifers are highly selected for nesting in the east. In Newfoundland, 43.6% of nests were in balsam fir, 30.8% in black spruce, 10.3% in moss, 5.1% in bare areas, 5.1% in snags, and 5.1% in unspecified locations. In New Brunswick, 32% of nests were in white spruce but it comprised only 9% of the available trees; 28% were in red spruce, and 40% were in balsam fir. In Vermont, 85% of 213 nests were in balsam fir and 15% were in red spruce. In New Hampshire, 86% of 50 nests were in balsam fir, 10% were in dead trees (predominantly balsam fir), and 4% were in red spruce. All nests on Kent Island were in white spruce as were nests on Grand Manan Island. Most nests are against the tree trunk but they are occasionally on a horizontal limb distant from the trunk, sandwiched between 2 trunks, or supported by live or dead branches away from the trunk. In New Brunswick, 50% of nests were oriented south to west relative to the trunk, but only 7.5% were oriented west to north. Southwest-facing nests offered maximum protection from occasional intense storms from the southeast and south-facing nests received maximum sunlight which may be important in damp, cool climates. Nests are not reused and a new nest is built for replacement or second clutches (Campbell et al. 2001; Chapman 1907; Dalley et al. 2008; DeLuca et al. 2020; Gross in Bent 1953; Harrison 1984; Porsild 1943; Sinclair et al. 2003).

The Blackpoll Warbler is territorial, but makes frequent forays off the territory. The maximum distance travelled from the centre of a territory in Newfoundland was 1,250 m. Despite the long-distance movements off territories, no evidence of polyterritoriality has been documented. In subalpine areas in New Hampshire, mean territory size was 1.5 ha. It preferred high-elevation communities and territory size decreased with elevation and density increased. Larger territories at

lower levels were not a result of decreased food abundance or increased competition, supporting the hypothesis that it is more adapted bioenergetically to cold, wet climate than other warbler species. Another New Hampshire study reported an average territory size of 0.89 ha (range 0.41-1.26 ha). In New Brunswick, territory sizes were 0.2-1.85 ha. In Newfoundland, territory sizes of males averaged 0.8 ha at the 50% isopleth (range 0.1-2.7 ha). At the 70% isopleth, the average was 1.5 ha (range 0.3-4.4 ha), and at the 90% isopleth, the average was 2.0 ha (range 0.5-7.9 ha). Home ranges averaged 1.3 ha at the 50% isopleth (range 0.3-8.1 ha). At the 70% isopleth, the average was 2.2 ha (range 0.6-15.7 ha), and at the 90% isopleth, the average was 4.3 ha (range 1.2-33.2 ha). Territory size was not affected by the amount of habitat that had been clear-cut, but home range size increased with the proportion of natural area at neighbourhood (115 m) and landscape (1,250 m) scales. Home range sizes were more variable in harvested than unharvested areas. Birds in landscapes that were naturally heterogeneous had increased space requirements, possibly because they were limited to foraging in trees and scrub along shorelines or edges of peatlands (Dalley et al. 2009; DeLuca et al. 2020; Leonard et al. 2008).

The rate of natal philopatry has been determined at only 2 locations, and in both cases sample sizes were small. In New Hampshire, 1 of 12 nestlings (8.3%) returned to breed and 14 of 20 (70.0%) returned in New Brunswick. The latter site was an island, and this may have influenced the extremely high return rate (DeLuca et al. 2020).

Variable return rates have been reported for adults, and the proportion of adults returning to a given area may vary considerably annually. In New Brunswick, 27-75% of adult males returned (average 48%), and 33-58% of females returned (average 49%). In 1 year, all 12 returning males defended a territory that included part of the previous year's territory; 11 of 12 females settled on a territory that included portions of their former territory. These data were collected on an 80-ha island where almost no predation occurred. In New Hampshire, 40-70% of adult males returned. Only 1 of 16 returning males moved the location of his territory. Reproductive success the previous year did not influence site fidelity. Another New Hampshire study reported return rates of 47-61% for adult males. They returned to within 200 m of their previous territories but the new territories did not necessarily overlap with the old ones. Lower return rates occurred in Newfoundland: 28.4% of males and 26.2% of females. One banded as an adult in a clear-cut was recaptured on territory in a natural forest opening 820 m distant the following year. The return rates were too low to be explained by mortality alone and suggested that there were landscape-scale movements of adults that may have included breeding dispersal, transience, and extra-territorial forays. The results are consistent with other observations that most boreal songbirds use home ranges far larger than their defended territories and that individuals may respond to landscape-scale habitat. There was no difference in return rates in natural and harvested landscapes. Site fidelity may be lower in the Boreal Forest Region due to regular large-scale disturbances and the shifting mosaic of stands (DeLuca et al. 2020; Eliason 1986; Whitaker et al. 2008).

Limiting Factors

Peck and James (1987) concluded that eggs were most likely to be present in Ontario nests in the last half of June and first week of July. Several days may elapse between nest-site selection and the initiation of nest building. In New Brunswick, 1-3 weeks elapsed between when the female was first

seen on the territory and when the first egg was laid. Nests take 3-4 days to build. One female started building a new nest 2 days after the first clutch was lost and the first replacement egg was laid 6 days after the loss. The first egg is laid 8-10 days after the initiation of nest building for first nests, but as soon as 4 days for later and second nests. When second broods are raised, there is an average of 9.1 days between fledging of the first brood and initiation of the second clutch (range 3-13 days). Eggs are laid at the rate of 1 a day. The incubation period is 11-12 days. The hatching period suggests that incubation begins before the clutch is complete. Hatching usually occurs over a 24-hour period but may occasionally take 2 days. Young fledge when they are 8-10 days old, mostly at age 9-10 days (Dalley et al. 2008; DeLuca et al. 2020; Gross in Bent 1953).

On Kent Island, 13 of 19 females (68.4%) raised 2 broods. Those that raised second broods initiated egg laying an average of 5.1 days earlier than those that raised a single brood. No female that initiated her clutch more than 10 days after the first egg of the season was laid had a second brood. Two females that switched mates after the first brood and mated with a previously unmated male had second broods. The previously unmated males were not present when the females initiated their first broods. The second broods on Kent Island appear to be unique, possibly because of extremely low rates of predation that allowed most birds to complete their first brood early enough to start a second brood. Of more than 300 pairs observed in Vermont and New Hampshire, none attempted a second brood. This may have been due to low success rates of initial nests compared with Kent Island. At more northern latitudes, it is unlikely that the Blackpoll Warbler has time to raise 2 broods due to the shortness of the season. If the first clutch is lost, a replacement clutch may be laid. Of 4 Ontario nests, 3 contained 4 eggs and 1 contained 5 eggs. Clutches of 2-5 eggs have been reported throughout its range with 3-5 eggs typical and 4 eggs most frequent. The mean clutch size in Newfoundland was 3.85 eggs and 67% of clutches had 4 eggs. On Kent Island, clutch size was 3-5 eggs with 5-egg clutches most frequent. The average clutch size for first clutches was 4.8 eggs (range 3-5 eggs) and second clutches averaged 3.4 eggs (range 3-4 eggs). Females older than 2 years laid significantly more eggs in a season (average 7.9, range 4-9) than yearlings (average 5.8, range 3-8). Mean clutch size in Vermont was 4.1 eggs and clutches averaged 4.0 eggs in New Hampshire with a range of 2-5 eggs at both sites (Chapman 1907; Dalley et al. 2009; DeLuca et al. 2020; Eliason 1986; Gross in Bent 1953; Peck and James 1987).

Both sexes are capable of breeding in their first year, but some yearling males may not breed. In New Brunswick, 4 of 12 yearling males (33.3%) bred but some additional ones may have bred outside the study area. Usually all females are mated regardless of their age and almost all birds 2 years old or older nest every year. Nonetheless, some after-second-year males may not obtain a mate. In Newfoundland, 1 study determined that 47.9-50.2% of captured birds were unmarked transients. The researchers concluded that these were most likely birds making forays from nearby territories rather than nonterritorial floaters. A radiotelemetry study in the same area determined that only 1 of 35 males (2.9%) was a nonterritorial floater but all birds made regular extra-territorial forays as far as 1 km from their territory centre. The Blackpoll Warbler is typically monogamous but polygyny was observed on Kent Island. At this site, bigamy occurred every year at rates of 8-40% of males. Bigamy occurred in first broods only and all second broods were by monogamous pairs. Polygyny was attributed to the high site fidelity of returning birds. Females tended to breed near their former territories; 91.7% of returning females nested in a territory that included a portion of the previous

year's territory. In 1 year, 6 females returned to an area where they had nested the previous year. Only 3 males returned and this resulted in 3 bigamous matings. In 1 case, a female returned to her territory but her previous mate was already mated with a yearling female. The older female also mated with the male and initiated her nest earlier than the yearling, thus becoming the primary female. In most cases, bigamy occurred when no unmated males were available near former nest sites of females. Territories of bigamous males supported significantly more large coniferous trees than those of monogamous or unmated males. This population was unusual in that it was confined to an island where adult return rates were exceptionally high. Polygyny rates are likely to be much lower in other areas, although this requires further study. Pair bonds of monogamous birds are maintained throughout the breeding season even when a second brood is initiated. On Kent Island, females that mated with a polygynous male for the first brood mated with a previously unmated male to raise their second brood. Several pairs reunited in subsequent years but this is less likely to occur in other portions of its range where adult return rates are much lower. Extra-pair copulations have not been observed and no studies have been undertaken on paternity of nestlings. Both mated and unmated birds enter territories of other males and approach the females, suggesting that extra-pair copulations are part of the mating system (DeLuca et al. 2020; Eliason 1986; Leonard et al. 2008; Whitaker et al. 2008).

On Kent Island, 90% of foraging observations of the Blackpoll Warbler were in conifers where it fed in the midcanopy in trees as tall as 10 m, often probing in closed buds at the tips of branches. It rarely used conifers shorter than 2 m and less than 8 cm DBH for foraging. In Newfoundland, it frequently foraged on regenerating balsam fir in remnant patches of timber within clear-cuts (DeLuca et al. 2020; Leonard et al. 2008). Morse (1979) characterized its foraging techniques in subalpine areas of New Hampshire. It foraged at medium heights in conifers, using the inner parts of limbs most frequently. It foraged at heights of 3-15 m, but mostly at 6-9 m, which did not differ significantly from the profile of the forest. Forty-four percent of foraging occurred on inner limbs, 24% on outer limbs, 18% on dead branches, 9% on deciduous species, 2% at tips of branches, and 1% each on the ground and trunks. In white birch, it exhibited a stronger tendency to forage on small outer parts of limbs than it did in firs. In white birch, 61% of foraging was on outer parts of limbs, 32% on inner parts of limbs, 4% on the tips of foliage, and 3% on dead limbs. Almost all foraging was by gleaning although a few prey attacks were by hawking and hovering. Sabo (1980) conducted similar studies in the same general area. Above elevation 1,200 m, average canopy height was 7.6 m compared with 13.1 m below 900 m. Average foraging heights at these elevations were 3.3 and 5.6 m, respectively. This is consistent with other observations that the Blackpoll Warbler forages at midheight of trees. The percent conifer volume declined from 95% to 64% going down the mountain and its usage of conifers declined from 69% to 35% accordingly. Foraging techniques were 44.6% leaf gleaning, 30.0% twig gleaning, 10.9% leaf hawking, 8.0% twig hawking and hovering, 4.3% leaf hovering, 0.9% branch gleaning, 0.3% bole pecking, 0.2% bole gleaning, 0.1% litter pecking, and 0% branch pecking, litter gleaning, and fallen log manoeuvres. Foraging occurred at similar rates distant from (56.4%) and near (43.6%) the trunk.

Nestlings are fed caterpillars, spiders, and flies. At first, young are fed small green caterpillars and aphids, but spiders and large adult insects are delivered by the time they are 6 days old. Little information is available about the adult diet during the breeding season. The Blackpoll Warbler is

predominantly insectivorous but presumably eats spiders as well. It has been confirmed eating mosquitoes and balsam woolly adelgids and fed on locusts during an outbreak in New Brunswick. It does not appear to respond to spruce budworm outbreaks, although limited research has been done on this (DeLuca et al. 2020; Eliason 1986; Gross in Bent 1953; Morris et al. 1958; Porsild 1943).

The Blackpoll Warbler is rarely parasitized by the Brown-headed Cowbird, with only 2 cases of parasitism reported in North America. There is limited overlap in the ranges of the 2 species and the cowbird rarely occurs in the habitats preferred by the Blackpoll Warbler. In the southern portion of this warbler's range, 0 of 41 New Brunswick nests, 0 of 50 New Hampshire nests, and 0 of 213 Vermont nests were parasitized. No parasitism has been documented in Ontario or British Columbia (Campbell et al. 2001; DeLuca et al. 2020; Peck and James 1987).

Habitat loss is not a significant factor in Ontario because of the northern range of the Blackpoll Warbler, although mining activities may have localized effects. Clear-cutting temporarily removes habitat, but these areas tend to be recolonized about 10 years after harvesting. In Newfoundland, low levels of forest harvest appeared to have limited influence on nest-site use and nest success. Fledging success was higher in areas with more clear-cut habitat within 20 m of the nest in some years but there was no relationship in other years. Areas that were clear-cut were more productive than unharvested areas and potentially supported a higher biomass of arthropods. Researchers in Newfoundland concluded that moderate levels of clear-cutting did not adversely affect the Blackpoll Warbler and it appeared to be beneficial in certain areas or years. Only 5.9% of this landscape was subjected to clear-cutting, so their results may not be broadly applicable (Dalley et al. 2008, 2009; DeLuca et al. 2020; Leonard et al. 2008; Whitaker et al. 2008).

On Anticosti Island, the Blackpoll Warbler was negatively affected by high deer densities in mature forests. Deer heavily browsed white birch and balsam fir and reduced shrub and sapling coverage (Cardinal et al. 2012). In Ontario, the Blackpoll Warbler nests north of the range of the white-tailed deer. Moose and caribou occur within its Ontario range, but densities of these 2 ungulates are not high enough to alter habitat structure.

Dalley et al. (2008) examined habitat characteristics relative to nest success in Newfoundland. The only consistent parameter that affected nest success was that successful nests had more large downed wood within 5 m of the nest than unsuccessful nests. Successful nests tended to have more open areas created by clear-cuts within 20 m than unsuccessful nests, but this relationship was not significant in every year.

The Blackpoll and Bay-breasted warblers are morphologically very similar and both forage mostly at midheight in the interior portions of conifers. Thus, they may be in direct competition with each other for food resources. Although the ranges of these 2 warblers greatly overlap, they rarely occur in the same locations. In New England, the Blackpoll Warbler is associated with high elevations. The Bay-breasted Warbler is associated with lower levels and spruce budworm outbreaks. The Blackpoll Warbler nests further north into the taiga and tundra than the Bay-breasted Warbler. Adaptations of the Blackpoll Warbler to colder weather include a relatively large body mass and probably a lower critical temperature and heat transfer coefficient. It has insulation with the most thickly developed semiplumes and down plumules among the warblers, a typical adaptation

to cold-climate thermoregulation. Most areas of coexistence of the Blackpoll and Bay-breasted warblers are at sites with abundant budworms (Morse 1979, 1989; Sabo 1980).

Degradation of subalpine spruce–balsam fir forests as a result of acid precipitation may harm populations in southeastern Canada and the northeastern United States, but this is unlikely to be an issue in Ontario. In the northeastern United States, the ecotone between hardwoods and montane spruce–balsam fir forests has shifted approximately 100 m upslope in the past 40 years. The lower levels of montane spruce–balsam fir forests appear to be sinks for the Blackpoll Warbler. It has been estimated that a 1°C increase in average temperature would eliminate more than half of the montane spruce–fir forest and that a 3°C increase would almost eliminate it entirely (DeLuca et al. 2020).

Status

It is likely that the historical range and abundance of the Blackpoll Warbler was similar to present conditions, but early ornithologists were uncertain of its breeding range and status. The first nest for the province was found on 2 July 1940 at Fort Severn on the Hudson Bay coast. Young were also observed near the Shagamu River and Lake Attawapiskat (Baillie 1960). The first atlas established the range of the Blackpoll Warbler as including the entire Tundra Region, most of the Hudson Bay Lowland, the extreme northwest corner of the Boreal Forest Region, and scattered areas south of Moosonee. From North Caribou Lake north to the Manitoba border, it was the most abundant species in spruce scrub (Welsh in Cadman et al. 1987). Welsh and Fillman (1980) reported it in low density near Hearst in the southern Boreal Forest Region. James (1991) considered it a common summer resident in the northern Hudson Bay Lowland south to Big Trout Lake and Moosonee, and rare south to Kesagami Lake. Wilson and McRae (1993) found it most consistently at Shagamu, but did not find it breeding in the tundra at Brant or at Moosonee.

The second atlas indicated a similar breeding range for the Blackpoll Warbler, although it nested further south in the western portion of the Boreal Forest Region than during the first atlas. The southern extent of continuous breeding range appeared to be in the vicinity of latitude 51°N, from Woodland Caribou Provincial Park to Moosonee. Breeding evidence was obtained in the Moosonee area southward 100 km to Kesagami Lake. Its probability of observation increased significantly province-wide and in the Hudson Bay Lowland since the first atlas. It was most abundant in the northeastern Hudson Bay Lowland inland from the coast in an area bounded by the Winisk and Attawapiskat rivers. It was more common in the Hudson Bay Lowland than in the Boreal Forest Region (Sutherland in Cadman et al. 2007).

Breeding Bird Survey (BBS) data for 1966-2009 indicated that the Blackpoll Warbler declined at a nonsignificant rate of 5.8% per year. This suggested that it was experiencing a widespread decline. The BBS data are unreliable for this species. Most routes are at the southern extremity of its range outside its core range. Populations at the periphery of the range are more likely to fluctuate than those in the core. At present, the Blackpoll Warbler is not well covered by any surveys (Anonymous 2009c; DeLuca et al. 2020; Nadeau in Gauthier and Aubry 1996). BBS results indicate that it decreased at annual rates of 3.456% in Canada and 4.0% in Ontario 1970-2021. Trends for 2011-21 were annual decreases of 5.39% in Canada and 2.78% in Ontario. All results were of low reliability except that the long-term trend for Ontario was of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young cannot fly strongly when they leave the nest but are adept at flying 9 days after leaving the nest. They begin to wander off the territory 20-25 days after fledging and are independent 25 days after leaving the nest. Both parents were observed feeding the same fledglings in 3 broods so brood division apparently does not take place (DeLuca et al. 2020).

In the Yukon, fledglings remained in low willows while the adults foraged in spruce, in open spruce with abundant willow and Labrador tea, in small spruce and willow along a creek, and in a trembling aspen stand (Sinclair et al. 2003). In Quebec, Major and Desrochers (2012) netted birds during the postfledging period in 5-12-year-old clear-cuts in balsam fir forest containing some black spruce, white spruce, and white birch. In the first year, they captured 14 Blackpoll Warblers but only 4 the following year.

Mitchell et al. (2010a) radiotracked juveniles in Newfoundland during the postfledging period. At the finest scale, they were associated with dense understorey woody stems and dense foliage above breast height. They were more likely to be observed at locations with coarse woody debris. Juveniles were very sensitive to the amount of clear-cut habitat at both the 115-m and 1,250-m scales. At 115 m, they were positively associated with high amounts of clear-cut land cover. The relationship was curvilinear at the 1,250-m scale. Individuals were positively associated with clear-cuts when 5% or less of the landscape was clear-cut but negatively correlated with clear-cuts above this value. Young appeared to seek dense cover that offered protection from predators and locations with high prey availability. At 16% of sites, birds were observed on the ground or in understorey vegetation. Birds may select locations with higher amounts of coarse woody debris to mitigate potential costs associated with exposure to wind.

Mitchell et al. (2009) studied the effects of clear-cuts on the movement of newly independent fledgling Blackpoll Warblers in boreal forests in Newfoundland. Medium movement rate was 303 m per day (range 4-7,380 m). Movement rate increased and residency time decreased as the proportion of clear-cut land increased, but if there was a high proportion of clear-cut land along the movement path to exit the neighbourhood, connectivity was impaired and movement rate was reduced. Clear-cuts may be low-quality habitat during the postfledging period.

Brown and Taylor (2015) determined that both adult and juvenile Blackpoll Warblers in Atlantic Canada moved distances more than 200 km prior to initiating autumn migration. Birds left Nova Scotia between 20 August and 14 September and departed across the Atlantic Ocean for their long-distance flight between 28 September and 13 October. Adults were detected as far as 484 km from the breeding area and juveniles were detected 200 km from their natal areas. Sixty-six percent of adults and 30% of juveniles moved west across the Gulf of Maine; 66% of adults were detected as far south as Cape Cod but no juveniles were detected that far south. Adults moved longitudinally slightly westward. Juveniles tended to move slightly eastward of their starting location.

MIGRATION

Most migration is nocturnal, but long-distance flights may continue into the daylight hours. At high latitudes, some movement may occur during the day because of the short nights. Autumn premigratory movements in a southward direction have been observed during day in the Churchill area. While making short-distance flights or while foraging during migration, the Blackpoll Warbler

may occur individually, in mixed flocks with other warblers, or in small single-species flocks. During the long-distance autumn flight, it travels in large flocks consisting solely of Blackpoll Warblers. It has the longest migration route of any passerine, breeding further north than any other warblers and wintering further south. Those breeding in the northwest travel about 8,000 km to reach the wintering grounds and none travel less than 4,000 km. It is the only warbler, and possibly the only passerine, to make an extensive transoceanic flight during migration (Badzinski 2002; DeLuca et al. 2020; Gross in Bent 1953; Jehl 2004; McNair and Nisbet 2011; Mitchell et al. 2010a, 2011; Morse 1989; Murray 1989; Nisbet et al. 1995).

The autumn migration route is complicated and has been the subject of considerable debate in the scientific literature. It is now agreed that migrants concentrate along the Atlantic coast from Virginia to Nova Scotia prior to making a transoceanic flight to northern South America. Birds from northwestern Canada and Alaska migrate in a southeastward direction to the Atlantic coast, travelling through southern Ontario and the states just south of the Great Lakes. At Churchill, birds appear to travel southward first prior to turning southeastward. Birds coalesce first into small flocks and then into larger flocks as they stream toward the northeastern deciduous forest. Birds breeding in northwestern Newfoundland initially move southeastward. Debate ensued on whether these birds were moving in a direction that was consistent with the transoceanic flight. It appears as though this is not the case because birds continuing in this direction would have to reorient their flight to the south while en route. Some Newfoundland birds may initially migrate southwest to Nova Scotia, New Brunswick, or New England before undertaking the transoceanic flight. In addition to the transoceanic flight theory, it has been hypothesized that the migration route was through the southeastern United States. It is generally agreed now that this is not the case. The Blackpoll Warbler is abundant in northern North Carolina during autumn migration but rare in South Carolina and areas further south. Sightings of large numbers in Florida coincide with extreme weather conditions whereby birds may have been grounded due to adverse weather. Transoceanic flight has been confirmed by radar and the fact that flocks occasionally appear on ships in the Atlantic Ocean. Birds remain at staging areas along the coast for 2-3 weeks prior to taking the transoceanic flight, building up fat reserves and waiting for a favourable wind. Birds initiate their flight when there are northwestern tail winds following passage of a cold front. The flight across the Atlantic Ocean is nonstop for a distance of about 3,000 km and requires the birds to travel continuously for 88 hours. They travel in large flocks at high altitudes averaging 3,000 m but are as high as 6,500 m at Antigua. The southern flight is predominantly passive, with birds gliding with the prevailing winds (Badzinski 2002; DeLuca et al. 2020; Jehl 2004; McNair and Nisbet 2011; Mitchell et al. 2010a, 2011; Morse 1989; Murray 1989; Nisbet et al. 1995).

Smetzer et al. (2017) and Smetzer and King (2018) used stable isotopes and the Motus Wildlife Tracking System to study the autumn migration of the Blackpoll Warbler in the vicinity of the Gulf of Maine. The range of isotopes indicated that they captured birds from a wide geographic area from the Maritime Provinces and New England to regions further west. The average stopover period was 3.5 days; 63% of birds were females and 74% were juveniles. Stopover flights of less than 50 km were directed mostly northward to inland sites, but 10% of flights were oriented offshore. All these latter flights were nocturnal suggesting that they were abandoned migratory flights. Of 6 migratory flights, 3 were directed offshore, 2 along the coast, and 1 inland. Three birds moved northward to

the Maritime Provinces and were last detected departing south over water from southeastern Nova Scotia. More stopover than migratory flights were made suggesting that it required high energy inputs to complete migratory flights. It appeared to actively select coastal or overwater routes for migratory flights. There may be greater hazards associated with coastal routes such as wind farms and communication towers. The average stopover period was 14.4 days and 59% of warblers made at least 1 stop in the Gulf of Maine that exceeded 7 days. Four birds stayed at the capture site for a mean duration of 12 days and a maximum of 22 days. Eight-three percent of birds stopped at 1 or more sites before continuing migration for a range of 1-25 days (mean 5.3 days) at individual stopover sites. Birds averaged 2.84 stops (range 1-6) and spent an average of 15.1 days on stopover throughout the study area. Those from more southern breeding areas made significantly more stopover bouts and spent significantly more total time in stopover than birds originating from more northern areas. Movement rate averaged only 0.69 km per day, with birds travelling via multiple short flights rather than in single sustained movements. The median distance of sustained flights was 42.73 km. The sample consisted almost entirely of hatch-year birds, but it is unlikely that age was the cause of the prolonged stopovers. They may be an adaptation for accumulating large fat stores to fuel long migratory flights. Brown and Taylor (2017) also used the Motus system and stable isotopes to monitor autumn migration of the Blackpoll Warbler in the Gulf of Maine area. Ninety-one percent of flights were nocturnal and 80% occurred between sunset and midnight. Only 13 of 75 movements (13.3%) were considered migratory with the remainder being local movements. One made a 200-km flight inland within New England. Many made flights that were not toward their migratory goal. The probability of making a properly oriented flight increased later in the season. Those that moved in indirect patterns were last detected at the same latitude or further north than their capture location. Adults tended to make more flights and moved in more tortuous patterns than juveniles. Adults and individuals from more western natal origins were more likely to move southwest over time. Results suggested that flights are not as costly to migratory birds as commonly assumed.

Males arrive before females in spring and adults arrive before yearlings. At Long Point, the mean capture dates for males were 22.8 May for adults, 24.7 May for yearlings, and 24.5 May for birds of undetermined age. For females, mean capture dates were 30.5 May for adults, 28.2 May for yearlings, and 30 May for birds of undetermined age. The Blackpoll Warbler was the only species studied for which female yearlings arrived before adults, but none of the results were significant (Stewart et al. 2002). At Prince Edward Point, the median date of arrival was 11.9 days earlier for males (16.9 May) than for females (28.8 May). Results were not significant due to the small sample size (Francis and Cooke 1986). On Kent Island, adult males arrived 6 days before adult females, who arrived 4 days before yearling males. Females arrived over a longer period with some old females arriving before any young males. Depending upon where early adult males settled, some females returned to areas where there were no unmated males present. This contributed to bigamy but the later arriving males were available to mate with polygynously mated females for their second brood (Eliason 1986). In New Brunswick, 1 male arrived 17 days earlier in his second year than when he was a yearling. In Vermont and New Hampshire, the first females are typically seen 2-3 days after the males arrive (DeLuca et al. 2020).

The Blackpoll Warbler is one of the last warblers to arrive in spring. Average arrival in southern Ontario is mid-May and the peak flight occurs in the last 2 weeks of May. Migrants may be present from early May to mid-June (Black and Roy 2010; Curry 2006; Fleming 1907; Keast 1980; LaForest 1993; Lancaster et al. 2004; Weir 2008). In the southern Shield, migration extends from mid-May to mid-June (Mills 1981; Tozer 2012). Wilson and McRae (1993) reported migrants at Ekwan on 2, 14, 15, and 19 June.

Morris et al. (2016) determined that younger birds moved through western sites in autumn before adults but the reverse was true in the east. Younger birds were in poorer condition and migrated slower due to shorter flights and/or longer stops. Adults and yearlings initiated their autumn migration through Virginia during the same 5-day period (Stewart 1986). In the southern Shield, average arrival is mid-August, average departure is mid-September, and migrants may be present from mid-July to early October (Mills 1981; Tozer 2012). Peak migration in southern Ontario is from mid-August to mid-September, with most gone by mid-October. Migrants may be present from late July to mid-November (Black and Roy 2010; Curry 2006; Fleming 1907; Keast 1980; LaForest 1993; Lancaster et al. 2004; Weir 2008). The midpoint of autumn migration at Long Point is 12 September (Mills 2005a).

During migration, the Blackpoll Warbler uses a much wider variety of habitats than during the breeding season. Where conifers such as spruce and tamarack are available, it may use them preferentially, although it is uncommon in spruce forests in Maine during spring migration. In the Yukon and British Columbia, it is frequently found in deciduous cover. Conifers are scarce or absent in the southern portions of its migration routes. In the Yukon, it is found in shrubby mixed forests adjacent to wetlands and in drier upland sites. Migration habitat in British Columbia includes a variety of forested habitats such as lakeside stands of trembling aspen and willow, riparian stands of cottonwood and willow, and groves of white birch; muskegs, including those dominated by black spruce, dwarf birch, and willow; dense stands of old-growth pine and white spruce; and mixed forests bordering marshes, fields, roadsides, and other openings. In riparian coniferous stands in British Columbia, it was negatively correlated with dense deciduous vegetation along streamsides and was most common in coniferous forests away from streams. In Illinois, forest edges and bottomland forests were the primary habitats it used during spring in the south. In central portions of the state, it occurred in high densities in all woody habitats, but was most abundant in upland forests where oaks predominated. In spring in Maryland, it occurred in large numbers in mature deciduous forests. During spring in North Carolina, the number of observations per hour were 1.31 in wet thickets, 1.13 in oak-hickory forests, 0.47 in floodplain forests, 0.16 in pine forests, and 0.07 in pine-hardwood stands. It was not observed in dry thickets or beech forests. During migration, the Blackpoll Warbler may occur in gardens, backyards, urban parks and shade trees, and orchards (Campbell et al. 2001; Chapman 1907; DeLuca et al. 2020; Graber et al. 1983; Gross in Bent 1953; Morse 1979; Parnell 1969; Sinclair et al. 2003; Wiebe and Martin 1998). Suomala et al. (2010) compared numbers of migrating Blackpoll Warblers during both migration periods on 2 islands in Maine. One was predominantly forest; the other was dominated by shrubs and saplings. There was no significant difference in numbers in spring or autumn over 2 years, but the trend was that it was more abundant on the shrubby island. During spring migration in Ohio, it was significantly more abundant in mature upland forests than in mature riparian forests. Upland forests had significantly

less canopy cover (74% compared with 83%) and more shrub coverage (39% compared with 19%; Rodewald and Matthews 2005). In 2 different years, Rodewald and Brittingham (2002, 2004) examined the habitat preferences of autumn migrants in Pennsylvania. In 1 year, the Blackpoll Warbler was equally abundant in all the habitats they studied. In the other year, it was significantly more abundant in forest-agricultural edges, in suburban forests, in pole-stage forests, and in forest-interior than it was in shrub-sapling stage forests.

Several studies summarized the Blackpoll Warbler's foraging techniques during migration. In Illinois, it searched from tree to tree in the central part of the state where prey was scarce, and from branch to branch in the south where prey was abundant. It foraged throughout the morning and at an increased rate between 1100 and 1200 hours, and also fed in the evening after 1500 hours until 1700 hours. It strongly selected for oaks and honey locust and used most other plants less than their availability. Oaks supported 64-82% of all leafroller moth caterpillars and this may be why they were favoured (Graber and Graber 1983). During spring migration in North Carolina, 27.1% of foraging by the Blackpoll Warbler occurred in the canopy, 68.8% in low trees, 3.3% in shrubs, and 0.8% on the ground. In the canopy, 17.4% of foraging occurred in the top of the crown, 11.5% in the inner crown, 8.2% in the lower crown, and 0% on the bole. In low trees, 8.2% of foraging occurred at the top of the crown, 46.7% in the inner crown, 13.9% in the lower crown, and 0% on the bole. In shrubs, 0.8% of foraging was at the top of the crown, 2.5% in the inner crown, and 0% in the lower crown and in dense thickets, brush piles, and grasses. On the ground, 0.8% of foraging occurred in the open, and 0% in dense thickets, grasses, and at water's edge. Singing birds were seen 1.8 m to more than 17 m from the ground (average 8 m). Nonsinging birds occurred within the same range of heights (average 6 m; Parnell 1969). During migration in Maine, all foraging in deciduous species took place in the canopy. Foraging occurred at heights of 0-24 m but mostly at 6-21 m which was not significantly different from tree height distribution. Seventy percent of foraging occurred on outer limbs, 16% at tips of branches, 12% on inner limbs, 1% on dead limbs, and 0% on the ground and tree trunks. It foraged significantly more at the periphery of trees during migration in Maryland than during the breeding season in New Hampshire. This was probably related to differences in the location of foliage in deciduous and coniferous trees. In Maryland deciduous trees, inner parts of branches consisted of limbs 3 cm or larger that did not support leaves, bark, or lichens that would be likely to provide hiding spaces for insects. In Maryland, almost all foraging was by gleaning, with some prey captured by hovering at vegetation or retrieving fallen food. On islands forested with spruce in Maine, spring migrants made heavy use of the inner parts of limbs (64% of foraging) and only occasional use of the tips of vegetation (4%) and dead limbs (4%). Seventy-nine percent of foraging occurred 6-9 m from the ground, slightly higher than in New Hampshire but that was likely a function of tree size. Migrants in spruce forests in Maine foraged in a similar manner to breeding birds in spruce forests in New Hampshire (Morse 1979). During autumn migration in New York, Lebbin et al. (2007) suspected that Blackpoll Warblers were foraging at night in areas illuminated by stadium lights, but could not confirm this.

More information is available on the Blackpoll Warbler's diet during migration than the breeding season. In spring in Illinois, most available prey consisted of caterpillars, particularly those of the linden looper and leafroller moths. The largest caterpillar eaten by any warbler was a 40-mm geometer moth larva consumed by a Blackpoll Warbler. Overall, the migration diet consists mostly

of larval and adult insects and other arthropods, although it may eat some seeds and fruit in autumn. Small fruits are available near Churchill in July and August but were apparently not eaten. Of 18 fecal samples analyzed in autumn in Rhode Island, 72.2% contained fruit and 100% contained insects. Fruit comprised 41% of identifiable food and included pokeweed, southern arrowwood, chokecherry, and bayberry. One was observed eating a yew berry during autumn migration in Ohio. The diet of 4 autumn migrants in Illinois consisted of 67% cankerworms. Most remaining prey consisted of beetles, especially currant-tip borers, plus 4% ants, 4% gnats, traces of true bugs and mites, and some undetermined seeds. Four killed at a tower near Prince Edward Point in autumn had eaten an average of 20 beetles 5-7 mm long. An autumn flock completely eradicated aphids on some poplar trees. During spring migration in Maryland, it fed on mayflies, pine sawflies, ants, weevils, wasps, and bees. It also eats winged termites, mosquitoes, and scale insects (DeLuca et al. 2020; Graber and Graber 1983; Graber et al. 1983; Gross in Bent 1953; Jehl 2004; Keast 1980; Tramer and Tramer 1977).

Migration is particularly hazardous for the Blackpoll Warbler because of its long-distance transoceanic flight in autumn. If headwinds are encountered during the 88-hour flight, it is unlikely that it can remain aloft long enough to complete the crossing. Forty-four were found dead or dying on a ship 70 km from the Massachusetts mainland, but it is probable that a high proportion of birds that encounter unfavourable winds drop into the ocean and perish. Adults are more at risk of mortality during autumn migration than juveniles. Adults undergo a moult prior to migration but juveniles do not. Adults have the physiological burden of reproduction and of preparing their offspring for migratory flight, which are a cost to the adults and a benefit to the young (Morse 1989; Stewart 1986).

The Blackpoll Warbler occasionally collides with towers, lighthouses, buildings, and other tall structures during migration and such collisions are sometimes a major source of mortality. Fifty-eight were killed at the Lennox generating station chimneys 1972-82. In September 1929, 31 were killed at the Long Point Lighthouse on 7 September, 6 on 9 September, and 199 from 22 to 29 September. At a Wisconsin television tower, it was the eighth most commonly killed migrant in spring and ninth in autumn. Kill rates are typically low on average, but very high kills may occur at lighted structures on evenings when there is abnormally low cloud cover. High winds and adverse weather conditions that cause individuals to deviate from their normal offshore route have caused large kills in Florida where typically few strike tall structures. Single-night mortalities have exceeded 50 in West Virginia and 600 in Florida at individual structures during adverse weather conditions (DeLuca et al. 2020; Graber et al. 1983; Gross in Bent 1953; Roberts and Tamborski 1993; Weir 2008).

Mills (2005a) examined autumn migration periods for the Blackpoll Warbler at Long Point 1975-2000 to determine if climate change had altered its migration timing. It exhibited a significant autumn delaying trend, but only for juvenile birds. Juveniles migrated 1.9 days per decade later during the period that was examined. Smith and Paton (2011) found similar results in Rhode Island. Blackpoll Warblers significantly delayed autumn migration 1960-2007; temperatures increased by 0.03°C per decade over this period. On average, long-distance migrants migrated 3.3 days per decade later. Morris et al. (2016) summarized its autumn migration across the continent 1967-2013.

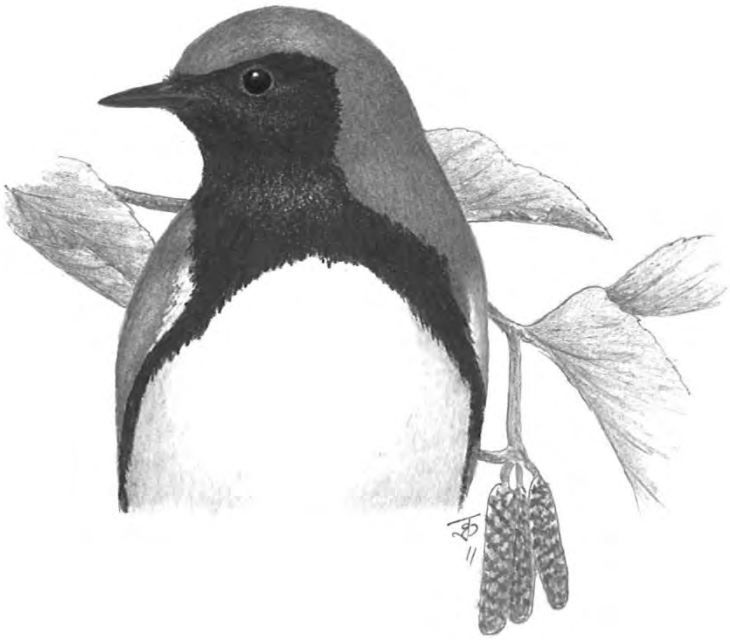
Autumn migration occurred about 1 day later per decade. Spring migration advanced at a rate of 0.5 day per decade continent-wide over a 30-year period (Covino et al. 2020b).

James (1991) considered the Blackpoll Warbler a common migrant in Ontario, although it tends to be uncommon in Elgin County, Niagara Region, Muskoka and Parry Sound districts, and Algonquin Provincial Park (Black and Roy 2010; Lancaster et al. 2004; Mills 1981; Tozer 2012).

Hussell et al. (1992) determined that there had been a nonsignificant increase in the number of migrant Blackpoll Warblers at Long Point of 0.7% 1961-88. Trends by period were: –1.7% 1961-70; +4.8% 1970-79; and +6.0% 1979-88. Its pattern of abundance on the BBS was similar to those of the Tennessee, Cape May, and Bay-breasted warblers suggesting that the Blackpoll Warbler might also respond to the abundance of spruce budworms. Badzinski (2002) analyzed banding station data across Canada. It declined at all stations except Long Point. Declines were most pronounced at Delta Marsh and Thunder Cape. Black (2017) reported a significant increase in May sightings at Port Weller 1993-2017.

Black-throated Blue Warbler

Setophaga caerulescens

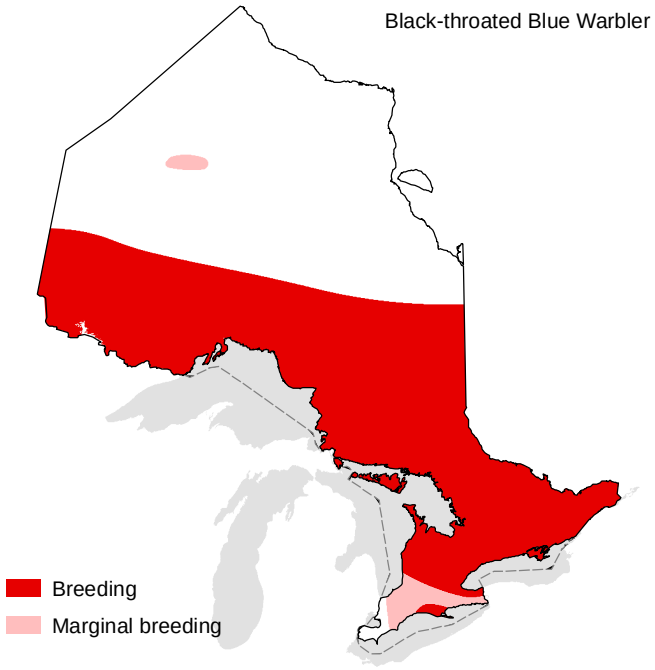


BREEDING SEASON

Habitat Requirements

Ontario Black-throated Blue Warbler nests were in mixed (66.7% of nests) and deciduous woods, all with a dense understorey. It selects deciduous understorey most frequently, but it also nests in woodlands with a coniferous understorey. Most nests were near open areas such as road edges, shorelines, and clearings (Peck and James 1987). It occurs mostly in deciduous or mixed forests in older second-growth or mature stands. It requires a fairly closed canopy and areas where there is some shrubby growth. In mixed forests, hemlock is the preferred coniferous species (James 1984b).

In the Boreal Forest Region near Manitouwadge, Venier et al. (2009) did not record the Black-throated Blue Warbler in forests 1-21 years old. It occurred at very low densities in forests 24-36 years old. It was 3 times as abundant in forests 60-223 years old, but still uncommon. At Quetico Park, Apfelbaum and Haney (1985) found it in very low densities in forests 112-176 years old. It was absent in forests 1-23, 67-73, or 367-370 years old. Near Hearst, it nested in clear-cuts 11-24 years old in upland mixed stands. It was second in abundance in a 19-year-old stand. It was absent in lowland coniferous stands of all ages (Welsh and Fillman 1980). In the Clay Belt, it occurred in 1 stand each



of trembling aspen, jack pine, tamarack–white cedar, balsam poplar, white spruce, and white birch. It was absent in black spruce. It occurred mostly in nutrient-rich sites in very wet to very dry sites (Welsh and Lougheed 1996). Smith (1957) reported it in mature white spruce forests in the Clay Belt west of Hearst and in black spruce stands in the Quebec portion of the Clay Belt.

Erskine (1977) concluded that the Black-throated Blue Warbler was not a regular inhabitant of spruce and balsam fir stands in the Boreal Forest Region, but it appeared in hemlock and mixed stands with hemlock in the transition area between that forest region and the Great Lakes–St. Lawrence Forest Region. It was common in sugar maple–beech and poplar-birch stands and occasional in pine stands.

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, Kirk et al. (2012) documented the Black-throated Blue Warbler in both mature and old-growth white pine stands. It was slightly more common in old-growth stands, but not significantly. Near Gogama in areas dominated by jack pine, it was common only in deciduous forests taller than 16 m where there was 50-75% coverage by tall shrubs. Jack pine was usually rare to absent in these stands, but occasionally constituted as much as 60% of the tree cover. It was not observed in pure jack pine stands. Highest densities occurred in a 40-42-year-old mixed jack pine–deciduous forest (James and Peck 1995a). In Algonquin Park, it was common in old pine forests with much beaked hazel in the understorey, and in sugar maple forests (MacLulich 1938). Kingsley and Nol (1999) reported it in all age classes of white pine forests in Algonquin Park. It occurred in 75% of plots in 2-9-year-old cuts, 70-81.8% of plots in 10-16-year-old cuts, and 71.4-73.3% of plots with no recent history of logging. Also in Algonquin Park, Martin (1960) reported it in pioneer poplar–white birch stands, in mixed hardwood-spruce–balsam fir stands, in pure balsam fir–spruce stands, and in hemlock. It also occurred in shrubby plots at forest edges. Within deciduous stands, it confined its activities from about 0.5 m above ground to the lower tree branches in the canopy. Algonquin Park nest sites were characterized by low canopy cover and a large amount of regeneration, particularly of hemlock (Creasey 2013). Mills (1981) considered the Black-throated Blue Warbler an abundant breeder in Parry Sound and Muskoka districts in rich deciduous and mixed forests where there was a thick understorey of shrubs and saplings. During the breeding season and in mid-summer, it was associated with deciduous hardwood forests. In autumn, it switched its habitat preferences and was associated more with white birch stands (Mills 2007). In Muskoka District and Haliburton County, it occurred in mixed and deciduous forests with moderate canopy volume and tree density, indicative of selective tree removal in mature woods or of immature woods. Singing posts were in areas of very high tree

density and the highest amounts of understorey. It required a higher density of understorey than any of the other species studied (Clark et al. 1983).

In Elgin County in the Carolinian Forest Region, 2 of 3 breeding season records were in hemlock-dominated ravines (Lancaster et al. 2004).

Throughout its range, the Black-throated Blue Warbler nests predominantly in deciduous and mixed forests. In the Maritime Provinces, New England, and Minnesota, it nests mostly in northern hardwoods dominated by sugar maple, beech, and yellow birch. These may contain either no or varying numbers of conifers, especially hemlock and balsam fir, but also pines, spruces, and white cedar. In Quebec, it is more abundant in the deciduous and mixed forests of the Great Lakes–St. Lawrence Forest Region than in the more northern coniferous forests or in the urbanized and agricultural areas in the south. In the Maritime Provinces and Ontario, it is common in intolerant hardwood stands dominated by species such as trembling aspen, balsam poplar, and white birch. It is much less common in coniferous stands and, in conifers, is most frequent in stands of hemlock and less frequent in spruce, balsam fir, and pine stands. In New Brunswick, it nests in spruce plantations as young as 6 years old; it is rare in Wisconsin coniferous plantations. In New Brunswick, forest types that it selected, in order of preference, included intolerant hardwoods, spruce, mixed intolerant and tolerant hardwoods, and intolerant hardwoods mixed with spruce. Stand types used less than their availability, in order of decreasing avoidance, included pine, spruce and balsam fir, spruce, and spruce with some intolerant hardwoods. Other forest types that it may inhabit include oak-hickory, red pine plantations, and hemlock–yellow birch. In mountainous areas of South Carolina, it breeds most frequently in heavily wooded ravines, along streams, near seepages, and in riverine forests where there is dense undergrowth. In addition to forests, the Black-throated Blue Warbler nests in clear-cuts and strip-cuts in deciduous, mixed, and coniferous forests. It may inhabit clear-cuts when they are as young as 6 years old. In Vermont, some territories were entirely within undisturbed forest, others were completely within clear-cuts, and some contained both habitats. In Pennsylvania, it nests in shrubby areas of hydro transmission line corridors where they pass through deciduous forest (Beals 1960; Bielefeldt and Rosenfield 1994; Brooks 1940, 1947b; Crawford and Titterington 1979; Darveau in Gauthier and Aubry 1996; Falardeau et al. 1999; Freedman and Johnson 1999; Gates and Giffen 1991; Harrison 1984; Holmes et al. 2020; Holway 1991; King et al. 1997; Lent and Capen 1995; Lind 1999; Morgan and Freedman 1986; Parker et al. 1999; Pitts 1993; Steffes 1999; Temple et al. 1979; Yahner et al. 2002).

Presence of a shrubby understorey appears to be the most important habitat component for the Black-throated Blue Warbler. Shrubs appear to provide superior habitat than saplings. In northern hardwoods near Sault Ste. Marie, its abundance was positively correlated with small deciduous shrubs rather than hardwood saplings. In many areas, it appears to prefer 1 species of shrub over others, but the species that it uses vary geographically. Important species in Ontario are beaked hazel and American yew and it uses these more than their availability wherever they occur. Small balsam fir and spruce are often important features of habitat and they are particularly critical where heavy browsing by white-tailed deer has reduced the density of deciduous woody plants. In New Hampshire, areas with dense coverage of hobblebush are highly selected. In other areas, mountain maple, striped maple, and mountain laurel are important understorey shrubs in occupied

habitats. Saplings of sugar maple and beech may also provide habitat but are less frequently used than shrubs or spruce and fir saplings. The shrub layer is extremely important to the Black-throated Blue Warbler because it nests almost exclusively in it. It rarely occurs in habitats with poorly developed understories. Selection of dense shrubby areas seems most closely related to its nesting requirements and not to foraging needs or other factors. Dense shrubs provide a suitable nest substrate, shelter from the elements, and concealment from predators and parasites. In Vermont, the importance of shrubs depended upon the landscape context. In forested landscapes, occupancy rates remained nearly unchanged as shrub cover decreased but in fragmented landscapes, a decrease in shrub cover resulted in lower occupancy. Sites with high shrub coverage had a 40% probability of occupancy regardless of landscape-level patterns. In sites with low shrub coverage, occupancy declined from 30% in contiguous landscapes to 10% in fragmented landscapes. In sites within the most fragmented landscapes and with the lowest shrub coverage, there was a 16% probability that it would become locally extirpated. In the same landscapes, this probability declined to 13% when shrub cover was maximized. In New Hampshire, sites that were consistently occupied in 3 consecutive years were characterized by more deciduous vegetation than sites occupied less frequently (80% for 3 years of occupancy, 78% for 2 years of occupancy, and 68% for 1 year of occupancy) and hobblebush density was consistently higher (70 stems per 25 m^2 for 3 years of occupancy compared with 56 for 2 years and 48 for 1 year). At consistently occupied sites, its abundance was higher, males arrived earlier, and 55% of all fledglings were produced from territories that overlapped high-occupancy areas. All sites occupied in 3 years were occupied in the fourth year. Seventy percent of Black-throated Blue Warblers occurred on the high-quality sites which represented less than 50% of the occupied locations. Most reproductive output occurred from few locations that all had dense deciduous shrubs. Other New Hampshire studies demonstrated the importance of deciduous shrubs, particularly hobblebush. The percent cover was significantly greater at nest sites than random areas (94% compared with 26% within a 0.15-m radius and 87% compared with 28% within 0.30 m). Shrub density was significantly greater at nest sites than random areas at all scales examined: 1 m, 1-2 m, 2-5 m, and 5-10 m. Hobblebush density was also significantly greater at nest sites. This shrub accounted for most of the shrub density at nest sites but not at random sites. The Black-throated Blue Warbler selected areas with denser hobblebush coverage below 1.5 m and more open areas between 1.5 and 3 m than at random spots. It also selected patches of hobblebush that were larger than random, with 52.5% of nests occurring in shrub patches with a radius of at least 10 m. Nests tended to be distant from edges of hobblebush patches. Its density tended to be low until shrub density reached 40 stems per 40 m^2 and increased significantly with increasing shrub density. It was consistently and significantly more abundant in areas of high shrub density than in low shrub density. In high-density areas, 68% of males and 71% of females were 2 years old or older. Only 35% of males and 36% of females were older in areas of low shrub density. More unpaired males occurred in low shrub-density areas and warblers in high shrub-density areas produced more fledglings, mainly through double brooding. All these factors indicate that areas of high shrub density are preferred and superior habitat. A positive correlation between warbler and shrub density was also noted in northeastern mixed forests and in deciduous forests in the mid-Atlantic states. In West Virginia, it was most likely to occur in areas of high shrub density. Shrubs were removed from a plot in New Hampshire. Prior to treatment, the plot supported 3 entire and 4 partial territories. In the first year after treatment, 1 male

retained his territory but failed to attract a mate and 1 pair had a territory that was mostly in the defoliated area but nested 50 m into the adjacent forest. There was 1 nest the second year and 0 the following year. There was a 61% decline in warbler density on the treated plot. In Michigan sugar maple stands that were subjected to high grazing pressure by deer, the Black-throated Warbler was positively correlated with the amount of balsam fir in the understorey. It was negatively correlated with deciduous understorey and was absent in areas with minimal understorey. Presence of balsam fir allows it to persist in hardwood communities that are heavily browsed (Beals 1960; Bent 1953; Chapman 1907; Cornell and Donovan 2010; Dimmig et al. 2020; Doran and Holmes 2005; Holmes and Pitt 2007; Holmes et al. 1996, 2020; Holway 1991; Kearns et al. 2006; Lind 1999; Robbins et al. 1989; Steele 1992, 1993; Temple et al. 1979).

The Black-throated Blue Warbler is usually found in older stands, but may occur in those as young as 6 years. Holmes et al. (2020) stated that it did not occur in young clear-cuts or second growth but becomes common once the canopy is well developed and the shrub layer is dense, usually more than 50 years after cutting. Although that may be the case in New Hampshire, it is not universally true. In Maine spruce–balsam fir stands, it occurred in clear-cuts with dense raspberries and regenerating hardwoods less than 2 m tall and in all later stages of succession, but was least abundant in closed forest, possibly because of limited shrub coverage. It was positively correlated with the number of hardwoods larger than 20 cm diameter at breast height (DBH) and negatively correlated with the amount of slash within 1 m of the ground, the number of dead trees larger than 10 cm DBH, and the number of conifers larger than 20 cm DBH. It was one of the more common species in dense hardwoods taller than 4.5 m with a DBH of 10-15 cm (Titterington et al. 1979). In Vermont, it was associated predominantly with deciduous forests with a dense understorey, usually in pole-sized timber with a mean DBH of 8-15 cm. Plots with these characteristics included a large stand that had been clear-cut 20 years previously and stands where recent selective logging opened the canopy and allowed a dense understorey to develop (Thompson and Capen 1979). In Pennsylvania, Haney (1999) identified the Black-throated Blue Warbler as having significant negative old-growth affinity. It most commonly inhabited deciduous habitats typical of younger regenerating forests. In Wisconsin northern hardwoods, it first appears at the pole-timber stage when trees reach a minimum of 22.5 cm DBH, with the trees well spaced and a developing shrub layer and understorey of saplings (Hoffman 1989a). In northeastern northern hardwoods, Noon et al. (1979) reported it in 15% of plots in mature undisturbed forests and 40% of plots in disturbed and successional forests. Temple et al. (1979) considered it a mature forest species in northeastern mixed forests. In New Hampshire and Maine, it was most abundant in sawtimber-sized forests followed by pole-timber and large sawtimber. It was least abundant in sapling-sized forest. It was one of the species most strongly associated with mature forest (DeGraaf et al. 1998; DeGraaf and Chadwick 1987). It is likely that its distribution is influenced predominantly by the density of shrubs rather than the age of forests.

Several studies examined microhabitat preferences of the Black-throated Blue Warbler. In New Hampshire and Maine, it was positively correlated with the number of both coniferous and deciduous trees larger than 10 cm DBH, the number of conifers 2-10 cm DBH, the number of snags larger than 10 cm DBH and more than 5 m tall, total foliage volume of conifers larger than 10 cm DBH, and total foliage volume of deciduous species smaller than 2 cm DBH. It was negatively

correlated with canopy closure, the number of deciduous trees 2-10 cm DBH, the number of woody stems per ha, and the total foliage volume of conifers 2-10 cm DBH (DeGraaf et al. 1998). In Vermont, it was associated with high numbers of dead trees, increasing successional age, and higher numbers of conifers than average. It was negatively associated with numbers of aspen and white pine and coverage by hophornbeam, red oak, sugar maple, and beech; it was associated with moderate amounts of red maple (Lent and Capen 1995). Also in Vermont, average habitat characteristics included 13.7% green ground cover, 13.6% ground coverage by slash, 88.4% canopy closure, 22.1 m canopy height, 12.5 m canopy depth, 13.3 m^2 basal area deciduous species, 13.8 m^2 basal area coniferous species, 12.7 cm DBH for deciduous trees, and 17.0 cm DBH for conifers (Thompson and Capen 1988). In the mid-Atlantic states, it was significantly associated with foliage density between 0.3 and 1 m (Robbins et al. 1989). In Maine, it was associated with medium-sized to large trees in predominantly deciduous forests (Collins 1983a). In North Carolina, it was positively correlated with canopy closure and was the only species that increased with canopy cover (Lumpkin and Pearson 2013).

Freemark and Collins (1992), Holmes et al. (2020), and Lumpkin and Pearson (2013) identified the Black-throated Blue Warbler as a forest-interior species without providing any supporting documentation. Harris and Reed (2001) noted that there were several cases of it clustering territories near clear-cut edges. It is not a forest-interior species in Ontario. Peck and James (1987) reported that many Ontario nests were found at edges and Martin (1960) documented highest densities in edge plots in Algonquin Park. Three studies specifically studied the Black-throated Blue Warbler in relation to edge. In New Hampshire, King et al. (1997) established plots adjacent to clear-cuts 6 years old and younger. It was significantly more abundant in edge areas than forest interior and regularly defended territories within clear-cuts. Gates and Giffen (1991) examined edge effects along a forest-stream ecotone. It was significantly correlated with the bottomland hemlock–yellow birch–red maple forest along the stream and negatively correlated with the adjacent mature upland deciduous forest. The creek was bordered by a dense thicket of rhododendrons that probably attracted the warblers. Pitts (1993) reported a nest in South Carolina that was 8 m from a power-line right-of-way clearing. Harris and Reed (2002) studied the distribution and ecology of the Black-throated Blue Warbler in relation to forest-clear-cut edges in Maine. They surveyed 5 edge sites and 56 sites a minimum of 300 m from any clear-cut edges or roads. Clear-cuts abutting sites were 1-15 years old and were either completely devoid of trees or contained only a few dead trees and live saplings. Interior sites were dominated by trees at least 60 years old. There was a significantly higher proportion of yearling males (50.9%) at edges than in the interior (21.1%). Significantly more males were paired at edges (77.2%) than in the interior (55.4%) and in both areas, more yearlings were unmated than older birds. Of paired males, 34.1% of those at edge sites were observed with fledglings, significantly less than the 61.3% of males with fledglings in the interior. When all males were considered (paired and unpaired), there was no significant difference in the proportion of males with fledglings at edges (26.3%) or in the interior (39.9%). Fledging success was significantly correlated with male age, but only at edge sites where proportionately fewer yearlings fledged young. Males in the interior spent a greater amount of time in the understorey than males at edges even though the overall understorey density was lower in the interior. Males at edges spent most of their time in the canopy. There were several differences between edge and interior that had the

potential to affect reproduction and survival. These included differences in understorey vegetation density, prey abundance, predator densities, encounters with potential avian competitors, as well as age structure and pairing success of the warblers. These patterns did not consistently favour individuals nesting in interior over edge. There was no apparent net difference in the probability that a male establishing a territory at an edge or in the interior would produce fledglings. Male-age distributions and fledging-success patterns were consistent with the hypothesis that edge sites were inferior habitat and that yearling males may be prevented from settling in the interior by older males. Despite this, there was higher pairing success at edges, significantly higher understorey density, greater invertebrate density, and lower predator density that might indicate potential benefits of edge over interior. The results indicated that females did not avoid edges. Females' attraction to edge may be maladaptive, resulting in a lower probability of producing fledglings while males in interior sites remain unmated. It is most likely that the Black-throated Blue Warbler selects territories based on factors such as shrub density, food abundance, and predator density rather than distance from edge.

Based upon a literature review, Freemark and Collins (1992) concluded that the Black-throated Blue Warbler was area sensitive. Harris and Reed (2001) noted that it has been found in high densities in small fragments, but provided no information on the size of woodlots it inhabited. In the mid-Atlantic states, Robbins et al. (1989) determined that its abundance was positively correlated with forest size and that it rarely occurred in woodlands smaller than 100 ha. Its probability of occurrence was maximum (at approximately 20%) in woodlands larger than 3,000 ha and the probability was reduced to 50% of maximum at 1,000 ha. The 3 smallest forests in which it was seen a minimum of 2 times were 1,500, 1,500, and 1,120 ha. It was rare in this area and the conclusions were based on only 19 sightings. The results may not be representative of conditions in the core of its range. Beals (1960) studied the avifauna of islands ranging from a few hectares to more than 52 km^2 in Wisconsin. The Black-throated Blue Warbler was not confined to larger islands. Its distribution in southern Ontario according to the second atlas (Joos in Cadman et al. 2007) suggests that it may be area sensitive. It appears to be restricted to heavily forested landscapes such as the Bruce Peninsula, the Niagara Escarpment, the Oak Ridges Moraine, southeastern Ontario, the Norfolk Sand Plain, and the eastern shoreline of Lake Huron. No information is available on the size of forests it requires in southern Ontario, and this probably varies geographically depending upon the amount of forest within the landscape. Coleman et al. (2000) concluded that it probably requires a minimum of 100 ha of forest in locations off the Shield.

Ontario nests were in small trees and saplings. Conifers were slightly preferred, supporting 57.1% of nests in 5 species; 3 deciduous species were used. The most frequently used nest species were balsam fir (9 nests), maples (5 nests), hazel (4 nests), spruce (3 nests), and American yew (3 nests). Nests were between 2 or more upright trunks or branches or in crotches and were 0.2-1.7 m from the ground, with most 0.3-0.4 m up (Peck and James 1987). Baillie and Hope (1947) reported a nest 30 cm from the ground in a small balsam fir in Sudbury District. In Parry Sound and Muskoka districts, most nests were about 30 cm from the ground in small conifers (Mills 1981).

Throughout its range, the Black-throated Blue Warbler nests near the ground in a small shrub or sapling. In the Maritime Provinces, most nests are in small spruce or balsam fir and Quebec nests are

frequently in American yew. At 1 New Hampshire site, most nests were in hobblebush. All nests were in mountain laurel in another New Hampshire area. Other species that it nests in include blackberry, purple-flowered raspberry, sugar maple saplings, beech saplings, red oak saplings, small hemlocks, American fly honeysuckle, striped maple, mountain maple, grey alder, elderberry, and bracken fern. Most nests are in the crotch of a shrub or sapling and some are in clumps of dead leaves. Many have a dead branch or twig that forms part of the crotch and adds additional support for the nest. Almost all nests have a nearly complete canopy of vegetation over them, thereby concealing the nest, shading it, and protecting it from rain. The nest species is probably not important, with shrubs most likely to be selected based on their density, size of the patch, and the overhead cover they provide. No nests have been reported on the ground, but most are within 1 m of the ground and almost all are 1.5 m or less from the ground. In North Carolina, 95% of 563 nests were 0.95-1.30 m from the ground. One New Hampshire nest was 11.5 m from the ground in a yellow birch and another was 17 m from the ground in a hemlock. Nest heights typically average about 0.5 m from the ground or even lower. In North Carolina, early nests averaged 0.44 m from the ground; late nests averaged 1.81 m. One unusual nest was in the top of an overturned spruce. This was in an open woodlot so there may have been few typical nest sites available. Another was in a fallen tree amidst small twigs and last year's dead leaves. Nests are not known to be reused, but 1 nest was built on the platform of an old nest. It may incorporate material from old nests into a new one, including those of its own and other species (Bent 1953; Chapman 1907; Harding 1931; Harrison 1984; Holway 1991; Holmes 1986; Holmes et al. 1979, 1992, 2020; Kendeigh 1945; Lind 1999; Mousley 1924; Nice 1930a; Smith et al. 2018; Steele 1993; Stodola et al. 2010b).

When males first arrive, they range over large areas (5-10 ha) of the forest prior to settling in 1 location. In New York, males were frequently observed 150-180 m from their singing posts, and sang as they gradually worked their way back. Males in this population did not appear to be aggressive toward each other and frequently sang in the same or adjacent trees. It was doubtful if all the area that was used was defended, so it might better be defined as a home range. One polygynous New Hampshire male had nests 300 m apart. Ford (1996) interpreted this male as being polyterritorial, but there were no intervening males defending territories so it could also be interpreted as being a very large territory. Most New Hampshire studies concluded that territories are 1-4 ha, larger than reported elsewhere. Smallest territories occur where the shrub layer is dense and heterogeneous. In Quebec, territories are smaller than 2 ha. In Minnesota, territory sizes averaged 0.46 ha (range 0.21-0.77 ha), but the researcher acknowledged that the size of some territories may have been underestimated. In Algonquin Park, territories averaged 0.68 ha (range 0.10-1.55 ha; Darveau in Gauthier and Aubry 1996; Holmes et al. 2020; Kendeigh 1995; Lind 1999; Martin 1960; Nagy and Holmes 2005; Petit et al. 1988a). Near Quebec City, Black-throated Blue Warbler territories were not aggregated. Bourque and Desrochers (2006) concluded that it was strongly associated with habitat features and this may define its occupation pattern. Betts et al. (2008b) stated that there is evidence that it aggregates, suggesting that it may use the presence of other birds to cue in on suitable habitat. Holmes et al. (1979) stated that its distribution was patchy, coinciding with areas of high-density foliage.

Natal philopatry appears to be low. In New Hampshire, 22 of more than 5,000 nestlings (0.4%) returned. The closest returning bird was 300 m from its natal site but most were more than 500 m

away. One returning female bred 2.5 km from its natal site. The low apparent return rates may have been partially due to all studies being conducted on small plots (10-15 ha) in contiguous forest. Stable isotope analyses indicate that juveniles dispense over broad areas (Harding 1931; Holmes et al. 1992, 2020; Nagy and Holmes 2005).

Adult site fidelity is fairly high and once an adult has bred at a site, it is likely to return to breed. In New Hampshire, the annual survival rate of females was 40-45%. Within the same area, 37.4% of 99 adults returned in the first year after banding. Return rates were similar for the sexes (39% for males and 36% for females). Survival rates were estimated at 51% for males and 40% for females, and this difference was significant. Yearling males returned more frequently (42%) than older males (35%), but not significantly. The average distance between territory centres in subsequent years was 94 m for males and 153 m for females. Yearling males dispersed a median distance of 156 m compared with 83 m for older males. There were no significant differences in the distances dispersed by the sexes or age classes. Reproductive success the previous year did not affect return rates. Another New Hampshire study reported differing results. The overall mean dispersal distance was 193 m and females dispersed significantly greater distances (245 m) than males (163 m). Sixty-six percent of males and 46% of females returned to within 150 m of the previous year's territory. One percent of each sex dispersed longer distances (1,201-1,350 m for males and more than 1,350 m for females). Dispersal distances were shorter for older than younger males and also for males in higher-quality habitats than those in medium-quality habitats. Habitat quality was the most important predictor of female dispersal distance. Reproductive success was also important, with females that fledged more young dispersing shorter distances. In heavily browsed deciduous forests in Michigan, annual return rates for adults were 26% where the understorey was dominated by balsam fir and 11% in deciduous-dominated understories. These differences were not significant (Cline et al. 2013; Holmes and Sherry 1992; Kearns et al. 2006; Nagy and Holmes 2005; Sillett and Holmes 2002). Some males (probably yearlings) arrive later than average and establish territories in suboptimal habitat. As the breeding season progresses, many move to higher quality vacant habitat (Betts et al. 2008b).

Limiting Factors

Eggs have been reported in Ontario nests from the last week of May until the end of July, with most present in the last half of June (Peck and James 1987). In Algonquin Park, nests are under construction from mid-May to early July, eggs are present from late May to late July, nestlings are present from early June to early August, and dependent fledglings have been seen from late June to early August (Tozer 2012).

Pair formation usually occurs within a few hours of arrival but occasionally takes a few days. Nest building begins 3-7 days after arrival in favourable weather, but may be delayed as long as 14 days if it is cold or wet. Nests take 3-5 days to build and the first egg may be laid the day after the nest is complete. Eggs are laid at the rate of 1 per day. Incubation is usually initiated with the laying of the penultimate egg. The incubation period at 3 Ontario nests was 12 days. Elsewhere, incubation periods of 11-13 days have been reported, typically 12-13 days. Eggs tend to hatch on the same day and a 4-egg clutch hatched within a period of 1.5 hours; clutches occasionally hatch asynchronously. The nestling period is 8-12 days, mostly 11-12 days. The average nestling period in New Hampshire was 8.6 days compared with 11.4 days in North Carolina (Harding 1931; Holmes et al. 1979, 1992,

2020; Kendeigh 1945; Mousley 1924; Nagy and Holmes 2005; Nice 1930a; Peck and James 1998a; Pitts 1993; Stodola et al. 2010b).

Double broods probably occur in Ontario, but this has not been confirmed. Double brooding has been confirmed in Minnesota, North Carolina, and New Hampshire. Over a 20-year period in New Hampshire with a sample size of more than 2,000 nests, 3 attempts at third broods were documented. None of the third broods fledged young. In New Hampshire, the proportion of females that raised a second brood after successfully rearing a first brood ranged from 0% to 87% annually. On average, 53% of successful females initiated a second brood. In Michigan, 26-45% of birds raised 2 broods over 6 years. Females that raised a double brood nested on territories with greater food availability and produced heavier fledglings in their first brood compared with single-brooded females. The date of nest initiation and the age of females were not good predictors of whether a female would attempt a second brood. Females were more likely to be double brooded in years when food was abundant or when they were mated with an older male. Females raising more young in the first brood were less likely to double-brood. Despite the large number of females raising 2 broods in this population, some females failed to fledge any young. Replacement nests are common if a nest is lost due to predation or other factors. Females in New Hampshire made 1-4 nesting attempts (average 1.7, median and mode 2). These included replacement nests and multiple broods. There were few second broods in years when wet weather in late May and early June delayed nesting. In North Carolina, time until a new nest was started averaged 6.5 days following nest loss and 10.5 days after a successful nest (Holmes et al. 1992, 2020; Lind 1999; Nagy and Holmes 2005; Stodola et al. 2009). Clutches of 2-4 eggs have been reported in Ontario with 79.2% containing 4 eggs (average 3.71 eggs; Peck and James 1998a). Throughout the Black-throated Blue Warbler's range, clutches of 2-5 eggs have been reported. Four is the most frequent clutch size and 94.2% of New Hampshire clutches contained 4 eggs; 5-egg clutches are rare. The average clutch size in New Hampshire was 3.8 eggs. First clutches averaged 3.9 eggs, second clutches averaged 3.7 eggs, and third clutches averaged 3.6 eggs. Early clutches averaged 4.0 eggs and late clutches averaged 3.7 eggs. In North Carolina, average brood size was 3.39 for first nests and 3.23 for second nests (Bent 1953; Chapman 1907; Holmes et al. 1992; Nagy and Holmes 2005; Rodenhouse and Holmes 1992).

Both sexes are capable of breeding in their first year and all females of all age classes breed every year. In New Hampshire, the proportion of unmated males varied annually from 0% to 21.9%. Unmated males are mostly yearlings and birds in marginal habitat. Unmated males are most common in years when density is highest. Male removal studies in New Hampshire demonstrated that missing males were replaced primarily by neighbours, with little evidence of a floater population (Holmes et al. 1992, 2020). The mating system is typically monogamous, but some males are bigamists. In New Hampshire, polygyny rates ranged from 0% to 15% annually. Seven of 8 bigamous males were after-second-year birds and some females successfully raised 2 broods with a bigamous male. In the case of the yearling bigamous male, both his females raised 2 broods. Bigamous males raised significantly more fledglings (average 7.2, range 3-12) than monogamous males (average 4.4, range 0-8). Most pair bonds are retained through the entire breeding season, including replacement nests and multiple broods; divorce occasionally occurs. When both members of a pair return in a subsequent year a high proportion reunite. Of 20 cases when both

pair members returned, 16 (80%) reunited (Cline et al. 2013; Holmes et al. 1992, 2020; Petit et al. 1988a).

Extra-pair fertilizations are an important component of the Black-throated Blue Warbler's mating strategy, but intraspecific brood parasitism appears to be rare. In New Hampshire, 44.7% of 17 broods contained extra-pair young. Another study at the same site determined that 43% of 900 nestlings were extra-pair and 56% of 152 broods contained extra-pair young. In Vermont, 33.2% of nestlings were extra-pair and 52.9% of broods contained extra-pair young. In North Carolina, 32% of nestlings were extra-pair and 57% of broods contained extra-pair young. Females that had more than 2 neighbouring females with overlapping fertile periods were most likely to have extra-pair young. Synchrony of nesting in adjacent territories was an important factor regulating extra-pair fertilizations. Males that guarded their females closely during the incubation period were less likely to have extra-pair young in their nests. Extra-pair sires had a significantly higher annual return rate (67%) than those who were cuckolded (42%). This suggests that females may select high-quality males as extra-pair mates. In the same study area, 68.0% of extra-pair sires occupied a territory adjacent to the one supporting its extra-pair young and in most cases the sire was less than 2 territories away. There were 4 cases in which the male was separated from his extra-pair young by 2 or more territories. In addition, 70.2% of young whose sires were not identified were at the edge of the study plot where some neighbouring males had not been sampled. The probability of a male obtaining extra-pair copulations decreases with increasing distance to females and breeding density. Frequency of extra-pair copulations increases with breeding synchrony. Older males are more likely to sire extra-pair young than young males, which is probably associated with territory quality (Chuang et al. 1999; Holmes et al. 2020; Webster et al. 2001).

The Black-throated Blue Warbler forages mostly in the shrub and subcanopy layer of deciduous and mixed forests and is ecologically separated from the canopy-dwelling warblers. In New Hampshire, it actively selected layers 3-6 m and 6-9 m from the ground for foraging. Heights of 0-1 m, 1-3 m, and over 9 m were underutilized. Males did not use the shrub stratum for foraging and significantly overused the sparse foliage in the sapling and subcanopy strata. Females and males feeding fledglings foraged differently, overusing tall shrub foliage 1-3 m from the ground. Females significantly overused tall shrub foliage and underused subcanopy foliage. Horizontally, foraging males selected areas with a high density of shrub or sapling foliage and overused these areas. Other density classes were used in proportion to their availability. Foraging females underutilized areas with high densities of shrub or sapling foliage and areas with high numbers of shrubs. All other areas were used in proportion to their availability. Males foraged higher than females, often over areas of dense shrub foliage. Females foraged low but did not show any clear selection for dense shrub patches. In New Hampshire, males foraged at significantly greater heights (average 5.9 m, range 2-16 m) than females (average 3.3 m, range 0-16 m). Male song perch heights averaged 8.1 m. Of all species studied, the Black-throated Blue Warbler exhibited the lowest overlap in usage of strata by the sexes at 62.7%. Females foraged significantly more on hobblebush, herbaceous species, and ferns than males. In Parry Sound District, it foraged at heights of 2-13 m during the breeding season and at 3-12.5 m in autumn (Holmes 1986; Holmes et al. 1979, 2020; Mills 2007; Robinson and Holmes 1984; Steele 1993). The Black-throated Warbler foraged mostly by hovering (about 65% of attacks) and 35% by gleaning in New Hampshire. In Vermont, gleaning was the primary foraging technique

(77% of attacks compared with 23% for hovering). Density of the warblers may determine which foraging technique is dominant. In 1 study, its density was decreased and those in areas of low density gleaned more than those in high-density areas. Males in high-density areas had less time available for foraging due to territorial defence requirements and compensated by using more aerial attack manoeuvres. Approximately 75% of prey attacks are directed to leaves with limited amounts of foraging on twigs, branches, tree trunks, and in the air. Most prey attacks are directed to lower leaf surfaces. In a laboratory study, the Black-throated Blue Warbler learned to locate prey more efficiently when it was distributed on lower leaf surfaces, and capture rates were higher on lower than upper leaf surfaces (Dobbs et al. 2007; Holmes 1986; Lent and Capen 1995; Robinson and Holmes 1982, 1984; Whelan 1989). In New Hampshire, there was no significant difference in the tree species that the sexes foraged on. Females tended to forage in herbaceous species and ferns more than males. Prey attacks in beech, sugar maple, and yellow birch were directed mostly to lower leaf surfaces. Prey items in beech and yellow birch were attacked in proportion to their availability on leaf, petiole, and twig surfaces. In sugar maple, it used the lower surface of leaves and the caterpillars there significantly more than expected. In all trees combined, 82% of attacks were directed toward lower leaf surfaces, 10% to upper leaf surfaces, 8% to twigs, and 0% to petioles (Holmes 1986; Holmes and Schultz 1988).

Nestlings are fed predominantly insects, particularly caterpillars. On their first day, New Hampshire young were fed small insects, white grubs, and large numbers of 1-cm long smooth green caterpillars. On days 2-8, the diet consisted chiefly of these caterpillars, insects, grubs, other types of caterpillars, and occasionally mayflies. On days 9 and 10, dragonflies and mayflies were the staples of the diet, but caterpillars and grubs were still consumed. Other food items eaten by nestlings included slugs, winged ants, cabbage white butterflies, and moths. Other studies confirmed that green caterpillars and, to a lesser extent, grubs are important in the diet of nestlings. Quantitative sampling of nestlings' diets indicated that 58-87% of food consists of caterpillars. They have also been fed crane flies, other flies, some hymenopterans, and occasional beetles (Goodbred and Holmes 1996; Harding 1931; Mousley 1924; Nice 1930a; Rodenhouse and Holmes 1992).

During the breeding season, adults are predominantly insectivorous, although they eat some spiders. In New Hampshire, stomach samples consisted of 50.5% beetles, 27.6% caterpillars, 12.0% flies, 5.2% soft-winged bugs (mostly leafhoppers), and 5.2% hymenopterans. Other food items include spiders and harvestmen, dobsonflies, stink bugs, caddisflies, stoneflies, lacewings, damselflies, snails, crickets, and sawflies (Holmes et al. 2020; Robinson and Holmes 1982; Rodenhouse and Holmes 1992). Near Manitouwadge, the Black-throated Blue Warbler responded positively to a spruce budworm outbreak in mature forest, but not significantly (Venier et al. 2009). In a laboratory, Whelan et al. (1989) offered gypsy moth larvae to this warbler. One of 5 birds offered second-instar larvae accepted it and 1 of 3 offered third to sixth instar larvae accepted. In another trial, warblers were simultaneously offered 4 types of potential prey items. Zero of 12 birds chose gypsy moth larvae, 1 of 9 consumed a tussock moth larva, 12 birds each selected a cabbage looper, and 7 of 8 accepted mealworms. Smooth prey was selected over hairy prey. The authors concluded that it was unlikely to eat gypsy moth caterpillars if alternate prey was available. In New Hampshire, Rodenhouse and Holmes (1992) experimentally reduced prey abundance by spraying plots with Bt, which kills caterpillars. There were significant differences in nestling growth rates among years and

plots, but this could not be related to food abundance. Growth rates were influenced more by weather conditions, particularly precipitation. Rainfall probably increases food requirements but reduces foraging time and the availability of some insects. When food was abundant, all pairs attempted first broods, all pairs renested after nest failure, 75% of birds with successful first nests attempted a second brood, and 4 young fledged from each nesting attempt. When food was limited, fewer pairs made multiple nesting attempts such that productivity was reduced below replacement level. In times of low caterpillar biomass, even a brief period of adverse weather can create food scarcity. In contrast, insect irruptions can increase productivity.

The Black-throated Blue Warbler is an infrequent host of the Brown-headed Cowbird and it appears to accept cowbird eggs. In most cases, a single cowbird egg results in complete reproductive failure. Only about 20% of parasitized nests in Vermont fledged a single warbler. In Ontario, 4 of 26 nests (15.4%) were parasitized; in Quebec, 2 of 21 nests (9.5%) were parasitized. Parasitism rates are much lower in forested landscapes than in smaller forest patches. Zero of more than 5,300 nests in New Hampshire were parasitized, although 1 female was observed feeding a cowbird fledgling. In unfragmented forest in Michigan, 1 of 160 nests (0.6%) was parasitized. In small forest fragments in Vermont, 25 of 203 nests (12.3%) were parasitized (Darveau in Gauthier and Aubry 1996; Holmes et al. 2020; Peck and James 1998a).

Habitat loss and degradation do not appear to be significant limiting factors in Ontario. Forest cover has increased south of the Shield in the past half century, which may improve habitat suitability for the Black-throated Blue Warbler. There is a possibility that this trend will reverse itself because of the high value of agricultural land. Invasive species such as garlic mustard may inhibit shrub and sapling establishment and reduce habitat quality. In North Carolina, its abundance was negatively correlated with the number of buildings within 200 m (Lumpkin and Pearson 2013). Establishing a single house within a woodlot may reduce its suitability for the Black-throated Blue Warbler. In Quebec, Bélisle et al. (2000) translocated territorial males during the breeding season. Birds took more time and were less likely to return to their territories as the percent coverage by forest decreased. Fragmentation may disrupt habitat selection processes, reduce colonization of isolated patches, and ultimately alter population structure and dynamics.

The Black-throated Blue Warbler is not significantly affected by forest management provided that the shrub layer is maintained or enhanced (Holmes et al. 2020). Several studies examined the effects of selective logging on it in Algonquin Park. Jobes et al. (2010) found that it was significantly more abundant in recently logged sites 1-5 years old and in uncut stands than in stands logged 15-20 years previously. Old logged stands had a reduced shrub layer and reduced canopy cover, reducing their suitability for edge and shrub-associated species. Uncut stands contained high shrub densities, probably a result of natural gap disturbances, and this created suitable habitat. A significant increase in shrub density occurred shortly after harvesting, providing better habitat. Tozer et al. (2010) found no significant difference in its abundance in control plots and those where single- and group-selection harvest occurred. Abundance of the shrub-nesting guild showed no response in the first year postharvest but increased the next year in response to typical and group-selection harvest. Creasey (2010, 2013) found that single-tree selection in Algonquin Park created significant habitat changes but had no effect on this warbler's reproductive success. Holmes and Pitt (2007)

examined the effect of selection harvesting in northern hardwoods near Sault Ste. Marie. In 1 plot, it increased in abundance within 1-2 years after harvesting. In the other plot, it declined initially but increased 3-8 years after cutting. The initial decline was attributed to the change in abundance of American yew which declined from 21.1% coverage prior to cutting to 1.2-2.0% coverage 1 and 2 years after cutting. Density of this shrub recovered in the third year after harvesting. In the Canadian Shield in Ontario, there was no difference in its abundance in early successional stands after clear-cutting and fires, but it was significantly less abundant in mid-successional clear-cuts than in similarly aged stands after fire. It was significantly less abundant in early successional stands than in mature stands, but there was no difference in its abundance in mid-successional and mature stands (Zimmerling et al. 2017). Very similar results to the Ontario studies have been documented elsewhere. Densities in new cuts and control areas are often similar, but sometimes densities are much higher in new cuts than uncut areas, depending upon shrub densities in the unharvested areas. Density starts to decline 14-18 years postharvest as the canopy fills in and shrubs are replaced by saplings and pole-sized trees. In New Brunswick, it reached highest densities in selection cuts and 61% of fledglings were produced in the harvested areas. In another New Brunswick study, shrub density declined by 13.7% in the first year postharvest due to skidder damage, returned to original levels in the second year, and then increased steadily. An increase in the Black-throated Blue Warbler was evident in the fourth year postharvest (Bourque and Villard 2000; Haché et al. 2013; Keller et al. 2003). In New York, Webb et al. (1977) found no evidence of effects on the Black-throated Blue Warbler when 25%, 50%, 75%, or 100% of merchantable timber was removed from forest stands. In Maine, Harris and Reed (2001) examined the effects on this warbler of 0.45-1.67-ha clear-cuts 1 to more than 15 years old in extensive northern hardwood woodlands. Broadcast calls and mounted birds were used to elicit territorial responses. Birds moved an average of 40 m in clear-cuts in response to these and readily crossed roads that constituted 10-30-m gaps. Three of 38 birds (7.9%) moved across clear-cuts. Males moved furthest into clear-cuts older than 15 years indicating that vegetation structure influenced movement into open areas. Small-scale habitat fragmentation by forestry may not disrupt territorial movement by the Black-throated Blue Warbler.

In New Hampshire, the Black-throated Blue Warbler population is regulated by food availability, nest predation, and local population density. These 3 factors explained 91% of the variation in the number of young fledged each year (Holmes et al. 2020).

Two studies in Quebec (Darveau et al. 1992; DesGranges et al. 1987) investigated the effects of sugar maple decline on the Black-throated Blue Warbler. In 1 study area, trees lost about 20% of their crown foliage and no effects were observed on the warbler. The other study found that it was significantly more abundant in stands that had suffered die-back due to the sugar maple borer than in healthy stands. It is likely that die-back of the canopy favoured shrub growth and improved warbler habitat.

High density of deer results in overbrowsing which can reduce habitat suitability for the Black-throated Blue Warbler. In a heavily browsed area in Michigan, it avoided areas with deciduous species in the understorey and selected sites with regenerating balsam fir, a species seldom browsed by deer (Gates and Giffen 1991; Kearns et al. 2006).

Taliaferro et al. (2001) examined the effects of soil calcium concentrations on the Black-throated Blue Warbler in New Hampshire (a calcium-poor habitat) and Vermont (a calcium-rich habitat). There were no significant differences in eggshell mass or thickness or in the concentration of calcium in the eggs. A diet of predominantly caterpillars did not provide a sufficient source of calcium. Ingestion of 8 average-sized (60 mg dry mass) snails during the egg-laying period would provide enough calcium for eggshell formation for a 4-egg clutch. Acid precipitation could become a limiting factor for snails which could lead to eggshell-formation issues for this warbler.

Graves (1997) examined the proportions of yearlings and adult males in breeding populations over much of the Black-throated Blue Warbler's range. The proportion of yearling males increased as relative abundance decreased toward the margins of the breeding range. The ratios of yearlings to adult males in 2 Ontario populations in the southern Canadian Shield were 0.67:1.0 and 1.0:1.0. The ratio was 0.17-0.80 and generally much lower than in Ontario in the core of the range in the southern Appalachian Mountains. Populations with high proportions of yearlings may be sink populations because fewer second broods are produced by yearlings.

In New Hampshire, Biasiolli (2009) documented introduced species of slugs actively feeding on nestlings. In most cases, adults successfully repel slugs and they may function as nest predators only under atypical conditions. In 1 case of slug predation, the young had fallen out of the nest and were on the ground. In the other case, the male had abandoned the nest and left its defence solely to the female. Only 2 cases of slug predation were observed at this site in more than 2,900 nests.

Venier et al. (1999) used breeding bird atlas data for Ontario and macroclimate information to model the distribution of the Black-throated Blue Warbler in the province. The final model included the maximum diurnal temperature range, the mean seasonal range in temperature, the annual range in temperature, the annual precipitation, the range in precipitation amount, and the total precipitation during the growing season. Price (2004) predicted that its breeding range in southern Ontario might contract if the average summer temperature increased by 2°C. Holmes et al. (2020) reported the results of climate modelling in New Hampshire. A projected increase in summer rainfall of 20% could reduce breeding productivity by as much as 26%. Alternatively, increasing temperatures might enhance productivity by increasing the food supply and lengthening the breeding season.

Status

It is likely that extensive deforestation by European settlers significantly decreased habitat for the Black-throated Blue Warbler and reduced its abundance (Curry 2006; Peck and James 1987).

McIlwraith (1894) concluded that it was likely that a few pairs of Black-throated Blue Warblers bred in the southern portion of the province and reported a nest from Listowel. In 1901, it was an abundant summer resident in Muskoka and Parry Sound districts (Mills 1981). Baillie and Harrington (1937) stated that it occurred sparingly in deciduous woods north to Lake of the Woods, southern Thunder Bay District, and the Kapuskasing area. The first atlas demonstrated that its breeding distribution was confined almost entirely to the Great Lakes–St. Lawrence Forest Region, although it occurred in the extreme southern portion of the Boreal Forest Region. It was widespread in the Canadian Shield with a noticeable absence around the Sudbury area which was still largely deforested at that time. It occurred sparingly south of the Shield, most frequently on Manitoulin

Island, the Bruce Peninsula, and the Niagara Escarpment. There were no records in the Carolinian Forest Region or in the southwest south of a line approximately from Goderich to Orangeville. Highest densities were reported from Algonquin Park, the districts of Muskoka and Parry Sound, and Haliburton County (Fraser in Cadman et al. 1987). James (1991) considered the Black-throated Blue Warbler common north to Wawa and Timmins and south to southern Georgian Bay and Ottawa and becoming rare north to Kenora, Red Lake, and Cochrane, and south to York Region and Kingston.

The second atlas revealed that the Black-throated Blue Warbler had extended its range southward since the first atlas. It was much more widespread in the Great Lakes–St. Lawrence Forest Region south of the Shield. It was also present in the Carolinian Forest Region, predominantly in the heavily forested area near Long Point with scattered records at Rondeau, in Hamilton and Niagara Region, and in a few other locations. Its range also extended further north, occurring regularly to latitude 50°N, from about Ear Falls to the Kesagami Lake area in the east. The most northerly record was at latitude 53°N near Weagamow Lake. Its probability of observation increased significantly province-wide and in all 4 regions where it occurred. It was abundant in Algonquin Park, Muskoka and Parry Sound districts, Haliburton County, the Algoma Highlands, and the Temagami–Lake Timiskaming area (Joos in Cadman et al. 2007). Tozer (2012) noted the high density in Algonquin Park where it is one of the most common warblers.

Breeding habitat for the Black-throated Blue Warbler is probably more extensive now in southern Ontario and throughout its range than it was 100-150 years ago. Results of the Breeding Bird Survey (BBS) suggest that it is stable or increasing over most of its range, with the largest increases in eastern Canada in Quebec and New Brunswick (Holmes et al. 2020). BBS results indicate that it increased at an annual rate of 1.06% in Canada and decreased at an annual rate of 0.165% in Ontario 1970-2021. The trends 2011-21 were annual decreases of 2.2% in Canada and 3.35% in Ontario. The long-term trends were highly reliable; the short-term trends were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Upon fledging, the young remain low in the understorey for 1-2 weeks, usually in the territory but sometimes moving as far as 200-300 m in the first 2 weeks. By 10-14 days after fledging, the young are flying well and actively foraging. Brood division may occur with 1 or 2 young going with each parent. When a second clutch is initiated, the male becomes the main and perhaps sole care provider for the fledglings of the first brood while the female initiates the second clutch. Adults may continue to feed fledglings 33 days after they leave the nest, but the normal period of dependency is 2-3 weeks after fledging. Family groups remain in breeding habitat in July and August, and occasionally into September (Holmes et al. 2020). These observations were made in a large contiguous woodland in New Hampshire. Postfledging habitat use may potentially differ in fragmented landscapes or where there are clear-cuts within forested landscapes.

In Pennsylvania, Stoleson (2013) captured 11 adults and 44 juveniles in clear-cuts during the postfledging period compared with 6 adults and 4 juveniles in adjacent mature forests. Coverage by shrubs was very similar in clear-cuts and forests but clear-cuts were dominated by raspberries and cherry seedlings whereas forests were dominated by beech and red maple seedlings. A significantly higher proportion of juveniles occurred in cuts than forests. In Michigan, it occurs in

dense patches of regenerating aspens, spruce, and red pine plantations with a dense deciduous sapling understorey during the postfledging period (Holmes et al. 2020).

Betts et al. (2008a) broadcast calls and songs during the postfledging period in areas in New Hampshire that did not support breeding Black-throated Blue Warblers. Warblers were seen more frequently at these sites than at control sites that were silent. In the subsequent breeding season, males were 4.1 times more likely to settle in treatment areas than in controls. Late in the season, singing was 5.1 times more likely to occur in territories that successfully fledged young than those that did not. Postbreeding song may be a cue for settling in an area the following year. During the breeding season in Vermont, Cornell and Donovan (2010) found that birds used habitat characteristics rather than conspecifics' songs as cues to settle in territories.

MIGRATION

The Black-throated Blue Warbler is a nocturnal migrant. One bird banded in Sault Ste. Marie was recovered in Cuba (Brewer et al. 2018; Holmes et al. 2020).

Males arrive in spring before females and adult males arrive before juveniles. The mean capture date for males at Prince Edward Point was 17.2 May compared with 22.9 May for females (Francis and Cooke 1986). At Long Point, the mean capture dates for males were: 11.1 May for adults, 14.6 May for juveniles, and 14.6 May for those of undetermined age. There were insufficient data to detect any timing differences in female age classes (Stewart et al. 2002). Elsewhere, males usually arrive 1-3 days before females, but often appear a week earlier (Holmes et al. 1992). The median stopover time for 48 Black-throated Blue Warblers at Long Point was 3.5 days (range 1-18 days). Post-departure flight paths were similar for the sexes and were mostly northward toward Georgian Bay, with some movement into Niagara Region and toward Lake Simcoe (Morbey et al. 2018). In southern and central Ontario, most migrants appear in early to mid-May. Some may arrive in late April and females are seen into early or mid-June (Black and Roy 2010; Curry 2006; Fleming 1907; Keast 1980; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012).

In autumn, no differential timing of migration by the sexes was apparent in Virginia. Migration of juveniles started earlier at the coast than for adults, and migration of all age classes began earlier inland and was well past its peak when numbers peaked at the coast. This suggested that distinct populations migrated through the 2 areas. Juveniles also pass through earlier than adults in Florida (Holmes et al. 2020; Stewart 1986). Most migrants pass through the southern Shield in September, with some arriving in late August; others remain until early October (Mills 1981; Tozer 2012). In the south, most birds arrive in mid- to late August and depart in early October, with some remaining into November or December (Black and Roy 2010; Curry 2006; Fleming 1907; Keast 1980; LaForest 1993; Lancaster et al. 2004).

Covino et al. (2020a) analyzed timing of Black-throated Blue Warbler migration for 1966-2015 from all United States banding stations. During spring, males consistently migrated earlier than females and adults migrated earlier than yearlings. In autumn, there was no difference in timing of migration by the sexes, but juveniles migrated earlier than adults. Early spring migrants passed through 1.1 days earlier per decade and the peak of migration also occurred earlier. In autumn, the peak of migration remained constant but became more protracted.

During migration, the Black-throated Blue Warbler remains mostly in shrubby or forested habitats where it shows a preference for low shrubs in various types of woodlands. Nonetheless, it may be seen almost everywhere that there is suitable shrub or tree cover, including in parks, gardens, orchards, and around human dwellings (Bent 1953; Graber et al. 1983; Holmes et al. 2020; McIlwraith 1894). During spring migration in North Carolina, numbers seen per hour were 0.54 in floodplain forests, 0.27 in beech forests, 0.08 in wet thickets, 0.07 in pine–hardwood forests, 0.03 in oak-hickory forests, and 0 in dry thickets and pine forests (Parnell 1969). In South Carolina, Bowen et al. (2007) examined usage of forest gaps, edges, and forest interior by migrating Black-throated Blue Warblers. Gaps were 0.013, 0.26, and 0.50 ha in area. Gaps were densely vegetated and contained early successional fruiting species such as sumac, blackberry, poison ivy, and hawthorns. In spring, 60% of captures were in gaps, 40% were in edges, and 0% were in forest. The differences in usage of the 3 habitat types were all significant. In autumn, 52% of captures were in gaps, 42% were in edges, and 6% were in forest. There was no significant difference in usage of gaps and edges, but these 2 habitats were used significantly more than forest. On 2 islands in the Gulf of Maine during both migration periods, more Black-throated Blue Warblers were captured on the island with greater tree density, canopy cover, and density of shrubs taller than 3 m (Suomala et al. 2010). During spring migration in Ohio, it was significantly more abundant in mature upland forests than mature riparian forests. Upland forests had significantly lower canopy cover (74% compared with 83%) and significantly more shrub cover (39% compared with 19%; Rodewald and Matthews 2005). During autumn migration, it was equally abundant in all habitats that Rodewald and Brittingham (2002, 2004) studied: shrub-sapling-stage forest, forest interior, pole-stage forest, suburban forest, forest-agricultural edge, and forest edge.

Parnell (1969) studied the foraging behaviour of Black-throated Blue Warblers during spring migration in North Carolina. Foraging occurred 18.7% of the time in the canopy, 72.9% in low trees, 8.5% in low shrubs, and 0% on the ground. In the canopy, 10.2% of foraging occurred in the inner crown and 8.5% in the lower crown; no foraging occurred at the top of the canopy or on the bole. In low trees, 3.4% of foraging occurred at the top of the crown, 32.2% in the inner crown, 37.3% in the lower crown, and 0% on the bole. In shrubs, 1.7% of foraging occurred at the top of the crown, 6.8% in the inner crown, and 0% in the lower crown, dense thickets, brush piles, or grasses. Singing males occurred at heights of 1.5 m to more than 15 m (average 6.7 m). Nonsinging birds occurred at heights of 0-12.8 m (average 5.5 m). Keast (1980) reported atypical foraging behaviour during a grounding at Point Pelee 28-30 April. These birds foraged 25% of the time on tree boles, 25% on exposed ground, 20% on branches, 20% on sapling trunks, 10% on low shrubs, and 0% on outer foliage, bare twigs, sapling twigs and foliage, on the ground in thickets, and in marshes. Foraging occurrence at different heights was 25% on the ground, 10% at 0.6-1.8 m, 0% at 3 m, 30% at 5 m, 20% at 7 m, 15% at 10 m, and 0% at 13 m and higher. During adverse autumn weather in Ohio after most fruit on trees and shrubs had been consumed, a female was observed creeping on a lawn, apparently gleaning tiny arthropods from the undersides of grass leaves and violet leaves (Tramer and Tramer 1977). During autumn migration in New York, Lebbin et al. (2007) observed the Black-throated Blue Warbler foraging at night in trees illuminated by stadium lights. It made aerial sallies after insects and appeared to glean insects from foliage. In Florida, Brooks (1986) reported a migrant plucking insects from spider webs.

During migration, the Black-throated Blue Warbler is still predominantly insectivorous, but consumes some fruit in autumn. During spring migration in Wisconsin, a male drank sugar water from a hummingbird feeder. During autumn migration in Quebec, a female hovered while she drank beech sap from old sapsucker holes. It is also possible that she was consuming insects attracted to the sap. A late November migrant in Michigan fed on suet and peanut butter at a feeder (Brooks 1986; Harrison 1984; Mousley 1917; Niemuth 1997).

The Black-throated Blue Warbler is highly vulnerable to striking buildings, communication towers, and other tall structures during migration. Loss et al. (2014) analyzed bird-building collisions in the United States and determined that it was 45.5 times more likely to strike a building of any type than on average for birds. It was 86.4 times more likely to strike low-rises and 78.5 times more likely to strike high-rises than average. It was not among the top 20 most vulnerable species for striking residences 1-3 stories tall. Weir (2008) reported that 567 were killed at the Lennox generating station chimneys near Kingston. At a Florida lighthouse, Black-throated Blue Warblers struck it more than any other bird species (Bent 1953).

Strode (2003) studied the effects of climate change on the migration of the Black-throated Blue Warbler in Illinois and North Dakota. Over 100 years, there was no significant change in spring temperature in Illinois but spring had advanced an average of 8.6 days in North Dakota since 1961. Spring also advanced north of Illinois. The Black-throated Blue Warbler exhibited no response to changing temperature patterns and now has as many as 20 fewer days to travel between southern Illinois and northern Minnesota. In New York, Zelt et al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season during 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming occurred during the second period. The spring arrival date was significantly earlier, the autumn departure date was significantly later, and the breeding season was significantly longer during the second period.

James (1991) considered the Black-throated Blue Warbler a common migrant in Ontario. It declined at a nonsignificant rate of 0.2% per year at Long Point Bird Observatory 1961-88. Trends during other periods were: 1961-70, −1.6%; 1970-79, +4.3%; and 1978-88, −1.1%. Its population trends were similar to those for the budworm specialists, suggesting that it might respond to some degree to changes in budworm numbers (Hussell et al. 1992).

Palm Warbler

Setophaga palmarum

BREEDING SEASON

Habitat Requirements

There are 2 easily recognized subspecies of the Palm Warbler (Pittaway 1995), both of which breed in Ontario. The Western Palm Warbler breeds from northeastern British Columbia east to Moosonee and Kapuskasing. The Yellow Palm Warbler breeds from Mer Bleue and the Alfred Bog in southeastern Ontario east to Newfoundland (Godfrey 1986; Rand 1944). There appear to be no differences in the breeding habitat or behaviour of the subspecies.

Ontario nest were typically in wet areas, particularly spruce or spruce-tamarack bogs, with lesser numbers in spruce swamps and treeless muskeg (Peck and James 1987).

Wilson and McRae (1993) concluded that the Palm Warbler bred throughout the Hudson Bay Lowland, but avoided the coastal strip. In the extensive tamarack fen inland from Moosonee, it was the second-most common breeding warbler. Manning (1952) also reported it near the edge of the Moosonee town clearing.

In the Boreal Forest Region from Pickle Lake north to the Manitoba boundary, the Palm Warbler was most abundant in coniferous scrub, followed by mixed scrub, deciduous scrub, coniferous forest with an understorey, and in heaths. It was absent in deciduous and mixed forest, coniferous

forest without an understorey, and tundra (McLaren and McLaren 1981). Near Pickle Lake, it was uncommon at edges of spruce forests surrounding large bogs as well as in tamarack bogs (James 1980). In the Clay Belt, Welsh and Lougheed (1996) found it only in black spruce forests. These were nutrient-poor wet stands. Also in the Clay Belt, Smith (1957) confirmed it breeding in a tamarack-alder bog. Erskine (1977) considered it characteristic of more open spruce bogs and observed that it was one of few species that was nearly confined to boreal coniferous forests during the breeding season. It occurred predominantly in bogs and fens and other sites with young or low spruce. It rarely occurred in mature spruce stands. North of Upsala, Harris (1990) found evidence of the Palm Warbler nesting in upland cutovers regenerating with jack pine. The area was on fine sandy soil and had been cut 9 years previously. The clear-cuts often exceeded 100 ha and were interspersed within stands of 60-80-year-old jack pines. Trees within territories averaged 3 m in height (range 2-5 m) and were mostly spaced such that one could walk between them without touching the branches. The ground cover consisted of red-stemmed feather moss, haircup mosses, and reindeer lichen with frequent patches of bare sandy soil. Logging slash was present at most occupied sites. The most abundant non-woody plants included bunchberry, bristly sarsaparilla, and Canada bluejoint. The shrub layer was predominantly ericaceous, being comprised of Labrador tea, velvetleaf blueberry, and lowbush blueberry, but beaked willow, pin cherry, and prickly rose were also present. In northwestern Ontario, this warbler appears to select nesting habitat on the basis of vegetation structure rather than species composition. Young jack pine stands were structurally similar in many respects to open bogs since both habitats consist of small conifers with open areas of ericaceous shrub cover. It probably traditionally nested in young jack pines that regenerated after fire in northwestern Ontario.

Near Gogama in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Palm Warbler was detected once during the breeding season in a 20-year-old jack pine stand (James and Peck 1995a). South of the Shield in this forest region, it is confined to large bogs and fens. Mer Bleue is approximately 3,500 ha in area and supports 10-20 pairs and the Alfred Bog is approximately 4,200 ha and supports more than 100 pairs (Leckie 2011).

Both subspecies of the Palm Warbler nest in 3 distinct habitats, although the structure of these habitats may be similar. It most frequently nests in bogs, fens, and peatlands with scattered trees and a dense shrub layer of predominantly ericaceous shrubs. Much less frequently, it nests in young jack pine stands with well-spaced trees and patches of bare soil intermingled among ericaceous shrubs. It rarely nests in coniferous plantations.

In bogs, fens, and other peatlands, the Palm Warbler appears to be restricted to large patches of suitable habitat. Although not all authors reported the size of the habitat patches they found it in, the smallest reported occupied area was 146 ha. This bog was part of a larger wetland complex that totalled 344 ha. Its distribution outside the Hudson Bay Lowland and Boreal Forest Region is dictated by the distribution of large bogs and fens (Ibarzabal and Morrier in Gauthier and Aubry 1996; Peterson 1984; Wilson 2020).

In bogs and fens, the Palm Warbler is predominantly an edge species, nesting near the interface between the surrounding coniferous forest and the bog or fen. It tends to avoid areas with no or dense trees. Areas with scattered conifers in sphagnum moss provide ideal habitat. It appears to require the presence of shrubs, particularly those in the heath family. Shrub species that are frequently within territories include Labrador tea, leatherleaf, swamp laurel, bog laurel, sheep laurel, bog rosemary, rhododendrons, bog cranberry, and blueberries. Other shrubs that may be present in lower densities include wild raisin, swamp birch, and alders. Preferred areas have dense coverage of shrubs 1-2 m tall. Sphagnum moss or occasionally other moss species are typical ground cover in these types of habitat. Other common ground species may include pitcher plant, cottongrass, common juniper, bogbean, orchids, and a variety of sedge species. Highest densities in Maine peatlands occurred in areas with a ground cover of sphagnum moss, a well-developed ericaceous shrub layer, and 25-50% forest cover by black spruce, tamarack, and white pine. In most areas, black spruce or tamarack are the dominant tree species, but it also inhabits fens with white cedar. Territories require trees of varying heights. Males sing from treetops about 6 m high from the beginning of the breeding season until nestlings are present, when low shrubs are used as singing perches. In Nova Scotia bog habitat, tamarack was the preferred perch tree, possibly because they were the tallest trees available and did not have any foliage early in the season so that singing males were more conspicuous. Presence of small seedlings is important because almost all nests in peatlands are hidden under seedlings. In addition to bogs and fens, the Palm Warbler nests in coniferous forests and burned peatlands. Suitable coniferous forests are open stands of black spruce or tamarack with a ground cover of sphagnum or other mosses, dense shrub coverage, and occasionally reindeer lichen. It prefers open areas with scattered trees or isolated clumps of dwarf trees. These stands include creeping ericaceous shrubs and occasionally loose growths of alder, dwarf willow, or birch. Trailing arbutus and sweet fern may be common shrubs. In British Columbia, spruce snags and spruce with dead tops were frequent features in nesting habitat. In extensively forested areas, it nested along road rights-of-way and oil exploration cut-lines that created open habitat. In Minnesota, the Palm Warbler was significantly more abundant in closed than open spruce stands. In closed stands, overall vegetation height was significantly higher (6.6 m compared with 5.5 m), and tree density per 0.1 ha was significantly higher (45 compared with 23). In Quebec, it occasionally nests in intolerant hardwood stands. Forest stands used for nesting are typically wet and nutrient poor (Bent 1953; Campbell et al. 2001; Collins 1981; Dawson 1979; Desrochers et al. 1998; Harrison 1984; Ibarzabal and Morrier in Gauthier and Aubry 1996; Jehl 2004; Kirk et al. 1996; Knight 1904; Niemi and Hanowski 1984b; Peterson 1984; Rand 1944; Tyler in Bent 1953; Walkinshaw and Wolf 1957; Welsh 1971; Wilson 2020). In Minnesota, the Palm Warbler was positively associated with non-productive black spruce–tamarack stands (Zlonis et al. 2017).

The second habitat used for nesting by the Palm Warbler consists of young pine stands on nutrient-poor sandy soils. In this habitat in Michigan, it is found in the same areas inhabited by the Kirtland's Warbler. Walkinshaw and Wolf (1957) described the occupied habitat as low-statured jack pines with alternating clearings and dense stands. The ground cover consisted of grasses and shrub coverage by bearberry, blueberries, wintergreen, trailing arbutus, and sweet fern. All nests were in semiopen areas where jack pines or spruces were not very dense. In New Brunswick, the Palm Warbler nested on dry sandy ridges vegetated by groves of small pines and scattered spruce seedlings (Philipp and Bowdish 1917). Rand (1944) reported that it nested in young open spruce stands. Wilson (2020) considered a report of this warbler nesting in sandy plains on the north shore of the Gulf of St. Lawrence to be exceptional. In Maine, Knight (1904) reported it nesting in shrubby pastures, but this is the only report of this habitat being used. The dry sandy habitats used by the Palm Warbler in Michigan, New Brunswick, and Quebec are very similar to the habitat described in northwestern Ontario by Harris (1990).

Coniferous plantations are the final habitat used by breeding Palm Warblers. Mossman et al. (1991) stated that it was a rare breeder in Wisconsin coniferous plantations. In New Brunswick, Freedman and Johnson (1999) reported it breeding in high density in spruce plantations 7-21 years old, with peak populations in 13-15-year-old plantations. No other details were provided in these studies. It is possible that the plantations that were used were on sandy soil and had a similar structure to the other dry habitats that it has been documented breeding in. It is also possible that some of the jack pine stands used in Michigan were plantations.

Most Ontario nests were on the ground, predominantly in hummocks of sphagnum moss (63.6% of nests). Single nests of a total of 11 were in sedge hummocks, in lichens, in the shelf of a root of a fallen tree, and elevated 0.9 m from the ground. Nests were frequently near or at bases of small trees or shrubs; 1 was under a fallen branch (Peck and James 1987, 1998a).

Birds nesting in bogs, fens, and open swamps usually sink their nest into the moss. Most are at the base of a small spruce seedling or other small woody vegetation and are well concealed from above. Occasionally nests are in hummocks of moss with no overhead cover. In a Nova Scotia bog, 6 of 7 nests were less than 30 cm from the ground on outside edges of hummocks of common juniper. The other was 30 cm from the ground in a clump of ferns. In dry habitats, nests may either be on the ground or as high as 35 cm from the ground in small conifers or occasionally in low hanging branches of a larger tree. There is 1 report of a nest 1.2 m from the ground (Knight 1904; Peterson 1984; Philipp and Bowdish 1917; Tyler in Bent 1953; Walkinshaw and Wolf 1957; Welsh 1971; Wilson 2020).

Although some authors stated that the Palm Warbler occurs in loosely aggregated colonies, most territories are widely scattered. There is no evidence of true colonial nesting. Males establish territories as soon as they arrive and maintain them until the nestlings fledge. All activities appear to be conducted within the territory. In Nova Scotia, territorial boundaries were established along natural edges such as rows of well-developed trees or a forest edge. In all areas, the territory could have been expanded into unoccupied areas, so territory size was determined by individual males. All territories of successful males contained a significant portion of open bog, but no completely open areas were selected for a territory. Of 3 males that did not breed, 2 had territories in almost

completely wooded areas and a significant proportion of the other territory was wooded. This suggested that wooded areas were inferior habitat. Territories in a Nova Scotia bog averaged 2.50 ha (range 1.02-3.26 ha). The largest territory was held by a bigamist male and it was different from other territories in that it had no neighbours and contained a swamp and a pond. Some unmated males held territories. Territory sizes of monogamously mated males were 1.12-2.62 ha. Some Nova Scotia territories had extensions in spring as large as 1.17 ha that were not always defended. Maine territories averaged 4.0 ha; territories in 1 Quebec area averaged 3.8 ha (range 0.7-13.7 ha). Territories in peatlands with scattered black spruce in the Lac-St.-Jean region were 1.3, 3.4, 3.6, and 13.2 ha (average 5.38 ha; Harrison 1984; Ibarzabal and Morrier in Gauthier and Aubry 1996; Knight 1908; Walkinshaw and Wolf 1957; Welsh 1971; Wilson 2020).

No information is available on natal philopatry. The only information on adult site fidelity is that 1 of 2 males in Maine returned the following year to the same territory. It did not maintain the territory (Wilson 2020).

Limiting Factors

Eggs have been reported in Ontario nests from the last week of May until the first week of July, with most present during the last 3 weeks of June (Peck and James 1998a).

It is unknown how long nest building takes. One apparently complete nest had an egg in it 2 days later. The incubation period is 11 days and the nestling period is 9-12 days, mostly 10 days (Bent 1953; Knight 1904; Peterson 1984; Welsh 1971; Wilson 2020).

Although some studies concluded that the Palm Warbler raises only a single brood, double brooding has been confirmed in Quebec and there is anecdotal information that suggests second broods may be fairly common. Most birds in a Nova Scotia bog had single clutches. Two cases of attempted second broods occurred, but both failed due to predation. Egg dates in Maine are suggestive of second clutches, with nests being constructed in early May and again in mid-June. One researcher had reason to believe that it frequently, if not regularly, raised 2 broods in Nova Scotia. Renesting may occur if the first clutch is lost. All Ontario nests contained either 4 or 5 eggs, mostly 4 (average 4.38 eggs). The clutch size is almost always 4 or 5 eggs. Of 61 Nova Scotia nests, 59% contained 5 eggs and 41% contained 4 eggs for an average of 4.59 eggs (Bent 1953; Harrison 1984; Ibarzabal and Morrier in Gauthier and Aubry 1996; Peck and James 1998a; Tyler in Bent 1953; Welsh 1971; Wilson 2020).

The age at first breeding is unknown, but is probably 1 year. In Nova Scotia, 3 of 10 males did not appear to breed and their territories were in inferior habitat. It is possible that these were nonbreeding yearlings. The Palm Warbler is typically monogamous but 2 cases of bigamy have been reported (Welsh 1971; Wilson 2020).

The Palm Warbler is the most terrestrial member of its genus, feeding on the ground, from scattered trees and shrubs in the territory, and in the air with flycatching sallies either from the ground or a low perch. It mostly gleans prey from leaves and cones but captures some prey on the ground and some by hawking. In a black spruce bog in Minnesota, it fed at an average height of 4.1 m; average tree height was 6.2 m. It also opportunistically captures arthropods feeding on carrion (Knight 1908; Wilson 2020).

The Palm Warbler is largely insectivorous, with the most important prey items including mayflies, beetles, lepidopterans, flies, soft-winged bugs, and hymenopterans. It also eats gnats, mosquitoes, ants, aphids, and grasshoppers. In late summer and autumn, it may eat small amounts of vegetable matter such as small seeds and raspberries. It may also consume plant nectar (Bent 1953; Knight 1908; Tyler in Bent 1953; Welsh 1971; Wilson 2020).

The Palm Warbler is rarely parasitized by the Brown-headed Cowbird. No instances of parasitism have been documented in Ontario. Knight (1908) reported a Maine nest containing 2 warblers and 2 cowbirds but the fate of the young warblers was not determined. Wilson (2020) reported that there were only 4 known cases of parasitism: 2 in Maine and 2 in Alberta. Harrison (1984) stated that 7 cases of parasitism were known, but provided no further details.

Habitat loss is a concern south of the Canadian Shield. The Palm Warbler is restricted to large bogs and fens in this region. These are often converted to agricultural uses or mined for peat. These habitats are very sensitive to changes in the quality and quantity of water that they receive. Minor changes in these parameters can greatly affect bogs and fens. They may become either flooded and marsh-like, or increased nutrient inputs may result in the habitat being converted to thicket swamp, habitat that is unsuitable for the Palm Warbler. Approximately two thirds of the Alfred Bog has already been drained and converted into farmlands (Leckie 2011). Degradation of peatlands due to peat mining has been identified as a significant concern for the Palm Warbler in southern Quebec (Ibarzabal and Morrier in Gauthier and Aubry 1996). Desrochers et al. (1998) compared vegetation and density of warblers in natural peatlands and those where peat had been harvested using 2 different methods. Block-cuts consist of alternating 2-m-wide ridges and trenches 6-15 m wide. Vacuum sites are split into 30-m-wide fields separated by drainage ditches. Most abandoned sites had a 2-3-m-deep layer of peat left unmined. There were significant differences between harvested and natural sites and differences in ericaceous shrubs and sphagnum moss persisted at least 20 years postharvest. Post–block-cuts had very little sphagnum and much bare ground compared with natural sites, but were otherwise similar. Post-vacuum sites had significantly less cover in all strata except for herbaceous vegetation. The Palm Warbler showed a significant response to peat harvesting, with numbers detected per point count of 0.61 in undisturbed peatland, 0.11 in post–block-cut, and 0 in post-vacuum. Block-mining is no longer used and the industry has turned to vacuum harvesting. An artificial nesting study in southern Quebec determined that nest predation rates were 12% in undisturbed peatlands and 78% in natural peatlands adjacent to areas where peat was being harvested. Calmé et al. (1998) concluded that it was important to conserve large patches of peatlands to maintain habitat for the Palm Warbler in southern Quebec.

In Alberta, the Palm Warbler was significantly less abundant at seismic lines and pipelines than in forest interior adjacent to these features. There was no difference in its abundance at well pads and in adjacent forest interior (Bayne et al. 2016).

In Maine, the Palm Warbler decreased 50-67% on sites where paper mill sludge was spread. The sludge contained low concentrations of dioxin derivatives (Wilson 2020).

Forest management has the potential to provide short-term benefits for the Palm Warbler. Suitable habitat may be created where none previously existed if forests are clear-cut. To provide any potential habitat, clear-cuts must be large (100 ha minimum), have regeneration by jack pine,

and be situated on dry, nutrient-poor sandy soils. In Ontario in the Canadian Shield, there was no difference in its abundance in early and mid-successional clear-cuts and stands of the same age after fire. It was significantly more abundant in early and mid-successional stands than in mature forests (Zimmerling et al. 2017).

Status

The first Ontario Palm Warbler nest was found in Mer Bleue in 1901. Baillie and Harrington (1937) had only 1 additional breeding record from an island in Lake of the Woods. During summer at that time, it had also been observed at the southern end of James Bay, in Algoma District, and near Sault Ste. Marie. They concluded that it might be a rare breeder in various areas of northern Ontario. The first atlas confirmed that the Palm Warbler nested throughout the Boreal Forest Region and Hudson Bay Lowland, although its distribution was spotty. It was likely overlooked in some areas due to difficulty in accessing its habitat. There were very few records in the Great Lakes–St. Lawrence Forest Region and the Canadian Shield and only 2 south of the Shield, reflecting the rarity of suitable habitat in these areas (Welsh in Cadman et al. 1987). James (1991) considered the Palm Warbler an uncommon summer resident in the Hudson Bay Lowland; becoming rare south to northern Lake Superior; and occasional and rare south of Wawa and Timmins south to the Bruce Peninsula and Ottawa.

The second atlas showed the same general distribution for the Palm Warbler, but it was found in many new squares and blocks in the north with the distribution appearing less spotty. Some of the apparent infilling of the distribution map may be attributed to greater atlasser effort to survey open peatlands distant from roads and densely treed river corridors. Its probability of observation increased significantly between the atlases province-wide and in the Boreal Forest Region and Hudson Bay Lowland. In the Great Lakes–St. Lawrence Forest Region, it occurred only in the area from Thunder Bay west to Lake of the Woods and in the Ottawa area. Its probability of observation was 75.5% in the Hudson Bay Lowland where it is one of the more common species. Its probability of observation was 40% in the Boreal Forest Region, reflecting the lower amount of peatlands in this region. It was estimated that Mer Bleue supported 10-20 pairs and that more than 100 pairs bred in the Alfred Bog (Sutherland in Cadman et al. 2007).

Breeding Bird Survey data indicate that the Palm Warbler decreased at an annual rate of 1.01% in Canada and increased at an annual rate of 2.82% in Ontario 1970-2021. Trends for 2011-21 were annual increases of 0.213% in Canada and 3.32% in Ontario. All results were of medium reliability except that the short-term trend for Ontario was of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

In Michigan, brood division appeared to occur, with each adult caring for 2 fledglings exclusively. The first morning after young left the nest, they ranged 1.9-47.5 m from the nest, all separated but in the same general area. Three fledglings hid among leatherleaf and dead grasses; the fourth perched on a jack pine branch 30 cm from the ground (Walkinshaw and Wolf 1957). In Nova Scotia, fledglings from 1 nest strayed from the territory and the male followed to feed them, not defending his territory again (Welsh 1971). Adults have been reported feeding young as late as the end of August, but these may have been from a replacement or second brood.

Manning (1952) collected some juveniles at the edge of willow thickets on Ship Sands Island near Moosonee in early September. This suggests that juveniles may flock together prior to autumn migration. It is possible that these birds were migrants but southward movement was not noted until 9 days later.

Bent (1953) reported that families roosted every night in conifers near the nest for weeks after the young were able to fly.

MIGRATION

The Palm Warbler is a medium-distance nocturnal migrant. Because of the routes that the subspecies follow, the Western Palm Warbler is the subspecies that is typically observed in Ontario and few Yellow Palm Warblers are encountered. At the end of the 19th century in Hamilton, opposite trends were noted. There were no records of the Western Palm Warbler and the Yellow Palm Warbler was an occasional migrant that was apparently absent some years. In Hamilton, the Western Palm Warbler is now a common migrant; the Yellow Palm Warbler is rare. During the day while migrating, the Palm Warbler often occurs in small flocks, typically 10 or fewer but occasionally as many as 200 have been documented together. It is an early spring migrant, so it commonly flocks with other early migrants and resident species such as chickadees, Yellow-rumped Warblers, Golden-crowned and Ruby-crowned kinglets, juncos, and various sparrow species. In autumn, it flocks mostly with chickadees and other warblers (Bent 1953; Campbell et al. 2001; Curry 2006; Knight 1904; Leckie 2011; Leighton et al. 2002; McIlwraith 1894; Pittaway 1995; Tyler in Bent 1953; Wilson 2020; Wilson and Watts 1997).

The Yellow Palm Warbler initiates spring migration before the Western Palm Warbler (Wilson and Watts 1997). It is probable that males migrate before females, but this has not been confirmed. In southern Ontario, the Palm Warbler typically arrives in early May or late April and has departed by the third week of May. Migrants may be present from mid-April until early June (Black and Roy 2010; Curry 2006; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Weir 2012). In the southern Shield, average arrival is early May, average departure is mid-May, and migrants may occur from late April to early June (Mills 1981; Tozer 2012). Kendeigh (1947) first observed this warbler north of Lake Nipigon on 26 May.

The western subspecies initiates autumn migration prior to the yellow subspecies, possibly because of its more southern wintering areas. In Virginia, the median date of autumn migration was 10.5 days earlier for the western subspecies than the yellow subspecies. All age classes moved south at the same time for both subspecies (Wilson and Watts 1997). In autumn, the length of stay at sites is weather dependent, with birds moving south rapidly before a severe or sudden cold wave (Wilson 2020). At a reclaimed landfill in New Jersey, the mean length of autumn stopover was 4.8 days, with a maximum of 14 days (Seewagen and Newhouse 2018). Manning (1952) noted a significant southward migration at Moosonee on 18 September. In the southern Shield, average autumn arrival is late August or early September and the average departure is early to mid-October (Mills 1981; Tozer 2012). In the south, most birds arrive in early to mid-September and leave in mid- to late October, with stragglers remaining into December (Black and Roy 2010; Curry 2006; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Weir 2008).

During migration, the Palm Warbler is usually found in low vegetation and even on the ground. In spring, it is often in the company of the Yellow-rumped Warbler, but is less inclined to use upland forests. In the Kingston area, the Palm Warbler is especially common at shoreline sites and on islands. In Algonquin Park during spring migration, it is usually found low in brushy clearings, bogs, and forest edges. It has a broad tolerance in its habitat use during migration, but favours alder and willow thickets in riparian areas and early successional shrubby areas or those dominated by early successional trees such as birches. It may occur in shrubby roadsides and pastures and even in cultivated fields at significant densities. In British Columbia, vegetated spits, causeways, dykes, parks, golf courses, and beaches are typical habitat. It also occurs in suburban gardens and rural residential lots. Because it is an early migrant, the ground may still be frozen when it reaches the breeding grounds. During a brief but heavy spring snowstorm, hundreds congregated on a narrow strip of bare pebbly beach at the water's edge. During spring migration in Ohio, the Palm Warbler was significantly more abundant in mature upland forests than in mature riparian forest. Upland forests had significantly less canopy cover (74% compared with 83%) and significantly more shrub cover (39% compared with 19%; Bent 1953; Campbell et al. 2001; Chapman 1907; Faanes and Andrew 1983; Graber et al. 1983; Knight 1904; Leighton et al. 2002; Rodewald and Matthews 2005; Tozer 2012; Tyler in Bent 1953; Weir 2008; Wilson 2020).

During autumn migration at Prince Edward Point, the Palm Warbler foraged at heights of 3-10 m. Thirty-three percent of foraging time was spent on outer leaves, 33% on sapling foliage, and 34% on sapling branches. No foraging occurred on twigs and inner leaves, outer or inner branches, trunks, low shrubs, or the ground (Keast 1980). During spring migration in North Carolina, 36% of foraging occurred in the canopy, 18.2% in low trees, 0% in shrubs, and 45.5% on the ground. In the canopy, 9.1% of foraging occurred in the top of the crown, 9.1% in the inner crown, 18.2% in the lower crown, and 0% on the bole. In low trees, 13.7% of foraging occurred in the top of the crown, 32.3% in the lower crown, and 0% in the middle crown and on the bole. On the ground, 9.1% of foraging occurred in grasses, 16.9% in the open, and 0% in dense thickets and at water's edge (Parnell 1969). During spring migration, it forages in the most likely locations for the early development of insects such as sunny sheltered shores of ponds and streams, old orchards on hillsides, and near water. In Pennsylvania, it fed exclusively on the ground during early spring migration, but fed exclusively in trees in May after trees began to bud and flower. During spring migration in Quebec, it captured larvae from fresh buds of tamarack and on snags (Wilson 2020). During exceptionally inclement spring weather, Palm Warblers fed in scattered groups with other species of warblers on the ice of Lake Manitoba. Beetles, midges, other flies, and spiders were on the ice at that time (McNicholl and Goossen 1980). During autumn migration in New York, Lebbin et al. (2011) observed Palm Warblers searching for food at night among the foliage of trees illuminated by lights from a football stadium. Graber and Graber (1983) studied the foraging behaviour of the Palm Warbler during spring migration in Illinois. It fed preferentially on shingle oaks and hickories and used other trees less than their availability. The amount of food obtained from various tree species included 45.2% from shingle oak, 5.1% from other oaks, 44.7% from hickories (predominantly pignut hickory), 5.0% from sassafras, and 0.6% from black cherry. Shingle oak accounted for 13.9% of available trees compared with 7.0% for other oaks, 3.1% for hickories, 27.5% for sassafras, 5.9% for black cherry, and 1.8% for flowering dogwood. The percent time spent in each tree species was

29.3% for shingle oak, 10.7% for other oaks, 31.0% for hickories, 26.7% for sassafras, 0.7% for black cherry, and 1.7% for flowering dogwood. Several available tree and shrub species were not used for foraging, including honey locust, hackberry, elm, white ash, redbud, maples, sumac, multiflora rose, grape, sycamore, red cedar, hophornbeam, black gum, and Japanese honeysuckle. Where food was abundant, it foraged branch-to-branch. Where food was scarce, it foraged tree-to-tree. Where food was abundant, it tended to forage leisurely all day and remain in the area for approximately 3 days. Where food was scarce, it foraged only in the morning until 1000 hours and after 1600 hours and apparently migrated that night. Caterpillars were the dominant prey available and all caterpillars that it consumed were hairless. It selected either smaller-sized larvae (less than 15 mm) or small species (especially leafrollers) out of proportion to their availability. Leafroller moths constituted 19% of available prey but comprised 57% of prey taken by all warbler species. Linden looper moths constituted 49% of available prey and 42% of the diet of warblers in the same genus as the Palm Warbler. Geometer moth caterpillars constituted 65% of available prey and 62% of the diet of warblers in this group.

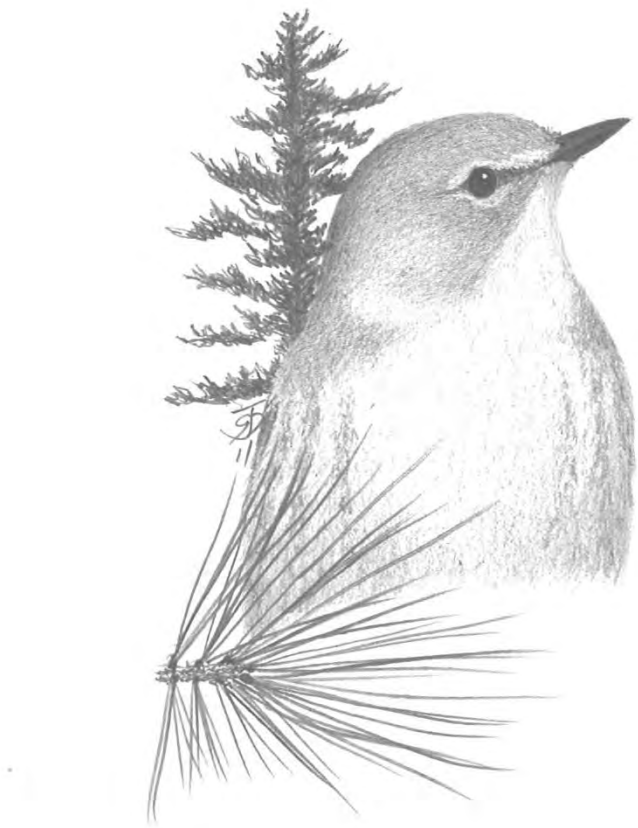
The Palm Warbler is often killed at television towers and other tall structures during migration. At 1 tower in Florida over a 25-year period, 1,827 were killed in autumn and 478 in spring, which represented 5.4% of all birds. It represented 6.6% of all birds killed at another Florida tower, 9% at a Florida power plant, 0.27% at Cape Canaveral, 9.1% at a tower in Illinois, and 1.4% at 9 other towers in Illinois (Graber et al. 1983; Leighton et al. 2002; Wilson 2020).

Strode (2003) studied the effects of climate change on the migration of the Palm Warbler in Illinois and North Dakota. Over 100 years, there was no significant spring temperature change in Illinois but spring had advanced by an average of 8.6 days in North Dakota since 1961. Spring also advanced north of Illinois. The Palm Warbler exhibited no response to changing temperature patterns and now has as many as 20 fewer days to travel between southern Illinois and northern Minnesota.

James (1991) considered the Palm Warbler a common migrant in Ontario. Most regional assessments concur with this, although Lancaster et al. (2004) considered it an uncommon migrant in Elgin County. It decreased at Long Point Bird Observatory at a nonsignificant rate of 1.5% per year 1961-88. Trends by period were: 1961-70, −6.6%; 1970-79, −1.0%; and 1979-88, +8.4%. The trends observed did not mirror those of the spruce budworm specialists (Hussell et al. 1992). At the Manomet Bird Observatory in Massachusetts, a significant decrease of 76% occurred in autumn for the Western Palm Warbler 1970-2001, but there was a significant increase of 26% in spring for the Yellow Palm Warbler (Wilson 2020).

Pine Warbler

Setophaga pinus

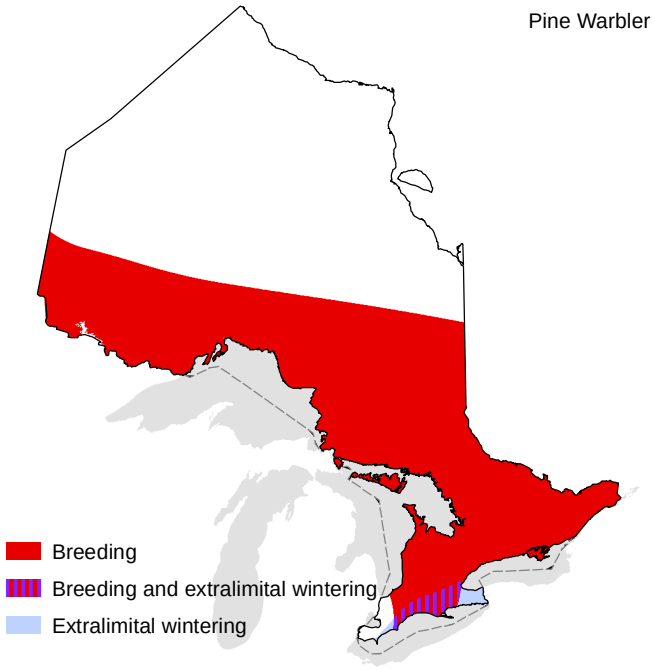


BREEDING SEASON

Habitat Requirements

Ontario Pine Warbler nests were usually in or at edges of open coniferous woods (8 of 14 nests, 57.1%) and 3 nests were in unspecified types of woodlands. Single nests were reported in each of an island with a few large pines, a mixed stand, and a lone tree in a village garden (Peck and James 1987). In Wellington County, 10 nests were in a mature coniferous woodland that was predominantly pine with some spruce (Peck and James 1998a). James (1984b) concluded that it occurred only in mature white pine or red pine forests and that these were typically somewhat open. It also nests in pitch pine stands in Ontario (Erskine 1977). Baillie and Harrington (1937) had a record of it nesting in a park in Simcoe.

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Pine Warbler is associated predominantly with red pine and white pine stands. It has nested in jack pine stands elsewhere, but was not reported in these types of stands near Gogama or Parry Sound (James 1979a;



James and Peck 1995a). In Algonquin Park, it was mainly associated with white pine stands 80-100 years old and 25-30 m tall. It also occurred in stands that had been cut 2-9 or 10-16 years previously (Kingsley and Nol 1999). Tozer (2012) concluded that it was a common breeder in the park wherever there was adequate cover with large pines present. Kirk et al. (2012) reported that it occurred in mature and old-growth white pine stands in central Ontario. It was more abundant in old-growth stands, but not significantly. Presence of medium-sized to large pines with a diameter at breast height (DBH) of more than 40 cm was a significant predictor of its presence. The density of supercanopy white pine was the most important variable in predicting its abundance, and stand age according to Forest Resource Inventory maps was equally important. It was locally distributed in white pine and red pine stands in Parry Sound and Muskoka districts (Mills 1981).

South of the Canadian Shield, the Pine Warbler occurs predominantly in white and red pine plantations that are a minimum of 40-50 cm DBH (Lancaster et al. 2004; Speirs and Orenstein 1975). It also occurs in mixed and even deciduous stands in the south, provided that some mature white pines are present.

No bird is more characteristic of pine forests than the Pine Warbler. It is essentially confined to pine or pine-hardwood stands and is rare in other stand types. It frequently inhabits sugar maple–white pine and pine-oak stands. Occasionally, it occurs in pure hardwood stands, but even these typically have a few pines in them that it focuses on. In predominantly deciduous stands, it invariably moves from 1 pine to another, ignoring the deciduous trees between them. As little as 10% pine coverage may attract it to deciduous stands. It responds directly to pine foliage and its abundance increases with the abundance of pines. It avoids stands containing spruce, balsam fir, tamarack, or hemlock unless pines are common. The Pine Warbler has used 15 species of pines. In the northeastern United States, it shuns white pine stands and highly selects pitch pine stands. In Ontario, white pines are preferred. In the western portion of its range in the United States, it prefers jack pine stands. In Quebec, its distribution coincides with that of pines where it nests predominantly in white pine stands. It is chiefly an upland species that rarely occurs in wetlands, possibly due to the scarcity of pines in swamps. It readily nests in pine plantations. These typically must be 40-50 years old to provide suitable habitat, but plantations as young as 3-5 years may support sparse populations. In both natural forests and plantations, it prefers stands where woody and herbaceous understorey is sparse. These conditions usually do not occur until trees form a closed canopy. In Texas, it favoured mature pine stands and demonstrated a strong positive association with

increasing proportions of pole-sized pines and canopy height. It avoided sapling-sized stands. It was absent where the average tree height was 13.5 m or less and reached highest densities in stands 18.9-26.2 m tall. In Arkansas, numbers recorded on point counts were 0.015 in 3-5-year-old plantations, 0.163 in 12-15-year-old plantations, 0.661 in stands that were thinned 17-23 years previously, and 0.870 in mature pine forests. Higher breeding densities occurred in forests with a more open midcanopy, lower canopy coverage, lower basal area of conifers and hardwoods, and a dense ground cover of grasses and forbs. In regenerating pine-oak forests in Virginia, it was found in increasing abundance in stands older than 10 years and was most abundant in stands older than 80 years. In mixed hemlock–white pine–hardwood stands in Pennsylvania, the Pine Warbler occurred in 36.4% of old-growth stands, 6.0% of stands statewide, and 5.7% of stands in the Appalachian Plateau. It was considered to have old-growth affinities (Beals 1960; Bent 1953; Bielefeldt and Rosenfield 1994; Brooks 1940; Brush 1987; Capen 1979; Chapman 1907; Graber et al. 1983; Haney 1999; Harrison 1984; Morse 1989; Mossman et al. 1991; Rich et al. 1994; Rodewald et al. 2020; Schroeder 1985; Spencer and Cotter in Gauthier and Aubry 1999; Temple et al. 1979; Yahner 1993).

Several studies examined microhabitat preferences of the Pine Warbler. In Minnesota, average habitat characteristics included 64.0% ground cover, 44.3% shrub cover, 75.7% canopy cover, 22.0 m canopy height, 66.7% coniferous cover, 4.9 tree species per 0.04-ha, 8.4 trees 7.5-15 cm DBH, 8.3 trees 15.1-23 cm DBH, 4.1 trees 23.1-30 cm DBH, 4.1 trees 30.1-38 cm DBH, 5.7 trees 38.1-53 cm DBH, 2.0 trees 53.1-68 cm DBH, and 1.1 trees larger than 68 cm DBH. It was in a guild of warblers that occupied habitats with tall canopies, moderate coniferous cover, few small trees, and more large trees. Species in this guild occur mainly in mature undisturbed forests containing conifers. Territories of most of these species had moderate ground and shrub coverage and greater than 75% canopy closure. They also consistently supported more than 50% coverage by conifers, mostly in the large tree classes. The Pine Warbler occurred regularly in red pine, white pine, and jack pine stands and was associated with large trees and large conifers more than any other species. The average canopy closure for the Pine Warbler was the least for warblers in this group. It occurred in habitats with variable amounts of pine. The other species in this guild had at least some spruce and balsam fir in their territories (Collins 1983a; Collins et al. 1982). In Maryland, it was positively correlated with the abundance of pines and shrub density and negatively correlated with canopy closure. In the mid-Atlantic states, it was positively correlated with canopy height, percent coverage by pines, the number of trees larger than 3 cm DBH, and foliage density 0.3-1.0 m from the ground. It was negatively correlated with slope, moisture, percent ground cover, and number of trees per 0.04 ha (Robbins et al. 1989). It was closely associated with pines and its probability of occurrence reflected the proportion and distribution of this forest type (Lynch 1987). In Tennessee, it selected for several habitat variables. The strongest of these were related to the number of canopy trees, the average size of the understorey vegetation, and the average size of canopy vegetation. It foraged in the upper canopy and frequented areas with a dense canopy and sparse understorey (Anderson and Shugart 1974). In Texas, the Pine Warbler was associated with mature pine forests. It was positively correlated with vegetation height and percent coverage by pines 17-32 cm DBH. It was negatively correlated with foliage density 3 m from the ground, percent coverage by pines 5-16 cm DBH, and the total number of stems 5-16 cm DBH (Conner et al. 1983).

Schroeder (1985) prepared a habitat suitability index model for the Pine Warbler. Its density in pine forests was inversely related to the percent coverage by deciduous species in the canopy. Forests with 30-80% deciduous cover in the upper third layer of dominant pines were considered to have very low suitability, and areas with more than 80% deciduous cover in the canopy were deemed unsuitable. Despite this, it is often found in stands with even greater deciduous cover. Optimal cover was considered pure, dense, mature pine stands (excluding white pine and some other pine species that this author thought were unsuitable) lacking a tall deciduous understorey. The habitat suitability for percent canopy closure by pines was 0 (completely unsuitable) for 25% or less closure, with a slow increase to 0.1 at 50% closure, and a sharp increase to 1.0 (optimum) at 90% and 100%. For average tree height, habitat suitability was 0 for trees 7 m tall and shorter with a straight-line increase to 1.0 at 20 m height. It was considered most abundant in stands 35-100 years old.

The Pine Warbler is often considered a forest-interior species, although most studies present no supporting documentation (Freemark and Collins 1992; Rodewald et al. 2020). A Florida study concluded that it was an edge species, with higher densities near edge than in forest interior (Rodewald et al. 2020). In southern Ontario, Austen et al. (2001) classified it as an interior species. It was positively associated with the amount of forest cover 100 m or further from forest edge, and this correlation was significant at the 10% level. This correlation does not necessarily mean that the Pine Warbler avoided edge. Peck and James (1987) reported that nests were often at edges of woods and 1 nest was in a lone pine tree. Near Brantford, Pine Warblers nested in a small grove of mature pines that were originally part of a larger deciduous forest. Many of the hardwoods had been clear-cut such that the pines were about 15-20 m from the main forest (personal observation). It is most likely that this warbler simply selects nest sites wherever there are large pines and that it does not actively pick edge or interior areas.

Most authors consider the Pine Warbler an area-sensitive species (Rodewald et al. 2020), but there are few data to support or reject this hypothesis. Freemark and Collins (1992) noted that some studies concluded that it was area sensitive and others reported the opposite. James (1984b) stated that it appeared to be area sensitive in Ontario, requiring at least 15-30 ha to sustain a viable population. In central Ontario, Kirk et al. (2012) found that patch size was not a significant predictor of its presence or abundance. In southern Ontario, it was significantly correlated with woodlot size and the amount of forest cover within 2 km. It was also associated with regional forest cover, but not significantly (Austen et al. 2001). Some studies suggest that this warbler is area sensitive in the province, but the presence of a nest in a single tree contradicts this. More study is required to determine if the Pine Warbler is area sensitive in Ontario. Results from Maryland and the mid-Atlantic states are also contradictory. In Maryland, Robbins (1979) concluded that 30 ha of forest were required to support a viable population. In the mid-Atlantic states, its abundance was significantly correlated with forest area, yet it demonstrated a constant probability of occurrence of 30% across all sizes of woodlands, including the smallest. In that study, it was not identified as an area-sensitive species (Robbins et al. 1989). In Minnesota, 1 pair nested on a 0.1-ha island that was isolated from the mainland and other pairs nested on islands as small as 0.9-1.1 ha (Howe 1979; Rodewald et al. 2020). In Tennessee, forests 10-15 ha support breeding Pine Warblers. Schroeder (1985) considered 10 ha to be the minimum patch size to support it.

All Ontario nests were in coniferous trees and usually in pines. Of nests in pines, 45.5% were in white pine, 36.4% were in red pine, and 18.2% were in jack pine. One nest was in a spruce. Nests ranged from the lowest branch in the tree to treetops, with most near the tops of trees. Most were near the end of lateral branches and one was 1.1 m from the trunk. Two nests were saddled on a horizontal branch and 2 were in clusters of pine needles. Nests were 3.7-20 m from the ground, with 8 averaging 8.5-15 m up (Peck and James 1987, 1998a). In Algonquin Park, white pine is used most frequently for nesting (Tozer 2012).

Throughout its range, the Pine Warbler nests almost exclusively in pines, with nests having been found in 15 species of pine with no clear preferences for species. In addition to the Ontario record of it nesting in spruce, it has been documented nesting at least once in each of red cedar, bald cypress, oak, and possibly hemlock. One nest in the Dominican Republic was on the ground, but ground nesting has not been documented in North America. Nests are typically high in a pine tree atop a horizontal or nearly horizontal branch, in a fork of a branch, in twigs or needles at the tip of a branch, at the end of ascending branches, or hidden among cones near the top of a tree. Most nests are 10-15 m from the ground (range 0.6-41.1 m). Nest heights are strongly dependent upon tree height and may be only 3-7.5 m in jack pine and pitch pine. Nests may be near the trunk or as far as 4.6 m from it. It has collected nest materials from an active American Crow nest when the crow was absent, an old Summer Tanager nest, an old Pine Warbler nest, and a nest that the female had just deserted (Bent 1953; Chapman 1907; Graber et al. 1983; Harrison 1984; Rodewald et al. 2020).

In Wellington County, 10 nests were found close together in a mature coniferous woods and it was concluded that a colonial situation was approximated. No other information on clustering of territories by the Pine Warbler is available. It is possible that territories are clustered to facilitate extra-pair copulation, but this aspect of its breeding strategy has not been studied. Little information is available on territory size and it is highly variable depending upon habitat quality. In mixed forests or deciduous forests with scattered pines, only a portion of the territory is used with birds restricting their activity to the pines. In Arkansas, 2 territories were about 0.9 ha. In Minnesota, 1 pair nested on a 0.1-ha island 450 m from the lakeshore, but most birds nested on islands 1.0 ha or larger. A polyterritorial polygynous male was discovered north of Kingston. The primary territory encompassed 1.95 ha and the secondary territory was 0.54 ha. The minimum distance between the edges of the territories was 398 m. There was a zone of unsuitable habitat between the 2 territories that was not occupied by other Pine Warblers. The male sang on both territories and chased both conspecifics and Yellow-rumped Warblers. He was less aggressive to Pine Warbler broadcast calls in the secondary territory (Conboy 2011; Peck and James 1998a; Rodewald et al. 2020).

No information is available on natal philopatry or site fidelity by adults. Twelve birds banded in Massachusetts were recaptured in subsequent years in the same 10-minute block of latitude and longitude suggesting that some exhibit a certain degree of site fidelity (Rodewald et al. 2020).

Limiting Factors

Eggs have been reported in Ontario nests from the second week of June until the first week of July (Peck and James 1987). In Algonquin Park, nest building occurs from mid-May to late June and dependent fledglings have been observed from early July to late August (Tozer 2012).

Nest construction and egg laying combined take about 14 days in favourable weather, although a week may elapse between nest building and the initiation of egg laying. This period was 25 days in 1 case. Long periods between completion of the nest and egg laying are likely to occur only in the south where the Pine Warbler is a resident species. Due to the shorter nesting period in Ontario, it is unlikely that there is a lengthy delay between nest completion and laying. It is probable that 1 egg is laid per day, but this has not been confirmed. It is unknown when incubation is initiated. The incubation period is not well documented and has been estimated at 10-13 days. The nestling period is estimated at 10 days, but there appear to be no supporting data (Bent 1953; Chapman 1907; Harrison 1984; Rodewald et al. 2020).

There is no direct evidence for multiple brooding but egg dates in the United States strongly suggest that second and possibly third broods may be raised. The Pine Warbler may renest multiple times in an attempt to raise a brood if nests are lost due to predation or other factors. This may partially explain the different peaks in egg dates. Ontario egg dates suggest that only a single brood is raised but this is based upon very few nests. Ontario nests contained 3-5 eggs and this is typical throughout its range. The most frequent clutch size is 4 eggs and 5-egg clutches are infrequent. Clutch size declines significantly with the date of clutch initiation but suggestions that first clutches contain 5 eggs and second clutches contain 4 eggs are unsubstantiated. The range-wide average of 266 clutches was 3.73 eggs and an average of 3.90 eggs was obtained from published records (Bent 1953; Chapman 1907; Harrison 1984; Peck and James 1987; Rodewald et al. 2020).

The age at first breeding has not been documented, but both sexes are probably capable of breeding in their first year. The proportion of yearling males that are successful in attracting females and breeding is unknown, and this probably varies among populations. The Pine Warbler is predominantly monogamous. The first case of polygyny was documented in Ontario north of Kingston. This was an after-second-year male that maintained 2 separate territories almost 400 m apart (Conboy 2012; Rodewald et al. 2020).

The Pine Warbler forages mainly while creeping slowly along tree trunks or limbs and forages predominantly in pine trees during the breeding season. There are no significant differences in the foraging behaviours of the sexes. Females tend to forage slightly higher than males. Foraging of Maryland females was centred near the height of nests, an average of 9 m from the ground. The lower density of vegetation in pine forests relative to that in spruce forests diminishes the advantage of males singing in treetops. In Maryland, males foraged at heights of 0-18 m, but mostly from 3 to 15 m and the mode was 6-9 m. Females foraged mostly from 6 to 12 m and the mode was 9-12 m. In Minnesota, foraging occurred at heights of 3-15^{+} m, but predominantly at 6-12 m with a mode of 6-9 m. About 40% of foraging was proximal to the trunk and 60% was distal. Seventy-five percent of foraging occurred in red pine, 22% in white pine, and about 2% each in spruce and deciduous trees. In New Jersey pine and oak barrens, it foraged mainly in pines and used oaks less than their availability. Based on 2 Maryland studies, 50-80% of foraging was on the distal half of limbs, 10-16% was on the proximal half of limbs, 26% was at the tips of branches, and a small proportion of foraging occurred on dead (3.5%) or deciduous (2.4%) growth. It also forages near and on the ground, especially in nonbreeding seasons, and is an adept flycatcher. In Maryland, 98% of foraging was by gleaning, 2% by hawking, and 0% by probing in cones. About 1.2% of time in Maryland was spent

probing and gleaning on tree trunks. In some areas of Maryland, the Pine Warbler coexists with the Yellow-throated Warbler. The Pine Warbler appears to be the dominant species despite the fact that the Yellow-throated Warbler forages higher in trees. The Pine Warbler foraged similarly in areas with and without Yellow-throated Warblers indicating that the presence of Yellow-throated Warblers did not influence its foraging behaviour. The 2 species can coexist because the Yellow-throated Warbler obtains much of its food by probing in cones. The Pine Warbler is incapable of accessing prey in cones because its skull is too wide and its bill is too short. During the breeding season in North Carolina, 68.8% of foraging occurred in the canopy, 25.0% in low trees, 0% in shrubs, and 6.2% on the ground. In the canopy, 31.3% of foraging occurred at the top of the crown, 25.0% in the inner crown, 12.5% in the lower crown, and 0% on the bole. In low trees, 6.2% of foraging occurred at the top of the crown, 12.5% in the inner crown, 6.3% in the lower crown, and 0% on the bole. On the ground, 6.2% of foraging occurred in the open and 0% in dense thickets, in grass, or at water's edge. During the breeding season, birds in the Grand Bahamas foraged almost exclusively on pine foliage; those on Andros Island foraged about equally on foliage and bark. The Pine Warbler may respond to seasonal changes in arthropod abundance. In May in New Jersey, its density was similar in oak-pine forests, one of which was heavily dominated by pine. In June and July, arthropod abundance was higher in the pine-dominated forests and higher densities of Pine Warblers occurred there (Bent 1953; Brush and Stiles 1990; Emlen and DeJong 1981; Ficken et al. 1968; Howe 1979; Morse 1974, 1989; Parnell 1969; Rodewald et al. 2020).

Nestling food items include small caterpillars, spiders, flies, and other insects. Adults eat mostly arthropods but also consume fruits and seeds, especially during autumn and winter. Fifteen stomachs analyzed during the breeding season contained a mean of 450 mg of food including 45 mg of caterpillars, 40 mg of soft-winged bugs, 10 mg of orthopterans, 5 mg of spiders, 5 mg of beetles, 4 mg of lepidopteran pupae, and 3 mg of hymenopterans. Twenty-one collected in Florida at all times of the year had consumed (by volume) 25.5% lepidopterans, 19% adult hymenopterans, 15.9% orthopterans, 12.9% beetles, 8.9% soft-winged bugs, 5.6% spiders, 3.4% flies, and lesser amounts of neuropterans, mecopterans, dragonflies, and damselflies. Cockroach eggs accounted for 13.2% of the mean food volume. Other prey items the Pine Warbler may consume include locusts, weevils, aphids, insect eggs, ants, and scale insects. It is unique among warblers in its ability to eat large quantities of seeds, especially those of pines (Bent 1953; Rodewald et al. 2020).

The frequency of parasitism by the Brown-headed Cowbird on the Pine Warbler is uncertain. Most authors consider parasitism rare, with only 15 records of parasitism known by 1985. Only 1 of 50 nests (2.0%) reported to United States nest records schemes was parasitized, but this was considered an underestimate since many observations were incomplete. In Ontario, 4 of 8 nests (50.0%) were parasitized, but this percentage will probably decline as more nests are reported. It is likely that parasitism rates in the Shield are near 0. The Pine Warbler is probably an acceptor of cowbird eggs and adults have been observed feeding cowbird fledglings. Occasionally it buries cowbird eggs in the nest. It is uncertain if the warbler does this deliberately or if it is because the cowbird laid the egg before nest construction was complete. In North Carolina, a female cowbird pulled all 4 Pine Warbler nestlings out of their nest and dropped them on the ground. There were no cowbird eggs in the nest. Killing a potential host's nestlings may trigger a replacement nest

which may provide an opportunity for parasitism (Beane and Alford 1990; Bent 1953; Harrison 1984; Peck and James 1998a; Rodewald et al. 2020).

Habitat loss and degradation do not appear to be significant for the Pine Warbler in Ontario. Habitat has increased in the south in recent years due to maturation of pine plantations. Old-growth forests in the southeastern United States have been almost entirely replaced by even-aged stands on shorter rotation periods. Birds that occupy younger pine forests or plantations may have lower nesting success. Forest clear-cutting is detrimental because warbler densities are much lower in young stands. Forest management such as single-tree and group selection remove fewer canopy trees and may have less of a negative effect (Rodewald et al. 2020).

Fire suppression in pine stands promotes the growth of hardwood regeneration which tends to result in lower densities of Pine Warblers. In Georgia, there was no difference in its abundance in unburned stands and those where prescribed burns were conducted at low, medium, and high intensities. The apparent lack of response may have been because it was not very abundant within the study area (Klaus et al. 2010; Rodewald et al. 2020). Rose and Simons (2016) studied the effects of fire in pine-oak forests in North Carolina on the Pine Warbler. It responded positively to fire, but only after high-intensity fires.

In Delaware, Tymkiw et al. (2013) found no differences in the abundance of the Pine Warbler in areas of low, moderate, or high white-tailed deer density.

Pine Warbler mortality was reported in Michigan in the late 1950s where DDT was used to control Dutch elm disease. Mortality has also been reported where arsenial spray has been used (Rodewald et al. 2020).

The Pine Warbler may be affected by weather extremes. There were widespread declines in the southeastern United States after the severe winters of 1976-77, 1977-78, and 1980-81, and after the summer droughts in 1980 and 1981 (Rodewald et al. 2020).

Price (2004) concluded that the breeding range of the Pine Warbler might expand in southern Ontario if the average summer temperature increased by 2°C.

Status

The Pine Warbler was probably much more common in Ontario prior to the widespread cutting of pines in the last half of the 19th century for ships' masts. McIlwraith (1894) considered it rather common in the Hamilton area but noted that it was not known to breed in the London area. Baillie and Harrington (1937) concluded that it bred in small numbers locally from the southern border to northern Algoma District and Renfrew County. They also had summer records from the vicinity of Lake of the Woods, suggesting that it bred there. In Elgin County, it was not reported by 1891, was considered a possible summer resident in 1954, and was a common breeder wherever mature pine stands occurred by 2000 (Lancaster et al. 2004). In 1965 in the Kingston area, it was a rare summer resident but was fairly common by the turn of the 21st century. The increase was attributed to maturation of pine plantations (Weir 2008). The first atlas demonstrated that the Pine Warbler occurred throughout the Great Lakes–St. Lawrence and Carolinian forest regions. It was most widely distributed in the Canadian Shield. South of the Shield, the distribution was spotty and correlated with presence of red or white pine stands and plantations. Concentrations occurred at Pinery and

Rondeau provincial parks, Long Point, the moraines between Cambridge and Hamilton, and at the base of the Bruce Peninsula. It was absent in the urbanized Toronto area and the intensive agricultural areas of Essex, Chatham-Kent, Lambton, Huron, and Niagara except for the locations previously mentioned (Eagles in Cadman et al. 1987). James (1991) considered the Pine Warbler an uncommon to locally common summer resident in the south that was occasional and rare in the north to Kenora, Thunder Bay, and Wawa.

The second atlas demonstrated that the range of the Pine Warbler had apparently expanded northward into the Boreal Forest Region, north to Cochrane, Timmins, Nakina, Armstrong, and Ear Falls. Distribution continued to be local north of Sault St. Marie and Sudbury. Its distribution south of the Shield was much more continuous, but it was still absent in Essex County and the Region of Niagara. Its probability of observation increased significantly from the first atlas province-wide and in all regions where it occurred. Overall, there was more than a 100% increase in its probability of observation with greatest increases south of the Shield. These increases were attributed to the maturation of pine plantations, but it is possible that atlassers were more proficient at recognizing its song. Highest densities of the Pine Warbler occurred in the Shield portion of the Great Lakes–St. Lawrence Forest Region. Highest abundances occurred along the eastern shoreline of Georgina Bay, the southern edge of the Shield, on the Frontenac Axis, and from eastern Algonquin Park northeast to the Ottawa River. These areas consistently have higher coverage by pine forests (Crins in Cadman et al. 2007). Curry (2006) noted that the Pine Warbler had increased significantly in the Hamilton area in the past 25 years due to maturation of pine plantations and growth of white pine in conservation areas.

The Pine Warbler appears to have increased significantly rangewide. From 1966 to 1996, Breeding Bird Survey (BBS) data indicated that it increased at a rate of 1.2% per year (Rodewald et al. 2020). BBS results indicate that it increased at annual rates of 2.81% in Canada and 2.55% in Ontario 1970-2021. Trends for 2011-21 were annual increases of 2.08% in Canada and 1.83% in Ontario. The long-term trends were highly reliable; the short-term trends were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Once the young fledge, both young and adults may move out of typical pine breeding habitat, but very little information is available. Family groups are often seen after the young fledge and these may form larger flocks in late August. In Arkansas, a flock of 15 juveniles was seen in early July. In Michigan, adults and young may move from the nesting area with taller pines into regenerating, shrubby, burned areas. Birds have been documented during the postfledging period at the peak of Mount Mitchell (2,037 m) in North Carolina, where no breeding occurs in the spruce–balsam fir forests. In Missouri, mist-netting was conducted during the postfledging season in an oak-pine-hickory forest 2-15 years after it was clear-cut. Only 8 Pine Warblers were captured during this period: 1 2 years after harvest, 1 3 years after harvest, 3 6 years after harvest, 2 7 years after harvest, and 1 9 years after harvest. The Pine Warbler has been seen in small flocks around buildings during the postfledging period, associating with Eastern Bluebirds and Chipping Sparrows (Bent 1953; Porneluzi et al. 2014; Rodewald et al. 2020).

MIGRATION

The Pine Warbler is a short-distance migrant in the northern portion of its range and a resident in the south. Populations that breed north of central Arkansas, southern Tennessee, southern Virginia, and Missouri are migratory. Those breeding in the southeastern United States and the West Indies are resident non-migratory birds. Migratory birds travel no further south than central Florida. Kills at towers indicate that it is a nocturnal migrant. One bird used different wintering areas (Arkansas and Mississippi) in subsequent years suggesting that some individuals may use different migratory corridors in some years. During migration, Pine Warblers often occur in mixed flocks with other warblers (Rodewald et al. 2020).

The Pine Warbler is one of the earliest warblers to arrive in spring. In Ontario, it typically arrives in mid-April. Some arrive in early April and there are some records from March, but these may represent overwintering birds (Black and Roy 2010; Curry 2006; Fleming 1907; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

Average departure from the southern Shield is in late September and the latest birds occur in late October (Mills 1981; Tozer 2012). In the south, autumn migration extends from mid-August to mid-October, with rare records through to December (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

Even during migration, the Pine Warbler demonstrates a clear preference for pines. During spring migration in North Carolina, numbers seen per hour were 1.86 in pine forest, 0.75 in pine-hardwood forests, 0.37 in floodplain forests, 0.07 in oak-hickory forests, and 0 in wet and dry thickets, beech forests, and oak forests. These results are typical, with it selecting pines wherever they are available. If pines are absent or scarce, it may occur in deciduous habitats, especially in spring, but it tends to be more confined to pines in autumn. It may heavily use deciduous habitats in some areas, and may also occur in orchards, residential areas, and rural residential lots. During autumn migration in Pennsylvania, it was equally abundant in forest edges, shrub-sapling-stage forests, forest interior, forest-agricultural edges, and suburban forests. It was not observed in pole-stage forests (Chapman 1907; Graber et al. 1983; Parnell 1969; Rodewald and Brittingham 2002; Rodewald et al. 2020).

During spring migration in North Carolina, 61.4% of foraging occurred in the canopy, 38.6% in low trees, and 0% in shrubs and on the ground. In the canopy, 15.8% of foraging occurred at the top of the crown, 19.3% in the inner crown, 26.3% in the lower crown, and 0% on the bole. In low trees, 10.5% of foraging occurred at the top of the crown, 22.8% in the inner crown, 5.3% in the lower crown, and 0% on the bole. Singing males were observed at heights of 4.6 m to more than 15 m (average 13.5 m). Nonsinging birds ranged from 5 to more than 15 m (average 12 m; Parnell 1969). During autumn migration at Prince Edward Point, feeding heights were 3-17 m with a peak around 10 m. Forty-four percent of foraging occurred on outer leaves, 22% on twigs and inner leaves, 20% on sapling foliage, and 11% on outer branches. The Pine Warbler was not observed foraging in the air, on inner branches, trunks, sapling branches, low shrubs, or the ground (Keast 1980). In autumn and winter, it regularly forages in the leaf litter on the forest floor and sometimes in open habitats near forest edge. On the ground, it flips over leaves, pieces of bark, or small stones with its bill in search of prey (Bent 1953; Rodewald et al. 2020; Tozer 2012). The Pine Warbler is often aggressive while in mixed-species flocks during autumn and winter. Individuals that it chases or supplants often

have food items in their bills, suggesting that it may occasionally steal or catch dropped food items from other birds. During spring migration and summer in Arkansas, 53% of prey was obtained from pine foliage, 23% from bark, 8% from the air, 8% from deciduous foliage, 4% from leaf litter, and 4% from pine cones. In autumn and winter, 43% of foraging observations were in pine foliage, 30% on bark, 13% in the air, 5% in leaf litter, 2% in deciduous foliage, and 2% in pine cones. In autumn and winter in Louisiana, 94% of food items were obtained by gleaning, 4.5% by sallying, and 1.5% by hanging. In Arkansas during the same period, 68% of food items were obtained by gleaning, 16% by sallying, and 16% by hanging. During spring and summer in Arkansas, 63% of food items were obtained by gleaning, 22% by sallying, and 15% by hanging (Rodewald et al. 2020).

Early spring migrants may appear at feeders where they eat suet and peanuts (Tozer 2012; personal observation). In late autumn in New York, Russack (1955) observed Pine Warblers feeding on pine needle scale insects. This insect occurred in both white and Scotch pines, but warblers were not observed foraging in Scotch pine. This is the only warbler that is known to regularly consume seeds, predominantly pine seeds and seeds at feeders. Away from feeders, the importance of seeds in the autumn and winter diet is unknown. In addition to feeding on pine seeds, it also consumes the fruit of dogwoods, wild grape, bayberry, Virginia creeper, and sumac (Bent 1953; Rodewald et al. 2020).

The Pine Warbler may strike tall structures during migration, but is much less likely to do so than other species. Only 2 were killed at the Lennox generating station chimneys (Graber et al. 1983; Rodewald et al. 2020; Weir 2008).

James (1991) considered the Pine Warbler a rare migrant in Ontario. Most regional works concur that it is rare to uncommon during migration, but it is a common spring and autumn migrant in Algonquin Park (Tozer 2012).

WINTER

The Pine Warbler is typically absent in winter where the average minimum January temperature drops below –1°C. Although some birds regularly winter as far north as Massachusetts, most occur from Virginia and southern Illinois south to Florida and the Gulf states. Despite most birds remaining in areas where temperatures seldom drop below –1°C on average, individuals have withstood much colder weather. An Illinois bird survived temperature as low as –14.4°C with a high of –7.8°C. One bird apparently survived blizzards and temperatures as low as –31.7°C in Minnesota. Another Minnesota bird appeared to be suffering stress in a light wind and –17.8°C. Many were killed in South Carolina after 13 cm of snow and near 0°C temperatures. Lack of access to suitable foraging substrates due to snow or ice may be more harmful than cold temperatures (Bent 1953; Rodewald et al. 2020; Root 1988; Tamar 1997). It is an avoider of snow and is most likely to occur where there are frequent changes between snow cover and bare ground (Keyser et al. 2023).

In its typical winter range, the Pine Warbler is most common in pine habitats with low-growing or sparse understorey, and is particularly abundant in the loblolly–shortleaf pine forests of the southeastern United States. Pine barrens are also characteristic habitats. Smaller numbers may occur in shrub and forest edge habitats as well as suburban areas where individuals or small groups may attend bird feeders. It may also forage on the ground in fields and pastures near forest habitat. It may visit deciduous forests, orchards, and lowland thickets in winter (Bent 1953; Chapman 1907;

Rodewald et al. 2020; Root 1988). In Ontario, it is probably associated with feeders, with habitat type being secondary to food availability.

Although the Pine Warbler may be aggressive to other species, there is no evidence that it defends a winter territory.

In winter, the Pine Warbler normally forages on the ground and proximal parts of pine limbs. It wedges pine seeds into bark crevices and pecks them open. It has been observed foraging amidst fallen leaves and tearing apart old oak leaves to eat the eggs and young of gall insects. It eats large numbers of scale insects and has fed on bean sprouts in a dumpster and on Manitoba maple sap. Although it may occur singly in winter, it most frequently joins mixed flocks that may contain chickadees, Tufted Titmouse, Downy Woodpecker, Brown Creeper, kinglets, Eastern Bluebird, Palm Warbler, Chipping Sparrow, Yellow-rumped Warbler, Dark-eyed Junco, Hermit Thrush, and White-throated Sparrow. It readily visits bird feeders where it dominates the House Finch and Downy Woodpecker but is subordinate to the Tufted Titmouse, Mourning Dove, Red-bellied Woodpecker, and House Sparrow (Bent 1953; Rodewald et al. 2020; Root 1988; Tamar 1997). The Pine Warbler typically visits feeders only in the coldest parts of winter with few sites reporting regular sightings throughout the winter. Favourite feeder foods are bird puddings, suet, and peanut butter mixes. Infrequently consumed foods include mixed seeds, cracked corn, black oil and striped sunflower seeds (only if they are broken up), water, and baked goods (Dunn and Tessaglia-Hymes 1999). It also eats cornmeal, nutmeats, bread, niger seeds, piecrust, millet, and peanuts (Harrison 1984; Rodewald et al. 2020; Tamar 1997). A wintering bird in Illinois made most visits to a platform feeder where black oil sunflower seeds and bread granules were provided, followed by a suet feeder, niger feeder, and suet crumbs on the ground (Tamar 1997).

James (1991) considered the Pine Warbler a rare and occasional winter resident in the south. It has overwintered in London and is very rare in winter in Elgin County. There are 9 records of it overwintering in Hamilton (Curry 2006; Lancaster et al. 2004).

Yellow-rumped Warbler

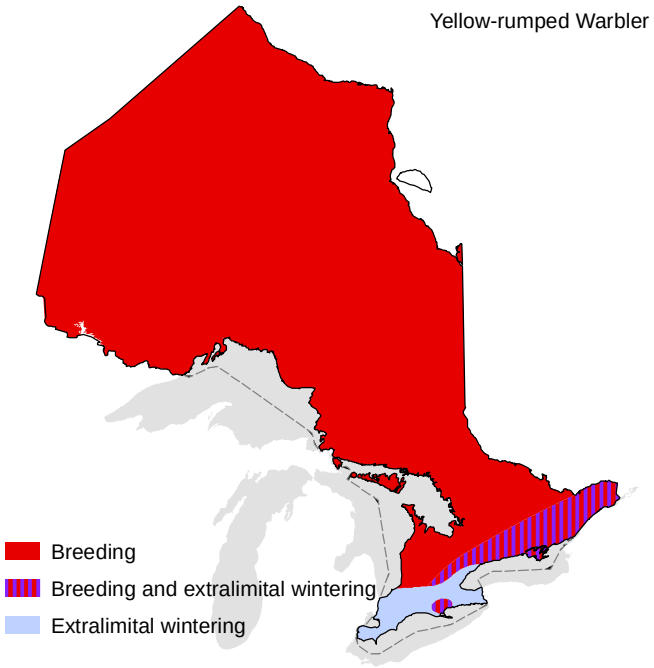
Setophaga coronata

BREEDING SEASON

Habitat Requirements

In Ontario, the Yellow-rumped Warbler usually breeds in mature and second-growth forests. It selected coniferous woods more (40.2% of nests) than mixed (37.3%) and deciduous (3.9%) woods; 81.4% of nests were in forested areas. Other nesting areas included on treed lawns and gardens of cottage and residential lots (6.9%), in spruce or tamarack bogs or fens (5.9%), at beaver ponds (2.9%), in hawthorn thickets (2.0%), and in a hedgerow (1.0%). Most nests were in open woods or at woodland edges, often near roads or water. Only 1 nest was reported from forest interior. It nested more frequently in dry than wet areas (Peck and James 1987). It breeds in coniferous and mixed forests where trees may range from short to very tall. Trees may be scattered, such as at edges or in openings and fens, or relatively dense. It has a wide tolerance to a variety of forest conditions, but prefers taller trees and open coniferous forests (James 1984b).

The Yellow-rumped Warbler occurred in all forested areas of the Hudson Bay Lowland. It was common in Moosonee, particularly in large forested areas (Wilson and McRae 1993). It bred in drier spruce forests on both the Hudson Bay and James Bay coasts (Manning 1952).



In the Boreal Forest Region from Pickle Lake north to the Manitoba border, the Yellow-rumped Warbler was most abundant in coniferous forests both with and without understorey, followed by deciduous scrub, mixed forests, heath, and coniferous scrub. It was absent in deciduous forests, mixed scrub, and tundra (McLaren and McLaren 1981). Near Pickle Lake, it was the most numerous warbler in all types of forest, but was still uncommon (James 1980). Near Lake Nipigon in spruce and balsam fir forests, it preferred semiopen to dense forests (Kendeigh 1947). Near Manitouwadge in spruce-fir forests, it was more abundant in stands 60-223 years old than in younger stands (Venier et al. 2009). In jack pine stands near White River, it was most abundant in stands 23-25 years old. It was a significant indicator of this age class of forest. Trees in this age class seldom exceeded 10 m in height. It was strongly associated with structure in the stratum 2.5-5 m from ground and negatively associated with coarse woody debris (Venier and Pearce 2005). Near Hearst, it nested in clear-cuts and uncut upland mixed and lowland coniferous forests. It occurred in clear-cuts as young as 6 years in both upland and lowland habitats (Welsh and Fillman 1980). In the Clay Belt, Welsh and Lougheed (1996) found breeding evidence in all types of forests that they examined: jack pine, black spruce, white spruce, white birch, trembling aspen, balsam poplar, white cedar, and tamarack. It occurred in stands situated on very wet to very dry soils on nutrient-poor to nutrient-rich sites.

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Yellow-rumped Warbler occurred in mature and old-growth white pine stands in approximately equal densities (Kirk et al. 2012). In jack pine stands near Gogama, it was one of the most common species in all habitats but occurred in mixed forests only where jack pine was the dominant tree. It began to colonize habitats when jack pines were 5-6 m tall and reached maximum densities once pines attained heights of 10-12 m. It preferred areas of forest that were slightly open but occurred almost everywhere, including in some very dense patches (James and Peck 1995a). Near Parry Sound, it occurred in moderate densities in young open stands of jack pine mixed with a variety of deciduous tree species (James 1979a). It was the most common warbler in Parry Sound and Muskoka districts wherever conifers were available, especially pines (Mills 1981). In Algonquin Park, the Yellow-rumped Warbler bred in stands dominated by black spruce, black spruce–white cedar, balsam fir–spruce, white birch–poplar–balsam fir–spruce, white birch–poplar, and hemlock. In mixed forests, it was not observed above 12 m, which represented the top of the coniferous forest canopy. In balsam fir–spruce stands, it occupied the central portion of the canopy. In black spruce–white cedar, it occurred from the ground to the top of the cedars, although the spruce extended another 9 m

above this. In white birch–poplar, it occurred from just below the tops of the shrubs to about 5 m below the canopy. In hemlock, it occurred from the shrub layer to mid-canopy. It was third in abundance in hemlock stands. Martin (1960) considered it characteristic of boreal forest. Martin (1960) and Kingsley and Nol (1999) reported it in young white pine stands in Algonquin Park, and it may be the most common species in these stands. In Muskoka District and Haliburton County, it was associated with mixed woods with some understorey, moderate canopy volume and tree density, and very low amounts of understorey vegetation. Its habitat was characteristic of areas in mature woods where selective tree removal had occurred or of immature woods that were regenerating on cleared cottage lots (Clark et al. 1983).

South of the Shield, the Yellow-rumped Warbler is associated with natural coniferous and mixed forests and coniferous plantations. McIlwraith (1894) reported breeding in a black ash–white cedar–balsam fir swamp near Listowel. It first occurred during the breeding season in the Hamilton region in 1974 in a coniferous plantation (Curry 2006).

The Yellow-rumped Warbler is the most common and widespread forest-dwelling warbler in Canada and North America. It is a habitat generalist, but prefers coniferous and mixed forests to those dominated by deciduous species. Although it prefers forests containing confers, it also nests in deciduous stands dominated by aspen, birch, or willow, especially in the Yukon. It prefers more mature stands and those that are open in nature, but also occurs in immature and dense stands. Erskine (1977) stated that it was one of the most typical boreal species where it is ubiquitous and often a dominant species along with the Swainson's Thrush and Dark-eyed Junco. In the Yukon, these 3 species are dominant in all forest types whether they are coniferous or deciduous, successional, or climax. In the Boreal Forest Region, the Yellow-rumped Warbler is characteristic of spruce and balsam fir forests, is found in most jack pine stands, and is often present in black spruce and tamarack bogs with more or taller trees. It is also characteristic of tundra and alpine ecotones at the edge of boreal forest. Erskine's (1977) conclusions are supported by those of Hunt and Flaspohler (2020), Morse (1974, 1976), Letourneau and Lafontaine (in Gauthier and Aubry 1996), Campbell et al. (2001), and Sinclair et al. (2003). East of the Rocky Mountains, 88% of nests were in forests, 6% were in wet areas, and 2% were in open or orchard-like habitats. Of nests in forests, 92% were in coniferous forests, 7% in mixed forests, and 1% in deciduous forests. Further south, pine forests become important and plantations 40-50 years old and older provide suitable habitat. In addition to Ontario, plantations have contributed to its southward range expansion in New York, Pennsylvania, and West Virginia. This warbler also nests in fens, young strip-cuts in Quebec, regenerating clear-cuts, small treed islands, open pastures with clumps of conifers, windbreaks, and human-influenced habitats. In British Columbia, 25% of nests were in human-influenced habitats including suburban, urban, and rural areas; cultivated farmlands; recreational areas; pastures; orchards; and logged areas. Backyard gardens and residential areas were the most reported nesting areas in human-influenced habitats (Back 1979; Bent 1953; Campbell et al. 2001; Capen 1979; Crawford and Titterington 1979; Dawson 1979; DeGraaf and Chadwick 1987; Falardeau et al. 1999; Freedman and Johnson 1999; Hoffman 1989a; Holmes and Sherry 2001; Hunt and Flaspohler 2020; Lent and Capen 1995; Morgan and Freedman 1986; Mossman et al. 1991; Niemi and Hanowski 1984b; Noon et al. 1979; Temple et al. 1979).

Some studies examined the Yellow-rumped Warbler's habitat preferences at the landscape scale or at multiple scales. In Saskatchewan, it was randomly distributed in fragmented and contiguously forested landscapes. It was most common in large forest fragments in areas of low forest cover within 5 km, and this relationship was significant (Hobson and Bayne 2000). In New Hampshire, it was found throughout alpine treed areas, but the population centre was in the high-altitude conifer region just below the krummholz (Sabo 1980). In Quebec, Drolet et al. (1999) examined 100-ha landscapes where forest cover ranged from a few to more than 90 ha. There were no significant differences in its abundance related to the amount of forest cover, edge, or core area within these landscapes. In Michigan, where it was one of the most abundant species, Crozier and Niemi (2003) studied its abundance in a naturally heterogeneous landscape of upland and lowland forests and wetlands. Its abundance was not related to any landscape parameters. In Newfoundland, Taylor and Krawchuk (2006) studied Yellow-rumped Warbler abundance in relation to amount of woodland cover at radii of 1,250 m (landscape scale), 150 m (neighbourhood scale), and 12.5 m (local scale). It was negatively associated with the amount of forest at the landscape scale but positively associated with forest at the local scale. The relationships between occurrence and forest cover were weak suggesting either that alternative scales were important to the warblers or that the researchers did not study the appropriate parameters. Another possibility is that it is a habitat generalist that is minimally affected by vegetation variables. In Newfoundland, Dalley et al. (2008) compared vegetation near nest sites to that of random sites. They considered the Yellow-rumped Warbler an ecological generalist but one that was largely confined to coniferous forests for breeding. Compared with random sites, nest sites had significantly more large downed wood and more stems 1-2 m tall and more than 2 m tall within a 1-m radius. Within a 5-m radius, nest sites had more canopy cover, more stems 1-2 m tall, and fewer stems taller than 2 m than random sites. Within this radius, successful nests had less high ground cover vegetation than unsuccessful nests. Nest sites had fewer openings and were located in areas with denser understorey 1-2 m tall. Vegetation taller than 2 m is found within the territory at random sites and is characteristic of the nest site at the larger scale, but is not selected for at the nest microsite scale.

Other studies examined the Yellow-rumped Warbler's preference for forest type. Flack (1976) determined that it was common in pure aspen stands in the western mountains and was not dependent upon conifers. In the western Boreal Forest Region, it was most abundant in black spruce forests. It was associated with dry nutrient-poor stands and moderately old stands (Kirk et al. 1996). In New Brunswick, its presence was correlated with high densities of coniferous stems. Stand types that it selected, in order of preference, included pines, spruce–tolerant hardwoods, and spruce–intolerant hardwoods. Stand types it used less than their availability, in declining order of avoidance, included intolerant hardwoods–tolerant hardwoods, intolerant hardwoods, spruce–balsam fir, and intolerant hardwoods–spruce (Parker et al. 1999). In Saskatchewan, it significantly selected for forest type and was most common in white spruce stands that were large but isolated. Spruce stands were preferred, followed by mixed stands. It made little use of trembling aspen stands (Hobson and Bayne 2000).

Some studies determined the Yellow-rumped Warbler's preference for stand age or seral stage. In balsam fir stands in Newfoundland, it was significantly more abundant in uncut stands older than 80 years than in 40-year-old second growth. It was also more common in mature stands than 60-

year-old stands, but not significantly. Uncut old stands had a more open structure with lower tree and small tree density, more gaps, fewer small deciduous trees, more varied tree height profile, shorter small trees, larger diameter living and dead trees, more dead wood on the ground, less litter cover, and more moss cover. It was associated with intermediate-aged stands on nutrient-poor sites with moderate amounts of deciduous species (Thompson et al. 1999). In the western Boreal Forest Region, the Yellow-rumped Warbler was in a guild of species associated with conifers. It was absent in stands 9 years old and younger and increased with increasing stand age, being most abundant in stands 80 years old, the oldest age class studied (Kirk et al. 1996). In Pennsylvania, it occurred in 9.1% of old-growth forests, 6.4% of stands state-wide, and 12.6% of stands in the Appalachian Plateau. Haney (1999) did not consider it to have positive or negative affinities for old-growth forests. In Maine, Titterington et al. (1979) determined that it was associated with coniferous overstorey. In spruce–balsam fir forests, it was present in low density in very recent clear-cuts characterized by dense slash and abundant bare ground. It was absent in the next 2 seral stages of regeneration, reappeared in low density when hardwood regeneration consisted of trees taller than 4.5 m with a diameter at breast height (DBH) of 10-15 cm, and was most abundant in spruce-fir forests with a dense canopy and an open forest floor. In aspen stands in Alberta, it was significantly more abundant in stands older than 120 years than in stands 23-26 or 51-63 years old. Schieck et al. (1995) considered it a canopy species associated with tree richness, downed woody material larger than 20 cm, canopy height, shrub richness, trees larger than 20 cm DBH, and conifer density. It was negatively correlated with aspen density. In black spruce stands in Quebec, it was least abundant in recent burns and clear-cuts and most abundant in stands 120 and 200 years old and those where clear-cutting had occurred 5-11 years previously (Imbeau et al. 1999).

Several studies determined microhabitat preferences of the Yellow-rumped Warbler. In New Hampshire and Maine, it was associated chiefly with white pine and balsam fir. It was positively correlated with the number of conifers 2-10 cm DBH and negatively correlated with percent ground cover, the number of deciduous trees larger than 10 cm DBH, and foliage volume of conifers less than 2 cm and 2-10 cm DBH (DeGraaf et al. 1998). Collins (1983a) compared its habitat preferences in Maine and Minnesota and found significant differences in amount of ground cover, canopy cover, and trees 15.1-23 cm DBH in territories. In Minnesota, it was in a group of forest and edge species occupying areas with high ground cover (70%) and moderate canopy cover. In Maine, it was in a group of forest species in areas with high percent canopy cover, variable coniferous cover, and many trees in the smaller size classes. In Minnesota, it was associated with large trees and large conifers; in Maine, it was associated with large trees and moderate canopy cover. Collins et al. (1982) determined that it was associated with mixed and coniferous forests supporting spruce or balsam fir in Minnesota. It was in a guild of species that occurred predominantly in mature undisturbed forests containing conifers. Distinctive features of the habitat of this group included greater than 50% coniferous coverage, mostly in the larger tree classes. Average habitat conditions in territories included 84.0% ground cover, 44.0% shrub cover, 66.0% canopy cover, 16.2 m canopy height, 58.0% coniferous cover, 4.8 tree species per 0.04 ha, 31.4 trees 7.5-15 cm DBH, 11.8 trees 15.1-23 cm DBH, 6.4 trees 23.1-30 cm DBH, 3.2 trees 30.1-38 cm DBH, 1.6 trees 38.1-53 cm DBH, 0.2 tree 53.1-68 cm DBH, and 0 tree larger than 68 cm DBH. Sabo (1980) characterized average habitat conditions in subalpine forests in New Hampshire territories as being at mid-slope and containing damp

depressions, 7.9 m canopy height, 59% canopy coverage, 72% conifer foliage volume, 33% conifer foliage volume 0-2 m from the ground, 17% deciduous leaf foliage volume above 5 m, and average DBH of live trees 10 cm.

Freemark and Collins (1992) considered the Yellow-rumped Warbler a forest-interior species, but this is incorrect. Only 1 Ontario nest was in forest interior and the remainder were in edge habitats (Peck and James 1987). Taylor and Krawchuk (2006) and Taylor and Taylor (1979) concluded that it was a forest-edge species that also occupied small openings. In Vermont, territories commonly bordered clear-cuts and occasionally extended a short distance into them (Lent and Capen 1995). In Alberta, Villard et al. (2007) predicted that it would avoid clear-cut edges but it did not exhibit edge avoidance. In Minnesota, there was no difference in the distance from the centre of the territory to transects in forests and on electrical transmission line cuts (Niemi and Hanowski 1984b). In Newfoundland, it was ubiquitous in balsam fir forests. It was equally abundant in riparian edge, forest–clear-cut edge, and forest interior (Whitaker and Montevecchi 1997, 1999). In Quebec, there was no significant difference in its abundance in riparian and nonriparian balsam fir stands, although it tended to be more abundant in riparian edges (LaRue et al. 1995). Wiebe and Martin (1998) studied populations in coniferous forests and dense deciduous riparian strips at edges of these forests in British Columbia. It was less common in riparian edges than in coniferous forests, but not significantly.

Freemark and Collins (1992) stated that there was uncertainty as to whether or not the Yellow-rumped Warbler is area sensitive. There appear to be no references to its being area sensitive in the literature. No relationship between Yellow-rumped Warbler presence or abundance and forest size was found in New Hampshire, Maine, or Saskatchewan (DeGraaf et al. 1998; Hobson and Bayne 2000). In Michigan, it was positively associated with patch size in jack pine stands but negatively correlated with patch size in red pine stands (Crozier and Niemi 2003). In Maine, it bred successfully on islands where forest size was only 0.35-1.50 ha (Morse 1971b, 1977). In Minnesota, it nested on islands 0.04-1.1 ha that were 30-450 m from the mainland. Its frequency of occurrence was 81% on small islands, 100% on large islands, and 91% on the mainland (Howe 1979).

Most Ontario nests were in living trees and shrubs, although 4 were in dead trees, 1 was on the top of a rail of a vine-clad trellis, and another was in the hollow top of a dead stub. Coniferous trees (6 species) were selected more frequently (93.3% of nests) than deciduous trees or shrubs (4 species). The most frequently used nest trees were pines (58 nests of which 41 were in white pine), spruces (40 nests), white cedar (28 nests), balsam fir (10 nests), and birches (5 nests). Nests were on horizontal branches, supported and often concealed by adjacent branches (74.5% of nests); in crotches (23.6%); or among a group of almost vertical branches (1.8%). Most nests were well concealed with 56.8% near the trunk; others were 0.5-4.3 m from the trunk. Nests were 0.6-20 m from the ground with most 2-6 m up (Peck and James 1987, 1998a). MacLulich (1938) reported a nest in Algonquin Park 1.2 m from the ground in a white cedar. Forty-four nests in Simcoe County were mostly in white pines at heights of 1.8-12.2 m (average 8.5 m). Twenty-eight were on horizontal limbs approximately two thirds of the distance out from the trunk but none were at the outermost tip of branches. Two were in the top clump of needles in young trees, 5 were on horizontal branches 0.9-4.6 m from the ground in small spruces, 5 were 4.6 m up in the crotch of a small cedar, and

another was 1.8 m up in a small balsam fir. At Garrison Petawawa, it nested in small jack pines. In northern Ontario, it nests in any species of conifer, but 1 nest was in a hawthorn (Bent 1953). In Muskoka and Parry Sound districts, almost all nests were in conifers, typically white pines, at heights of 2.4-13.7 m. One nest was in a white birch and another was in a white spruce (Mills 1981).

Most nests are on horizontal branches of conifers including pine, spruce, balsam fir, tamarack, hemlock, white cedar, and red cedar. The Yellow-rumped Warbler has also nested in white birch, alder, trembling aspen, apple, maple, hazelnut, snowberry, oak, and dogwood. Nests are occasionally placed over water or in dead trees and are rarely on the ground. Forty-four Maine nests were all in white spruce, red spruce, or balsam fir at heights of 1.8-13.1 m, but mostly at 3-6.1 m. Nests have been reported as high as 15.2 m from the ground. Average nest heights were 7.6 m in Wisconsin, 10.7 m in Arizona, 4.0 m in Newfoundland, 2.3 m in the United States east of the Rocky Mountains, and 7.1 m west of the mountains. One nest was on a wooden beam (Bent 1953; Campbell et al. 2001; Chapman 1907; Cruickshank 1956; Dalley et al. 2008; Harrison 1984; Hunt and Flaspohler 2020; Mousley 1916a; Nice 1930b; Sinclair et al. 2003).

North of Lake Nipigon early in the season, 1 male quickly covered more than 0.8 ha while singing and feeding and another covered 1.6 ha (Kendeigh 1947). In Algonquin Park, territories averaged 0.47 ha (range 0.05-1.82 ha; Martin 1960). On small islands 0.04-1.1 ha in Minnesota, birds commonly visited other islands or the nearby mainland. During 9 surveys on the most isolated island, which was 450 m from the mainland, birds were observed flying to or from it on 11 occasions (Howe 1979). In New Hampshire subalpine meadows, territories averaged 1.0 ha (Sabo 1980). In Maine, territories averaged 0.35 ha on small islands and 0.8 ha on the mainland. Larger territories on the mainland were attributed to the presence of numerous competing species (Morse 1976, 1977, 1989).

No information is available on natal philopatry rates. Band returns in the eastern United States suggested that the survival rate in the first year was 27.9% (Stewart 1988). Return rates to natal areas are probably low.

In Newfoundland, annual return rates of adult males were 27.0% in natural landscapes and 20.4% in landscapes containing clear-cuts. Return rates for females were 25.1% in natural landscapes and 20.6% in cut landscapes. A high proportion of birds that were captured were unbanded: 31.0% and 39.0% of males and 32.5% and 38.4% of females in natural and cut landscapes, respectively. Whitaker et al. (2008) attributed the low return and apparent survival rates to regular landscape-level movements of individuals.

Limiting Factors

Peck and James (1987) reported eggs in Ontario nests from the last week of May until the end of July, with most present in the last 3 weeks of June. A female was observed on a nest on 12 May in Muskoka District, suggesting an earlier egg date (Peck and James 1998a). In Algonquin Park, nests are under construction from early May to mid-July, eggs are present from late May to mid-July but mostly in June, and dependent fledglings have been observed from mid-June to early September (Tozer 2012).

It has been reported that it takes 10 days to build a nest. Although this may be true for southern resident birds, it is unlikely that northern migratory birds would take this long. The first egg is usually

laid within a day of nest completion. Eggs are laid at the rate of 1 a day but occasionally a day is skipped. Ontario nests had incubation periods of 11 days and at least 11 days. Incubation periods of 12-13 days have been reported elsewhere. The nestling period is 10-14 days (Bent 1953; Hunt and Flaspohler 2020; Peck and James 1987).

The Yellow-rumped Warbler typically raises a single brood. It has been reported to produce second broods in Nova Scotia and New England, and possibly Quebec, but double-brooding has yet to be confirmed with banded birds. Renesting may occur if the first nest is lost. In Ontario, clutches of 2-6 eggs were reported (mode 4 eggs, mean 3.88 eggs). Usually 4 or 5 eggs are laid and clutches of 3-6 eggs have been reported elsewhere. Other average clutch sizes include 4.38 in Wisconsin, 4.13 in Maine and Vermont, 3.86 in Arizona, 4.09 in the Prairie Provinces, and 3.70 in Newfoundland. In British Columbia, 65% of clutches contained 3 or 4 eggs (Bent 1953; Campbell et al. 2001; Dalley et al. 2009; Hunt and Flaspohler 2020; Létourneau and Lafontaine in Gauthier and Aubry 1996; MacArthur 1958; Peck and James 1998a; Sodhi 1995).

The age at first breeding is unknown but is probably 1 year. Morse (1971b) observed that the Yellow-rumped Warbler occasionally occurred on small islands in Maine where it did not breed. He concluded that these birds represented a floater population, but it is equally as likely that these were breeding birds wandering about in their larger home ranges. Howe (1979) observed that birds breeding on small islands in Minnesota frequently flew to other islands and the mainland. In Maine, Hensley and Cope (1951) experimentally removed Yellow-rumped Warblers and they were quickly replaced. They concluded that there was a surplus nonbreeding population. This is a plausible explanation because 2 times the numbers of birds ingressed to the site as were removed. It is possible that these were breeding birds that wandered far from their breeding territories (Whitaker et al. 2008). The Yellow-rumped Warbler is presumed to be monogamous, but this has not been confirmed (Hunt and Flaspohler 2020).

Several studies examined the foraging strategies of the Yellow-rumped Warbler. Greenberg et al. (1999) studied its foraging patterns in the Ontario Clay Belt and Mackenzie District and found that it was associated mostly with conifers. In the Clay Belt, 69.0% of foraging was in conifers, 60.0% in foliage, 30.8% by aerial attacks, 4.2% by hanging, 14.4% by hovering, and 15.0% by reaching at an average height of 9.4 m, which was 63.0% of tree height. In Mackenzie District, 88.8% of foraging was in conifers, 86.0% in foliage, 44.3% by aerial attacks, 5.2% by hanging, 14.7% by hovering, and 18.3% by reaching at an average height of 10.4 m, which was 71.0% of tree height. In Parry Sound District, it foraged predominantly in conifers during the breeding and postfledging seasons as well as during autumn migration. The range of foraging heights was 4-14 m during the breeding season and 5-16 m in autumn (Mills 2007). Sabo (1980) characterized its foraging techniques in subalpine forests in New Hampshire as 0.8% aerial flycatching, 39.5% leaf gleaning, 15.2% leaf hawking, 9.6% leaf hovering, 5.1% twig pecking, 17.9% twig gleaning, 6.5% twig hawking and hovering, 1.1% branch pecking, 1.9% branch gleaning, 1.9% bole pecking, 1.0% bole gleaning, and 0% litter pecking, litter gleaning, and fallen log manoeuvres. Foraging was conducted 50.4% proximal to the trunk and 49.6% distal; 60.4% of foraging occurred in conifers, 36.5% in deciduous foliage, and 0.3% on the forest floor. Foraging occurred from the ground to the upper canopy: 3.5% at 0.1-2 m, 39.9% at 2-5 m (the midstorey), 37.3% at 5-8 m (the midcanopy), and 19.1% above 8 m (the upper canopy). North

of Lake Nipigon, it foraged from the ground to treetops (Kendeigh 1947). On small islands in Minnesota, it foraged from the ground to above 15 m, but mostly at 3-12 m; 48% of foraging was on branches and twigs proximal to the trunk and 52% was distal. Sixty percent of foraging time was spent in red pine, 28% in white pine, 3% in balsam fir, 3% in spruce, 2% in deciduous trees, and 4% in other. It preferred medium-height pine foliage, which was the most abundant substrate, and used all parts of the tree. It foraged in many of the same locations as the Pine Warbler, but spread its activity among more tree species and heights. The Yellow-rumped Warbler appeared to be the most generalized of all pine forest canopy foragers on the islands (Howe 1979). On small islands in Maine, the Yellow-rumped Warbler demonstrated more plasticity in foraging than the Black-throated Green Warbler and in several cases deviated markedly from the mean of the large population of warblers. The Yellow-rumped Warbler foraged mostly on small limbs and spent lesser amounts of time on large limbs, tips of branches, dead limbs, and deciduous growth. In the absence of the Black-throated Green Warbler, it had a strong tendency to use the outer parts of foliage and small limbs on 1 island and regularly used the abundant deciduous vegetation on another island. The Yellow-rumped Warbler may modify its foraging techniques in the absence of the Black-throated Green Warbler. Male Yellow-rumped Warblers displayed greater foraging diversity on small islands than on the mainland where there was a larger guild of spruce-foraging warblers. Males had greater foraging diversity on islands supporting 2 warbler species than on islands with 3 species, but there was no evidence of this for females. The tendency of the Yellow-rumped Warbler to expand its areas of foraging in the absence of the Black-throated Green Warbler suggests that it restricts the foraging activities of the Yellow-rumped Warbler. In turn, the Yellow-rumped Warbler restricts the foraging activities of the Northern Parula (Morse 1971b). Also in Maine, Morse (1976) observed that the activity of the Red-breasted Nuthatch overlapped mostly with that of the Yellow-rumped Warbler, but the warbler did not forage on trunks. No simple relationship was found between the abundance of the Yellow-rumped Warbler and variables such as foliage characteristics and insect abundance and biomass. Prey abundance did not influence territory size. Maine birds foraged at heights of 0-13.7 m in a forest averaging 21.3 m tall. Mean foraging height was 7.8 m, 36.6% of tree height. On spruce, 14.6% of foraging occurred at the tips of foliage, 17.7% on twigs 5 mm or less in diameter, 0.8% on dead twigs, 30.0% on dead branches, 19.2% by flycatching, 0.8% on deciduous growth, and 3.1% on the ground. Gleaning represented 10.8% of foraging activities at the tips of foliage, 0.8% on dead twigs, and 29.2% on dead branches. Hovering constituted 3.8% of foraging at tips of foliage and 0.8% on dead branches. In branches covered with beard lichen, 1.5% of foraging was distal to the trunk and 12.3% was proximal (Morse 1967). Morse (1989) concluded that the Yellow-rumped Warbler concentrates foraging in the lower parts of trees where the habitat is open. It is one of the most flexible of the spruce-woods warblers that hawks for insects more than the other warblers, often from lower dead branches of the understorey. MacArthur (1958) observed the foraging locations and methods of warblers in spruce forests in Maine and Vermont. He concluded that differences in diet result from differences in feeding behaviour and positions in trees and that each species eats what food is available within the characteristic feeding zones by the characteristic methods of foraging. Trees were broken into 15 different feeding zones: 5 3-m tall intervals and 3 horizontal zones: B, which was the inner bare or lichen-covered branches; M, the middle area of old needles; and T, the terminal zone of new needles or buds. The area below the tree constituted a 16th zone. The areas with the highest percentage of observations were: below the tree, 12.9%; 3-6

m up in zone B, 11.8%; 15-18 m up in zone T, 11.8%; 12-15 m up in zone T, 10.6%; 6-9 m up in zone B, 9.1%. The percent time spent in the major areas was: 27.7% below the tree, 15.9% in zone B 3-6 m from the ground, and 9.8% in zone M 9-12 m from the ground. At least some foraging occurred in all zones, but it was least frequent in the interior and middle of the top 2 zones. It moved predominantly in a tangential direction while feeding, significantly different from the other warblers studied (Blackburnian, Bay-breasted, Cape May, and Black-throated Green warblers). Yellow-rumped and Cape May warblers hawked and undertook long flights significantly more than other species, which tended to search trees more thoroughly before moving on. The Yellow-rumped Warbler had the most widely distributed feeding zone and foraged extensively on the ground, predominantly on emerging crane flies. Its feeding behaviour was so flexible that there was no correlation between the insects captured and specific feeding zones. Its abundance was constant in plots with varying foliage volume over 6 m, only increasing slowly as foliage volume increased. This was probably due to its flycatching and ground-feeding habits that make it less dependent upon foliage. In these study areas, it was present in many habitats but never abundant. It may be a marginal species in New England spruce woods but, by being less specialized and more flexible in its foraging, it manages to maintain a constant low population. Cumming (2004) conducted a similar study in old-growth mixed woods in Saskatchewan. In conifers, 15% or more of foraging occurred in the middle outer zone, 10-14.9% in each of the outer and central parts of the second zone from the top and the central portion of the central zone, and 5-9.9% each in the top outer zone, in the inner portion of the second and third zones from the top, and in the inner and outer areas of the fourth zone from the top. Foraging was not documented in the inner and central portions of the top zone, the inner portion of the fourth zone, and the entire bottom zone. It used white spruce more than its availability and trembling aspen less than its availability, and was the most diversely foraging species in conifers. The bottoms of trees and large inner branches were used less than their availability. It appeared to be less affected by branch structure in conifers than the other warblers and used balsam fir in proportion to its availability. It used tall canopy trees significantly more than the Magnolia Warbler and Boreal Chickadee, and experienced the most overlap and probably the most competition from these species and the Ruby-crowned Kinglet. It occurred mostly in mid- to outer branches at mid- to upper heights in both coniferous and deciduous trees, the same areas used by Black-throated Green Warblers in the Maine and Vermont studies. No interaction was observed between these species and the Yellow-rumped Warbler was 8 times more abundant than the Black-throated Green Warbler. For this study, deciduous trees were divided into 3 vertical zones. In deciduous trees, 15% or more of foraging occurred in the outer top zone, 10-14.9% in the outer central zone, and 5-9.9% in the middle zone of all height classes. No foraging was observed in the inner zone of all height classes and in the lowest outer zone. Mean foraging heights were 7.0 m in conifers and 11.2 m in deciduous trees. The foraging strategies of the sexes were compared by Franzreb (1983) in Arizona and by Morse (1968) in Maine. In both cases, males foraged significantly higher than females: 17.7 m for males and 14.7 m for females in Arizona and 3-9 m for males and 3-6 m for females in Maine. In Maine, males hawked significantly more than females; females gleaned significantly more than males. Males foraging higher in trees may have increased opportunities for hawking. In Arizona, there was no difference between the sexes in methods of prey procurement, perch type, diameter of perch, or distance from the branch tip to the foraging site. Tree species selection differed significantly with females relying heavily on fir and males selecting spruce more frequently than

females. In both cases, habitat partitioning by the sexes appeared to be a result of concentrating their foraging activities near the location of their most important reproductive duties: singing and territorial defence by males and nesting by females. In Maine, males foraged lower than they sang, but their principal foraging areas were closer to their singing height than nest height. Malmborg and Willson (1988) studied Yellow-rumped Warblers feeding on fruit in Illinois woodlots in late summer and autumn. Ninety-six percent of foraging occurred in forest gaps, more than expected based on availability. In 1 year, it fed almost exclusively on fruits in treefall gaps, but not in the other year. It favoured foraging on isolated shrubs rather than clumps of shrubs. All birds left the area immediately after foraging, considerably more than expected, suggesting that it is a good disperser for the species that it consumed. More unusual foraging techniques include taking insects from spider webs and manure piles and skimming over water, gleaning insects from the surface (Harrison 1984; Hunt and Flaspohler 2020).

Nestlings are fed beetles, caterpillars, moths, lice from the adults' feet, and probably a variety of insects and possibly spiders (Bent 1953; Hunt and Flaspohler 2020; Nice 1930b). Adults eat predominantly insects and other small invertebrates early in the breeding season, but may eat some fruit and seeds late in the breeding season. Invertebrates that the Yellow-rumped Warbler has consumed include caterpillars, sawfly larvae, small grubs, leaf beetles, bark beetles, weevils, metallic wood-boring beetles, ants, scale insects, aphids and their eggs, grasshoppers and locusts, bugs, house flies and other flies, crane flies, caddisflies, chalcid wasps, ichneumonid wasps, gnats, spiders, budworm larvae and pupae, neuropterans, stink bugs, leafhoppers, and treehoppers. Six adults north of Lake Nipigon consumed 34.8% spiders, 28.9% beetles (scarab, ground, click, and leaf beetles), 11.8% lepidopterans, 7.8% hymenopterans, 5.9% aphids, 3.5% planthoppers, 2.4% neuropterans, 2.4% caddisflies, 1.6% mayflies, and 0.9% flies. In California, the diet consisted of 85% animal matter and 15% plant matter. The animal matter consisted of 26% hymenopterans (almost entirely ants but with some wasps and parasitic wasps), 20% bugs (scale insects, aphids, stink bugs, leafhoppers, and treehoppers, with aphids appearing to be favoured), 16% flies (house flies, crane flies, and gnats), 14% caterpillars, 6% beetles, and 2% other insects and spiders. Vegetable matter consisted of fruits and seeds, including those of beach grass; it has been documented puncturing grapes. In Maine, the average number of caterpillars in males' stomachs was 11.8, 57.1 times more than would be expected based upon availability. The caterpillar biomass in stomachs was 1.4-7.1 times greater than predicted if they ate average-sized larvae indicating that they selected for larger larvae. Caterpillars were the only food item taken more than expected. Foliage samples were dominated by aphids, but few were consumed. In Illinois woodlands in late summer and autumn, 100% of the diet was frugivorous in a year when fruit abundance was high. No fruit was consumed the following year when fruit abundance was moderate. In the year that it ate fruit, 77% was poison ivy, 15% was grape, and 8% was Virginia creeper. Fruit of elderberry, pokeweed, greenbrier, moonseed, and spicebush was present but not consumed. In Quebec, it eats red cedar berries and contributes to the dispersal of this plant. It was considered an important disperser of poison ivy in Illinois. It also eats the fruit of poison sumac and cranberries (Bent 1953; Hunt and Flaspohler 2020; Kendeigh 1947; Létourneau in Gauthier and Aubry 1996; Malmborg and Willson 1988; Morse 1976).

The Yellow-rumped Warbler readily consumes larger larvae and pupae of the black-headed budworm and the spruce budworm. In New Brunswick, variations in its density appeared to be

unrelated to black-headed budworm density. In Ontario near Manitouwadge and New Hampshire, its abundance did not change with increasing abundance of spruce budworms. In New Brunswick, it declined with increasing spruce budworm density. This was thought to be a response to the explosion in numbers of the budworm specialist warblers that may have outcompeted the Yellow-rumped Warbler. Over 2 years in Maine, spruce budworm larvae and pupae constituted 26% and 7% of the invertebrates it consumed (Crawford and Jennings 1989; Gage et al. 1970; Gillespie and Kendeigh 1982; Mitchell 1952; Morris et al. 1958; Venier et al. 2009).

The Yellow-rumped Warbler typically accepts Brown-headed Cowbird eggs. If a cowbird egg is laid before the first warbler egg, it may abandon the nest. It rarely buries cowbird eggs in the nest. It is likely that this occurs only when the egg is laid before the nest is completed. In Ontario, 39 of 139 nests (28.1%) were parasitized; 65% of nests in Simcoe County were parasitized. In Quebec, 6% of 33 nests were parasitized and in British Columbia, 21% of 118 nests were parasitized and 43 cases of adults feeding cowbird fledglings were documented. There is a case of a warbler feeding a young cowbird from the Yukon. In Maine, 5 of 13 nests (38.5%) were parasitized. In unfragmented forests in Wisconsin, 2 of 8 nests (25.0%) were parasitized, and 1 was 6 km from the nearest grassland opening. Of nests reported to United States nest records schemes, 11 of 79 (13.9%) east of the Rocky Mountains were parasitized and 2 of 9 (22.2%) west of the Rockies were parasitized. It may be subject to parasitism because of its preference for nesting near forest edges. Both warblers and cowbirds may fledge from parasitized nests but the effects of parasitism on the reproductive productivity of the warbler are unknown (Bent 1953; Campbell et al. 2001; Harrison 1984; Hunt and Flaspohler 2020; Létourneau and Lafontaine in Gauthier and Aubry 1996; Peck and James 1998a; Sinclair et al. 2003).

Habitat loss and degradation is currently not an issue for the Yellow-rumped Warbler. Considerable habitat was undoubtedly lost when European settlers cleared the forests. Maturation of coniferous plantations south of the Canadian Shield has increased the amount of available habitat.

In the Boreal Forest Region of Ontario, there was no change in abundance of the Yellow-rumped Warbler when 30-50% of trees were harvested, but populations began to decline once 70% of trees were removed. Harvesting with only 10% retention of trees caused 50-75% reductions. When data from the west and east were included, it exhibited a 25% decrease at less than 24% tree retention and a 50% decrease with less than 13% tree retention. It does not appear to be unduly affected by harvesting as long as residual trees are retained (Vanderwel et al. 2007, 2009). In Ontario in the Canadian Shield in early successional stands, there was no difference in its abundance in clear-cuts and burns. In mid-successional stands, it was significantly less abundant in clear-cuts than in stands created by fire. It was equally abundant in mid-successional and mature stands but significantly less abundant in early successional than mature stands (Zimmerling et al. 2017). Tittler et al. (2001) examined the effects of retaining residual trees in clear-cuts in Alberta. The Yellow-rumped Warbler population remained stable in control areas but declined in clear-cuts. In the third year after logging, it increased with increasing basal area in clear-cuts. It was the only forest species that benefitted from residual tree retention. Dalley et al. (2009) studied warbler survival rates relative to the amount of forest removed by clear-cutting in Newfoundland. Daily survival rate was essentially the same when 5-40% of the area within 20 m of the nest was harvested and, at the 115-m and 1,250-m scales,

survival remained steady regardless of intensity of harvest but it declined steadily as 10-100% of harvest was removed at these scales in a year with highly variable and inclement weather. The authors concluded that the Yellow-rumped Warbler may be threatened by high levels of harvesting. Also in Newfoundland, Whitaker et al. (2008) observed that there were apparently higher survival rates in natural landscapes than those containing clear-cuts. Nonetheless, they concluded that the Yellow-rumped Warbler is a habitat generalist that is typically unaffected by clear-cuts. It usually exhibits no response to selective thinning or a slightly positive response. In Algonquin Park, Jobes et al. (2004) found no differences in its numbers in control plots and those selectively thinned 1-5 and 15-20 years previously. It was associated predominantly with the presence of small conifers. Tozer et al. (2010) found no differences in abundance in controls and typical- and group-selection cuts in the park. In shelterwood cuts in white pine in the park, it occurred on 85.7-100% of control plots over 2 years, 90-100% of 10-16-year-old cuts, and 75% of 2-9-year-old cuts (Kingsley and Nol 1999). In New York, there was no significant difference in its abundance in stands where 0%, 25%, 50%, 75%, or 100% of merchantable trees were removed. In all forest types in Alberta, it increased when 25-75% of trees were harvested but declined when 80-100% of trees were removed (Harrison et al. 2008). In Minnesota, it tended to increase slightly when partial harvesting occurred (Hanowski et al. 2003, 2005) and it responded positively to single-tree selection in Idaho (Medin and Booth 1989).

In California, Bock and Lynch (1970) reported identical densities of the Yellow-rumped Warbler in areas burned by a natural fire and unburned areas. The fire affected most of the area except for several small pockets where a few mature spruce and fir remained. These were sufficient to maintain the low density of this species. Stephens et al. (2015) found that severity of burns affected the response of this warbler in Oregon. It decreased with increased severity of burns.

On Anticosti Island, the Yellow-rumped Warbler was negatively affected by deer browsing in mature forests. In areas of high deer density, white birch and balsam fir were scarce but abundance of spruce regeneration was unaffected (Cardinal et al. 2012). In Oregon, Earnst et al. (2012) monitored bird populations 1-3 and 10-12 years after cattle were removed from a formerly heavily grazed area. In the absence of cattle, substantial regeneration of aspen occurred and the Yellow-rumped Warbler increased significantly.

The Yellow-rumped Warbler may be adversely affected by chronic noise. In Alberta, it was significantly less abundant at noisy compressor stations than at quiet well pads. Bayne et al. (2008) concluded that noise could affect birds as far as 700 m into the forest.

In Wyoming, Gutzwiller and Anderson (1999) deliberately disturbed plots by having a person walk through them for an hour. In 1 area in 1 of 3 years, the mean abundance of the Yellow-rumped Warbler was 71% higher outside intruded areas. At another site, there was no significant difference over a 5-year period. The researchers acknowledged that the single significant difference could be spurious.

Blake et al. (1992) studied the effects of drought on breeding bird populations in Michigan and Wisconsin. The Yellow-rumped Warbler increased in drought areas, possibly because of the warmer winters associated with drought.

Cold and rainy or snowy springs may result in high mortality. Daily survival rates of nestlings were significantly lower in Newfoundland in a year with cold, inclement weather. On small islands in Maine, essentially all nest losses were due to weather events such as high winds and rain (Dalley et al. 2009; Hunt and Flaspohler 2020; Morse 1971b).

In Alberta, the Yellow-rumped Warbler exhibited no response to energy sector disturbances. There was no difference in its abundance at seismic lines, pipelines, or well pads than in forest interior adjacent to these features (Bayne et al. 2016).

No significant effects due to environmental contaminants have been documented. Levels of DDE, DDT, and dieldrin in birds collected at a Florida tower were too low to have deleterious effects and no adverse effects have been documented from insecticides used to kill spruce budworms (Hunt and Flaspohler 2020).

Competitive interactions among the Yellow-rumped Warbler and other warblers occur, but the relationships do not appear to be consistent geographically. Morse (1971b, 1989) studied the relationships of the wood-warblers in Maine. On small islands, a maximum of 3 warbler species was present, including the Black-throated Green Warbler, Yellow-rumped Warbler, and Northern Parula. This was the order of dominance. The presence of the Black-throated Green Warbler inhibited the Yellow-rumped Warbler from accessing some foraging locations. Because the Yellow-rumped Warbler had large territories and low density on the Maine mainland, it was concluded that the Magnolia Warbler and Blackburnian Warbler, in addition to the Black-throated Green Warbler, are socially dominant to the Yellow-rumped Warbler and may limit its numbers. During a spruce budworm infestation in New Brunswick, Yellow-rumped Warblers declined and Tennessee and Bay-breasted warblers increased significantly. This suggested that one or both of these species are socially dominant to the Yellow-rumped Warbler (Morris et al. 1958). This is the only location where a negative response to budworm populations has been reported for the Yellow-rumped Warbler. In most cases, its population does not fluctuate with changing budworm populations. In Minnesota, the Yellow-rumped Warbler displaced the Pine Warbler and Bay-breasted Warbler on 2 islands, suggesting that it was socially dominant to them (Howe 1979). In Alberta, the Yellow-rumped Warbler foraged in the portions of trees that were dominated by the Black-throated Green Warbler in Maine and Vermont, and the Yellow-rumped Warbler was 8 times more abundant than the Black-throated Green Warbler (Cumming 2004). This suggests either that the dominance roles were reversed or that there were sufficient resources that competition was not required. From Quebec westward, the Yellow-rumped Warbler is one of the most abundant forest-breeding warblers and its territory sizes are about half the size reported in Maine. This suggests that competition from other warbler species is not a significant limiting factor in most of its range.

Price (2004) concluded that the Yellow-rumped Warbler might disappear in southern Ontario if the average summer temperature increased by 2°C.

Status

Baillie and Harrington (1937) considered the Yellow-rumped Warbler a common summer resident, breeding from Wellington, north York, and Frontenac counties to the transcontinental railway (and probably to James Bay) west to Lake of the Woods. Several were observed in July 1930 along the Ontario-Manitoba border between latitudes 53°N and 54°N, suggesting that breeding occurred in

this area. The centre of abundance was between Georgian Bay and Ottawa where it was the most common warbler in many places. The first atlas defined its distribution better. It was widespread from the southern edge of the Canadian Shield to the Hudson Bay Lowland where it was ubiquitous, except in extreme northern squares that consisted entirely of tundra with no tree cover. It was rather spotty in distribution in the Great Lakes–St. Lawrence Forest Region south of the Shield, except for in the Bruce Peninsula and on Manitoulin Island, where it was widespread. It was rare in the Carolinian Forest Region, with scattered records at Turkey Point, Long Point, Kettle Point, and Woodstock. Highest abundance was reported from Algonquin Park, Parry Sound District, and Manitoulin Island (Crins in Cadman et al. 1987). James (1991) considered it a common summer resident across the province, south to Georgian Bay and Ottawa, rarely south to Norfolk County.

The second atlas revealed that the distribution of the Yellow-rumped Warbler was similar in the north to the first atlas, but it was much more widespread in the off-Shield portion of the Great Lakes–St. Lawrence Forest Region. Although it was found in a few more squares in the Carolinian Forest Region, it remained rare there where it was associated mostly with coniferous plantations on sandy soils. Its probability of observation increased significantly province-wide and in every region. The increase was attributed to colonization of maturing coniferous plantations and areas where mixed forests have regenerated on previously cleared land. Highest densities occurred in the northwest in the Boreal Forest Region. Moderate to high densities occurred from the southern edge of the Shield northward through the Hudson Bay Lowland (Crins in Cadman et al. 2007).

Hunt and Flaspohler (2020) stated that Breeding Bird Survey (BBS) data indicated a significant increase range-wide of 1.8% per year 1966-94, but with apparent declines of the Yellow-rumped Warbler in Ontario, Manitoba, central Alberta, and Newfoundland. Increases were particularly great in the northeastern United States where it has been expanding its range. BBS data indicate that it increased at annual rates of 0.2922% in Canada and 0.311% in Ontario 1970-2021. Trends for 2011-21 were annual decreases of 2.07% in Canada and 2.5% in Ontario. All results were of low reliability (A.C. Smith et al. 2023).

In Maine, MacArthur (1958) observed that the Yellow-rumped Warbler tends to increase following a decline and decline following an increase. The period of oscillation was 2.6 years indicating that populations were largely regulated by density-dependent factors rather than density-independent events such as catastrophes (storms and severe winters), some predation, and certain types of disease. It is uncertain if these regular population fluctuations occur throughout its range.

POSTFLEDGING PERIOD

Brood division appears to occur as soon as the fledglings leave the nest, but all fledglings may associate with the male if the female initiates another clutch. Juveniles have been found within 80 m of the nest 14 days after fledging. Young are dependent on the adults for at least 14 days after leaving the nest (Hunt and Flaspohler 2020).

As early as late July, both adults and juveniles form flocks and may join chickadees and other species. In the Yukon, the Yellow-rumped Warbler is most abundant in August when large numbers of juveniles congregate at productive wetlands. In Quebec clear-cuts in mature balsam fir, black spruce, and white birch forests, only 5 were captured during the postfledging period in 2 years.

Forty-eight juveniles were captured in Newfoundland clear-cuts in 2 years. At the 5-m scale, they were associated with dense understorey vegetation and dense foliage above breast height. At the 115-m scale, they were associated with patches downslope from their previous location in areas characterized by dense cover, but this relationship was significant in only 1 of 2 years. Small changes in elevation (10-30 m) were associated with significant changes in productivity and prey availability, so juveniles may continually move downslope to increasingly productive habitats. Juveniles appear to seek areas of dense vegetation that provide shelter from predators and the elements and that have high prey availability (Hunt and Flaspohler 2020; Major and Desrochers 2012; Mitchell et al. 2010b; Sinclair et al. 2003).

In Newfoundland, Mitchell et al. (2010a) documented broadscale movements of juveniles prior to migration. Young moved an average of 4,071 m (range 377-9,468 m). Juveniles moved both toward and along river valleys, moving down the elevational gradient of the rivers and in a clear orientation to the east. River valleys were associated with significantly higher productivity and prey availability and may provide optimal foraging habitat.

Mitchell et al. (2009) examined the effects of clear-cuts on the movement of recently independent Yellow-rumped Warbler fledglings through boreal forest habitat in Newfoundland. Median movement rate of juveniles was 353 m per day (range 24-6,154 m). Movement rate increased and residency time decreased as the proportion of clear-cut land increased, but if there was a high proportion of clear-cut land along the pathway used to exit the neighbourhood, movement rate was reduced and connectivity was impeded. Clear-cut lands may represent low-quality habitat for it during the postfledging period.

MIGRATION

The Yellow-rumped Warbler is a short-distance migrant. Populations in the southeastern United States and Pacific Coast of the United States are permanent residents; more northerly populations are migratory. Migration is predominantly nocturnal but movements may also occur during the day. Birds have been observed migrating along the Ohio River in Illinois during the day. During autumn in Louisiana, diurnal northeastward flights were made following a cold front with northeastward winds. All flights were into the wind, but this reverse migration allowed migrants to make a shorter over-water flight. Migration is quicker in spring than autumn, averaging 312 km per day in spring compared with 88 km per day in autumn. In Ohio, 2 Yellow-rumped Warblers stayed at a stopover site 4 and 8 days. One Wisconsin spring migrant stayed 5 days and the mean stopover duration in spring in Ohio was 5.9 days for 32 birds. It exhibits a facultative autumn migration that may continue into late winter. Birds may linger north of the typical wintering range when weather is favourable and food is abundant. If conditions decline, birds may move further south, and this is a common occurrence even in Florida and Arizona within the heart of the wintering range. In Arizona at the most northern study area, numbers peaked in October and declined to near 0 in November, typical of normal autumn migration. At the central study area, maximum numbers occurred in mid-December with a decline from then through early January. By early February, only 6 birds per km^2 were present compared with 1,125 in mid-December. At the southern site, there was an increase in January, consistent with the fact that birds moved further south as winter progressed. Changes in abundance at the northern sites coincided with declines in insect abundance, and cold fronts may

have been an influence in 1 year. In Florida, 67% of tower kills occurred in late December, 27% in January, and 6% in February. The distribution of dead birds around the towers correlated with wind direction, the same as for autumn migration. Both studies suggested that it may resume migration in late autumn or winter to avoid adverse weather or food shortages. In Alberta, autumn migration was initiated when the moult was approximately 50% complete. Two peaks of abundance were observed during migration. This may represent breeding populations near and distant to the study area moving past at different times, earlier migration of failed breeders, or differences between single- and double-brooded birds. During winter, males predominate in the northeastern and north-central United States. Females predominate in Florida, the West Indies, and Central America. Yearling males winter north of older males and yearling females winter south of older females. During winter, the number of females increases in the southeastern United States, suggesting that they may be more likely to exhibit facultative migration than males (Flockhart 2010; Graber et al. 1983; Hunt and Flaspohler 2020; MacDade et al. 2011; Slager and Rodewald 2015; Terrill and Crawford 1988; Terrill and Ohmart 1984; Yaukey 2010).

During spring migration, males arrive a few days to more than a week in advance of females. Adult males arrive before yearling males and adult females arrive before yearling females. At Prince Edward Point, the mean date of arrival for males (9.4 May) was 4 days earlier than for females (13.4 May). The difference may have been greater because many males arrived in April before sampling began. At Long Point, the mean capture dates for males was 0.3 May for adults, 3.6 May for yearlings, and 2.9 May for those of undetermined age. For females, median capture dates were 10.3 May for adults, 11.8 May for yearlings, and 10.6 May for those of undetermined age (Flockhart 2010; Francis and Cooke 1986; Hunt and Flaspohler 2020; Stewart et al. 2002). In southern Ontario, the Yellow-rumped Warbler arrives in early to mid-April and is common until mid-May. Most are gone by the end of May but a few remain into early June (Black and Roy 2010; Curry 2006; Fleming 1907; Keast 1980; LaForest 1993; Lancaster et al. 2004; Weir 2008). The midpoint of migration at Long Point is 8 May (Mills 2005a). In the southern Shield, average arrival is around the third week of April and the earliest birds arrive in early April (Mills 1981; Tozer 2012).

In autumn, there appear to be no differences in passage dates of the sexes or age classes (Dean et al. 2004; Flockhart 2010). In the southern Shield, migration may extend from mid-August until mid- to late October, with rare records in November and December (Mills 1981; Tozer 2012). Migration is also underway in mid-August in the south; 50% of the flight has gone through by mid-September with peaks in late September to mid-October. There are late records from November and December and some birds overwinter (Black and Roy 2010; Curry 2006; Fleming 1907; Keast 1980; LaForest 1993; Lancaster et al. 2004; Weir 2008). The midpoint of migration at Long Point is 8 October (Mills 2005a).

Four studies examined the phenology of Yellow-rumped Warbler migration in relation to climate change. At Long Point, there was no significant difference in timing of the first spring arrival date 1975-2000, although there was a trend toward earlier arrival. In autumn, it migrated significantly later at a rate of 3.5 days per decade. Only females showed a significant change in phenology, delaying migration by 2.3 days per decade (Mills 2005a). In Rhode Island, Smith and Paton (2011) analyzed 45 years of banding data and determined that it significantly delayed autumn migration

in recent years. All short-distance migrants combined delayed migration by an average of 3.0 days per decade. Over a 157-year period in Massachusetts, spring arrival of this warbler was significantly correlated with the mean temperature in the study area during the 2 months prior to its arrival (Ellwood et al. 2010). Strode (2003) analyzed arrival times of spring migrants over 100 years in Illinois and 40 years in Minnesota. Spring is arriving later in Illinois than formerly but earlier in Wisconsin so that migrants may have 20 fewer days to complete migration between these states. Over the 100 years, the Yellow-rumped Warbler was 1 of 2 out of 8 warblers that arrived significantly earlier in Illinois than in previous years, and it also arrived significantly earlier in North Dakota in recent years.

During migration, the Yellow-rumped Warbler may occur almost anywhere. It may inhabit forests of any type, all age classes, and both open and closed stands. In addition to forested areas, it occurs in shrubby areas, alpine meadows, backyard gardens, treed boulevards, orchards, power-line rights-of-way, hedgerows, city parks, and rural and suburban residential areas. It is much less frequent in grasslands and fallow and cultivated fields. Despite being a habitat generalist, it exhibits some habitat preferences during migration, and these are frequently related to food abundance. In western Canada, it is most abundant in shrubby riparian areas along lakes, rivers, and wetlands. In southern Illinois, highest densities of spring migrants occurred in pine plantations where it foraged in deciduous shrubs in the understorey. It made heaviest use of bottomland forests in central Illinois, but it also occurred in mature upland forests, forest edges, and shrubs, and rarely in corn stubble and pastures. In South Carolina, numbers seen per hour during spring migration were 4.36 in beech forests, 2.81 in oak-hickory forests, 2.23 in floodplain forests, 0.91 in pine forests, 0.78 in dry thickets, and 0.64 in wet thickets. During spring and autumn migration in British Columbia, it was negatively associated with deciduous riparian habitat in coniferous forests, and this relationship was significant in spring. In South Dakota during autumn migration, more were captured in a 3.5-ha woodlot than in contiguous riparian forests, but not significantly. On 2 islands in Maine, it was significantly more abundant in both spring and autumn on the island dominated by low sapling and shrub vegetation than on the treed island. Three birds, 1 in spring and 2 in autumn, that were banded on the treed island were recaptured on the shrubby island 0.7 km distant. Although habitat structure was probably an important factor in island selection, food abundance may also have affected its distribution. Bayberry, a favoured food, was moderately abundant on the shrubby island and absent on the treed island. In New Mexico, it was more abundant in cottonwood–Russian olive communities in autumn and declined in agricultural edges in autumn compared with spring. This may have been due to the greater abundance of fruit in communities with Russian olive in autumn. During spring migration in Wisconsin and Minnesota, it was significantly more abundant in floodplain forests. This was probably due to leaf phenology, with leaf-out occurring slightly earlier in floodplain forests. During autumn migration in Ohio, it was equally abundant in all habitats studied in 1 year. In another year, it was significantly more abundant in shrub-sapling-stage forests than other habitats, and was not detected in suburban habitats. Abundance in forest-agricultural habitat was significantly greater than in suburban forests and greater than in forest interior, but not significantly (Campbell et al. 2001; Chapman 1907; Dean et al. 2004; Graber et al. 1983; Kelly et al. 2000; Kirsch et al. 2013; Leighton et al. 2002; Létourneau and Lafontaine in Gauthier and Aubry 1996; Parnell 1969; Rodewald and Brittingham 2002, 2004; Sinclair et al. 2003; Suomala et al. 2010, 2012; Wiebe and Martin 1998).

Strode (2009) examined tree usage by the Yellow-rumped Warbler during spring migration in Illinois. Foraging was distributed unevenly among tree species in all 3 years. The greatest numbers of observations (40-48%) were in hackberry with 5-34% in white elm, red elm, bur oak, and sugar maple. Less than 5% of observations were in other trees (ash, basswood, black walnut, red oak, Ohio buckeye, and hickory), and none were observed in Kentucky coffee-tree. Early migrants selected hackberry in all 3 years and white elm in 2 of 3 years. Other species were used less than their availability, particularly ash, sugar maple, and basswood. Late-arriving migrants selected both white and red elm in 3 years, black walnut in 2 years, and bur oak and hickory in 1 year; other trees were used less than their availability. Preferences for tree species were linked both to tree phenology and insect availability. The median date of Yellow-rumped Warbler arrival was correlated with the date of 100% bud break on tree species. The date of median warbler counts in each of the 7 tree species surveyed for caterpillars correlated with the date of the maximum number of caterpillars. A preference for hackberries occurred early in the season because of its early leaf-out and the abundance of hackberry gall psyllids. Both elm species and bur oak supported higher densities of caterpillars and were preferred later in migration. Later migrants were females, suggesting that tree species selection may differ between the sexes. Opportunistic timing and tree species use suggest that it may experience little to no negative effects from climate change.

During spring migration in Wisconsin, Slager and Rodewald (2015) radiotracked a Yellow-rumped Warbler that left its diurnal home range to roost overnight. It flew about 2.6 km from its daytime activity centre to roost overnight in pine windbreaks within agricultural row crops. Shortly after sunrise the next morning, it flew 3.2 km to a different location for the day and returned to the same roost site that evening. No attempt was made to relocate it in subsequent evenings, so it was unknown if it returned to the same roost each night. It was also unknown if it roosted alone or communally. The bird roosted in dense coniferous cover that may have offered better protection from predators because deciduous trees had just begun to leaf out. Disjunct roosting was observed by only 1 of 30 birds, so this may be a rare behaviour. It is possible that migrants may take the presence of suitable roosting habitat into account when selecting stopover sites. In British Columbia, migrants roosted on small ledges on a face in a gravel pit (Campbell et al. 2001).

During spring migration in Wisconsin, 1 Yellow-rumped Warbler used different home ranges in each of 5 days, but all were within 1-2 km of each other. Daily home ranges were 5.1-9.0 ha (Slager and Rodewald 2015). In South Dakota, autumn migrants exhibited high site tenacity, with 30 of 33 radiotracked birds (90.9%) remaining at their relocation site. Birds that were captured were randomly relocated at a woodland corridor or woodlot site other than where they were initially captured. For the 3 individuals that moved, maximum distances moved were 2.5, 1.9, and 1.5 km. Minimum stopover duration was 1-17 days and more than 80% of birds left for migration within a week. Mean temporary home ranges were 0.08 km^2 in corridors and 0.03 km^2 in woodlots. Birds at stopover sites with smaller woodland areas had smaller home ranges. Habitat type did not have a significant effect on stopover duration, movement rate, or temporary home range size. Birds with lower movement rates tended to stay longer. Birds moved at higher rates later in autumn. Birds departed more frequently on clear nights with a mean cloud cover of 15.9% on departure nights. Departure nights had less tail wind and more head wind, lower temperatures, and lower barometric pressure than nondeparture nights (Liu and Swanson 2015).

During the daytime, the Yellow-rumped Warbler may join mixed-species flocks, particularly in autumn. It is an early spring migrant that is most likely to be found in the company of kinglets, Pine Warblers, and Palm Warblers. It may accompany a wide variety of species in autumn. When resources are limited, the Yellow-rumped Warbler may attack other species, but typically only those that have food in their bills or that are close to fruit-bearing shrubs. Kilham (1961) observed it attacking Red-bellied Woodpecker, Red-headed Woodpecker, Hairy Woodpecker, Downy Woodpecker, Carolina Chickadee, Blue Jay, and Northern Cardinal. No aggression occurs if food is abundant.

At Prince Edward Point, the Yellow-rumped Warbler fed at heights of 0-9 m during autumn migration, most frequently around 2 m, and mostly at heights of 7 m or less. It fed only to a small extent in the outer foliage, concentrating mainly in the outer branches and core of the tree and occasionally descending to the ground. Foraging locations consisted of 21% on outer leaves, 18% on the ground, 15% on inner branches, 12% on twigs and inner leaves, 12% on outer branches, 10% on sapling branches, 9% on sapling foliage, and 3% on low shrubs. No foraging was observed in the air or on trunks (Keast 1980). During spring migration in South Carolina, singing birds were observed at heights of 0-15 m (average 6 m). Nonsinging birds occurred within the same range of heights, but at an average of 10 m. It was the only species studied for which singing males were not higher up than other birds. Fifty-three percent of foraging occurred in the canopy, 40.4% in low trees, 6.7% in shrubs, and 0% on the ground. In the canopy, 24.0% of foraging occurred at the top of the crown, 18.5% in the inner crown, 10.5% in the lower crown, and 0% on the bole. In low trees, 8.7% of foraging occurred at the top of the crown, 18.8% in the inner crown, 12.9% in the lower crown, and 0% on the bole. In shrubs, 1.1% of foraging occurred at the top of the crown, 1.4% in the inner crown, 2.4% in the lower crown, 1.8% in dense thickets, and 0% in brush piles and grasses (Parnell 1969). From early to late spring, foliage gleaning increases; hovering and hawking decrease (Hunt and Flaspohler 2020). During migration, the Yellow-rumped Warbler may cling to walls and gutters of houses in search of insects. It may drink sap (and probably eat insects) from Yellow-bellied Sapsucker wells and injured sugar maple trees and probe burdock burs for insects (Bent 1953; Graber et al. 1983; Létourneau and Lafontaine in Gauthier and Aubry 1996; Mousley 1917; Underwood and Underwood 2013). Moore and Simm (1985) artificially prolonged daylight to stimulate migration response in captive warblers. Those in migratory disposition foraged more efficiently by consuming more food items per foraging bout, handling food items more rapidly, and feeding selectively on larger prey. Harrison (1984) reported an autumn migrant that followed the wake of a boat in Delaware Bay, feeding on the insects that were stirred up. Two separate incidents of it feeding on ice during adverse weather conditions in spring in Manitoba have been documented. Warblers appeared to be foraging on small flies, midges, beetles, and spiders that were on the ice (McNicholl and Goossen 1980). During adverse conditions during autumn migration in Ohio, a juvenile crept through a lawn apparently picking tiny arthropods off the undersides of grass blades and violet leaves. By this time, all local fruit supplies had been depleted (Tramer and Tramer 1977). During autumn migration in New York, large numbers foraged nocturnally, using aerial sally movements to capture insects from foliage or in the air. The area was illuminated by lights from a football stadium (Lebbin et al. 2007). In Algonquin Park during autumn migration, it caught insects on exposed waterlily roots in the mud of a pond, 50 foraged along the muddy shores of a pond, and one captured insects on the walls of the visitor centre (Tozer 2012).

The diet of the Yellow-rumped Warbler changes from predominantly insects in spring to fruit in autumn and winter, although it still consumes insects where they are available. In April and May in Illinois, it fed heavily on geometer moth and other caterpillars. The stomachs of 5 birds contained 4 hymenopterans (1 ichneumonid wasp), 3 beetles (2 scarab beetles), 3 true bugs, 2 flies, 1 caterpillar, 1 spider, and 1 seed (Graber et al. 1983). In Arizona, insect sweep samples reflected the diets of the birds collected. At 1 site, aphids constituted the vast majority of available insects and these represented the greatest volume of food consumed. At another site, midges comprised the majority of both the available insects and the diet. Items comprising at least 10% of the diet at 3 locations included leafhoppers, aphids, hymenopterans, beetles, midges, and assassin bugs. Other food items included adult and larvae lepidopterans, ants, metallic wood-boring beetles, weevils, spiders, true bugs, flower flies, treehoppers, and sap beetles (Terrill and Ohmart 1984). MacDade et al. (2011) studied the breath composition of spring migrant Yellow-rumped Warblers along the Lake Erie shoreline of Ohio. A combination of aquatic and terrestrial food items was consumed. Midges were the dominant aquatic prey and results demonstrated increasing consumption of aquatic prey as the season progressed. Midge emergence is temperature sensitive and increases in frequency as spring weather and water temperatures become more favourable. It opportunistically supplemented its diet with midges as their availability increased. In Idaho, Carlisle et al. (2012) compared the diet of autumn migrants to the availability of arthropods. Prey items consumed in greater proportion than their availability included, in order of preference, beetles, spittle bugs, leafhoppers, larvae, and lepidopterans. Invertebrates consumed less than their availability, in order of greatest avoidance, included bugs, spiders, stilt bugs, jumping plant lice, hymenopterans, flies, stink bugs, ants, and moths. In the eastern United States, it feeds extensively on bayberry in autumn and winter, and its abundance and distribution is closely tied to this plant. In the west, it eats waxmyrtle. The pulp of these fruits is covered with a solid waxy material that consists predominantly of saturated long-chain fatty acids. The Yellow-rumped Warbler possesses several gastrointestinal traits that allow it to assimilate more than 80% of this wax, compared with less than 50% for most vertebrates (Place and Stiles 1992). S.B. Smith et al. (2007) determined that it could not satisfy its daily protein requirement by eating high-energy fruits such as bayberry and southern arrowwood. It must eat both insects and fruit to satisfy its dietary needs in autumn and winter. Although bayberry is a staple in much of its range, it eats other fruits, seeds, and insects in autumn and winter. There are numerous records of it eating poison ivy berries and this is probably a staple in Ontario where bayberry is rare. Other fruits it eats include those of red cedar, juniper, Virginia creeper, viburnums, honeysuckles, mountain-ash, spikenard, greenbriers, and dogwoods. It also eats sunflower and goldenrod seeds. During autumn migration in Illinois, it fed on hackberry thorn gall midges as they emerged by the thousands (Bent 1953; Graber et al. 1983).

During migration, the Yellow-rumped Warbler commonly strikes communication towers, lighthouses, and other tall structures. It was the most commonly killed species at a Florida tower, constituting 7% of all casualties. It is rare at tower kills in Pennsylvania. At the Lennox generating station chimneys near Kingston, 55 were killed 1972-82 out of 22,779 songbirds (Bent 1953; Graber et al. 1983; Hunt and Flaspohler 2020; Weir 2008).

DeGroote and Rodewald (2010) examined blood parasites in Ohio spring migrants. Avian haematozoa occurred in 58.3% of spring migrant Yellow-rumped Warblers and the intensity of

infection increased with later capture, a relationship that was most pronounced for yearling birds. Parasitism could influence birds during migration and the subsequent breeding season, with reduced reproductive performance, particularly by yearlings.

James (1991) considered the Yellow-rumped Warbler a common to locally abundant migrant. At Long Point, it is the third most frequently banded species (Anonymous 2010b). At Long Point, Hussell et al. (1992) reported a significant increase of migrant Yellow-rumped Warblers of 2.6% per year 1961-88. Trends by period were: 1961-70, –0.2%; 1970-79, +0.7%; and 1979-88, +8.7%. More recent results from Long Point confirm that it continues to increase in both spring and autumn (Anonymous 2010b).

WINTER

Root (1988) concluded that the winter distribution of the Yellow-rumped Warbler was strongly influenced by temperature. In most areas where it occurs, the annual frost-free period is at least 180 days and the January temperature rarely drops below –4°C. Highest concentrations in the east are coincident with the distribution of bayberry, which covers the coastal plain from New Jersey to Louisiana.

In Illinois, Graber et al. (1983) observed that the Yellow-rumped Warbler could withstand a temperature of –29°C provided that poison ivy fruit was abundant. It was consistently more numerous in bottomland forests than other habitats, although good numbers also occurred in upland pine forests. In bottomland forests, there appeared to be an alternate-year pattern of high and low numbers that did not occur in upland forests. This may be related to availability of poison ivy berries, but this requires further study. It also appeared to be correlated with the number of trees at least 10 cm DBH, increasing as the number of trees increased above 395 per ha and declining as the number of trees declined. This relationship may also be correlated with fruit abundance. In Pennsylvania, Wilz and Giampa (1978) observed the Yellow-rumped Warbler in 2 habitats, and it was the dominant species in both areas. These habitats included pines 15-18 m tall with scattered 1-m tall bayberry in the understorey, and cottonwood 4.5-18 m tall with the highest density of bayberry 0.9-3 m tall in the area. In South Carolina, Kwit et al. (2004) could not conclusively separate the effects of habitat type from fruit availability. When habitat type was held constant, there was a positive correlation between this warbler's abundance and bayberry fruit mass. It occurred in pine stands, regenerating clear-cuts, and bottomland forests. Twelve percent of observations were in bottomland hardwoods and 11% in upland habitats even though bayberry did not occur in these areas. It remained uncertain whether it used regenerating habitats because of plentiful bayberry fruit. In an urban area and urban edge in northern California, its abundance increased with the availability of shrubs and/or trees and decreased with abundance of roads and structures. Kalinowski and Johnson (2010) concluded that it may be among the most vulnerable species to habitat changes associated with urbanization. In winter in Louisiana, it prefers open deciduous woods but also inhabits bare open fields, roadsides, hedgerows, neglected city lots, and trees and shrubbery in parks. It may also occur on sandy ocean beaches where it flycatches from half-buried logs and posts (Chapman 1907).

In winter, the Yellow-rumped Warbler roosts nocturnally in the thickest available treetops, which are mostly conifers, but also in nooks and crannies about buildings and even in holes in hay and

straw stacks in barnyards. Occasionally, as many as 50 roost together but more often individuals roost alone. In Arizona, one fluttered against a glass door through which it could see a Christmas tree. The homeowners opened the door and it flew in and roosted in the tree overnight until it was let out the following morning. It returned the following evening, but was not let inside (Bent 1953; Dunn and Tessaglia-Hymes 1999; Graber et al. 1983).

Monroy-Ojeda et al. (2013) studied winter fidelity of the Yellow-rumped Warbler in Mexico. Six percent of migratory birds exhibited winter site fidelity, 5.1% were residents that occurred in more than 1 year, and 0.6% exhibited both winter site fidelity and residency.

The Yellow-rumped Warbler may defend food resources from other species during adverse weather conditions when food is limited. In Florida, 1 warbler set up in an area of 2,000 m^2 in urban backyards. It remained there for 14 days while the temperature remained below 21°C with nightly decreases to below 4°C. During this period, it searched the lawn for food or sat on an exposed perch from which it sallied for passing insects. It attacked Palm Warblers and Ruby-crowned Kinglets when they attempted to forage in this area and was usually successful in driving them away. American Robins, Northern Cardinals, and White-throated Sparrows were attracted to the yard by bread and seeds. This food was not used by the warbler and it did not attack these species. When the weather warmed up to 23°C and above 4°C nightly, it joined a flock of foraging birds that contained Yellow-rumped Warblers and was not seen again. It was possible that the colder than normal temperatures and consequent shortage of insects caused it to form a temporary territory, but it reverted to more normal flock-foraging behaviour when temperatures increased (Woolfenden 1962).

In its main winter range, the Yellow-rumped Warbler is closely associated with bayberry in the east and waxmyrtle in the west. Autumn migration may be delayed where bayberry abounds, with birds moving further south once weather deteriorates or bayberry fruit becomes depleted. In many areas, it appears to subsist almost entirely on bayberry and has little competition for them from other species because few can digest it. Even low numbers of bayberries can support large numbers of warblers. At a Pennsylvania site, birds were never observed feeding where bayberry was absent. During periods of heavy snow cover, warblers fed almost exclusively on bayberry. Ground foraging became more common once bayberry fruit became scarce, and it also fed at fallen, partly decayed logs and on spider eggs under the eaves of a beach house (Bent 1953; Borgmann et al. 2004; Campbell et al. 2001; Chapman 1907; Hausman 1927; MacArthur 1958; Root 1988; Wilz and Giampa 1978). Outside the range of bayberry, poison ivy fruit is probably the most important winter food. In Illinois, fluctuations in warbler numbers were thought to be related to the abundance of poison ivy berries, and these were the most important food. Wintering birds in Elgin County were observed eating poison ivy berries, suggesting that they may be an important food item in Ontario (Graber et al. 1983; Lancaster et al. 2004). In winter, the Yellow-rumped Warbler may consume other types of fruit, including all those identified in the autumn diet; it may also consume some nectar. In winter, it gleans fruit or insects from leaves or branches, and rarely from dead leaves. Sixteen stomachs collected in Alabama in winter contained predominantly flies, beetles, ants and other hymenopterans, caterpillars, aphids, and spiders. Other winter foods include gall-forming insects, willow buds, frozen apples, honeydew from aphids, insect eggs, pitch pine seeds, and grass seeds (Bent 1953; Chapman 1907; Hunt and Flaspohler 2020). Beal and McAtee (1912) summarized the

contents of 383 stomachs collected in the western United States during winter. The diet was comprised of 84.7% animal food and 15.3% vegetable matter. Hymenopterans (wasps and ants) were the dominant food item, constituting 26.2% of the diet; most were ants. Flies comprised 16.4% of the diet, mostly gnats, house flies, and crane flies. Bugs constituted 19.1% of the diet, including aphids, scale insects, stink bugs, leafhoppers, and treehoppers. Lepidopterans formed 14.2% of the diet with a few adult moths and pupae consumed in addition to caterpillars. Beetles constituted 6.7% of the diet and included carrion and lady beetles and weevils. A few other insects and spiders constituted the remainder of the animal food. The vegetable food consisted of 9.2% weed seeds, 5% wild fruits, and vegetative rubbish.

The Yellow-rumped Warbler visits all designs of feeders and samples a variety of foods. It is an irregular feeder visitor, with only about 10% of sites hosting it all season. It is less likely to visit rural than urban feeders, possibly because there is more natural food in rural areas. Favourite foods include suet, bird puddings, and water, and small numbers show a preference for peanut hearts, peanut butter mixes, and fresh fruit. Infrequently chosen items include black oil sunflower seeds, sugar water, and baked goods (Dunn and Tessaglia-Hymes 1999). In Muskoka, one coming to a feeder ate oatmeal (Mills 1981). In Illinois, it ate cheese at feeders (Graber et al. 1983).

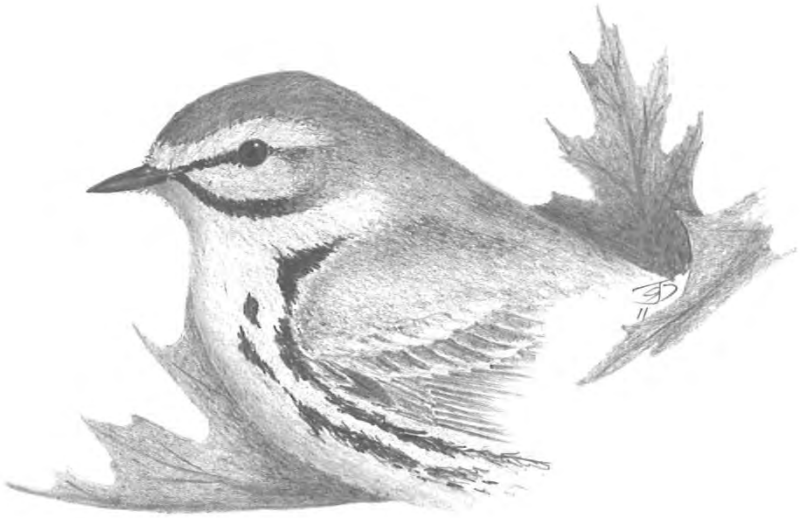
Graber et al. (1983) observed great variations in the number of wintering Yellow-rumped Warblers and tentatively concluded that this could be related to the supply of poison ivy berries, the staple in the diet. Regardless of initial numbers, declines of 40-45% occurred from before 10 January to after 31 January. They were uncertain if this decline was due to migration or mortality. Given this species' penchant for facultative winter migration, it is likely that some of the decline was attributable to migration. Nonetheless, mortality may also occur during severe winters. During very cold weather and heavy snow that persisted for a month in Illinois, Graber and Graber (1979) noted significant changes in its density. Density in bottomland forest was 16.8 per km^2 prior to the adverse weather and 1.5 afterwards, a decline of 91.2%. In upland forest, density was 7.9 before and 12.6 after, an increase of 59.4%. No birds were observed in urban residential areas during either period. Some birds appeared to have switched from bottomland forest (the preferred winter habitat) to upland forest as a result of the adverse weather, possibly because some upland forests had an abundance of poison ivy berries. Overall densities were much lower and 2 dead warblers were observed, indicating that some mortality had occurred. When sudden severe winter weather occurs, some birds may not be able to find adequate food resources or move further south in time to avoid mortality.

James (1991) considered the Yellow-rumped Warbler a rare winter resident in the south north to Peterborough and Ottawa. In the Hamilton area, McIlwraith (1894) stated that it stayed into late autumn but there were no winter records. The first Hamilton winter record occurred in 1951 and it has gradually become more common in winter, with as many as 7 or 8 occurring some winters. The increase is probably due to a combination of increased observer effort and milder winters (Curry 2006). Scattered winter records are available from Kingston (Weir 2008) and Elgin County (Lancaster et al. 2004).

Christmas Bird Count data indicate that the Yellow-rumped Warbler increased at an annual rate of 1.86% in Ontario 1970-2021 and decreased at an annual rate of 6.72% 2009-21 (National Audubon Society 2022).

Prairie Warbler

Setophaga discolor

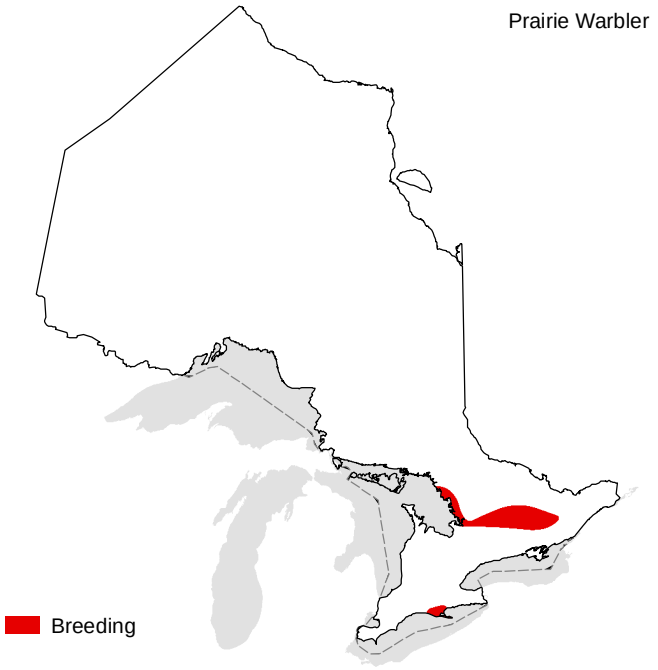


BREEDING SEASON

Habitat Requirements

Ontario Prairie Warbler nests were usually in areas of open, low growth, with juniper and stunted oak predominating. Breeding sites were either sandy (54.5% of nests) or rocky (45.5%) and almost always dry. One nest was in a pine plantation and another was in an overgrown meadow. Many nests were near shorelines of lakes (Peck and James 1987).

Most of Ontario's population breeds in the southern Canadian Shield in the Great Lakes–St. Lawrence Forest Region. The main habitat the Prairie Warbler uses is granite rock barrens along the Georgian Bay coast that are sparsely vegetated with stunted white pine, red pine, and red or white oak with patches of common juniper. This habitat is open in nature and only about 50% vegetated. It occurs in similar habitat along the southern edge of the Shield, particularly in Peterborough and Frontenac counties. In Frontenac County, cliffs and steep rocky inclines along lakes are favoured habitats, especially if fire has recently opened the forest. In the same county, it nests on wide hydro transmission line corridors where they pass through areas of exposed bedrock. Almost all occupied habitats on the Shield are characterized by sparse vegetation on exposed bedrock with common juniper and stunted oaks and pines (Austen et al. 1994; Harrington 1922; James 1996c, 1999e;



Lambert and Smith 1984, 1985; Mills 1981; Weir 2008). North of Parry Sound and Dillon Cove, Niskanen (1997) reported a pair nesting in unusual habitat. The territory included a bare bedrock outcrop with fairly typical habitat, although all the pine trees were dead. The nesting area was in the drier margins of a wetland dominated by sweet gale, reed canary grass, reed grass, and manna grass. The territory had a newly constructed cottage road on 1 side and a small back bay on another.

The Prairie Warbler inhabits a variety of habitats south of the Shield, almost all of which are on sandy or rocky substrates. The sand dunes along Lake Huron from Pinery Provincial Park to Wasaga Beach formerly supported the highest population south of the Shield. It used the interdunal meadows for nesting. These consist of open habitat with scattered oaks and clumps of low woody vegetation including common juniper, fragrant sumac, grape, chokecherry, sand cherry, and red cedar. It is likely that the presence of common juniper and red cedar saplings made this area most attractive. Near St. Williams and Turkey Point, it formerly nested in young red pine and white pine plantations and deciduous shrubby areas on the Norfolk Sand Plain. These areas were abandoned once the pines matured, but a few pairs still occur irregularly. A third habitat used south of the Shield is limestone alvar planted with conifers and these provided good habitat when the trees were small. Nesting in this habitat occurred on the Flamborough Plain near Rockton and Kirkwall. It rarely nests in regenerating old fields in Ontario. It has been documented using this habitat in Waterloo Region, Prince Edward County, and near Campbellville. This habitat is clearly not preferred because it is abundant but rarely used. Another potential habitat used in Ontario is bog or fen, but this is hypothetical. A singing male was present for about 10 days in June 2001 in the Wainfleet Bog but was not found after that. It is most likely that this was an unmated male that subsequently moved on (Austen et al. 1994; Bent 1953; Black and Roy 2010; Curry 2006; Lambert and Smith 1984, 1985).

Most Prairie Warblers in the United States breed in disturbed anthropogenic habitats. In many states, breeding is confined to upland old-field meadows that are often on poor soils that inhibit regeneration. Although it may nest in habitats over a wide moisture regime, it is typically found in dry areas. In addition to old fields, it nests in logged areas, power-line rights-of-way, strip-mined areas, young plantations, and in openings in pine forests that are as old as 40 years. In Indiana, it bred in abandoned fields 0.8-4 ha in area, separated from each other by fragments of woods and treed fence lines. Trees were scattered in distribution in most fields, but some contained planted rows of black locust, black walnut, sugar maple, or white pine. One territory supported a total of 2,263 trees at a density of 1,594 trees per ha. Half the trees were 1.5 m or less in height and 90% were

a maximum of 4.6 m tall. Tangles of blackberry and other raspberries were common in these fields. The principal grasses present included little bluestem, oldfield three-awn, and Canada bluegrass and the prominent herbaceous species were plantain-leaved pussytoes, oxeye daisy, and goldenrods. Average habitat characteristics consisted of trees 6-13 m tall, 5-25% tree cover, 9-24% shrub coverage, and 1-10% bare soil. In Indiana, occupied areas were hilly and had no standing water except for puddles after rain. Limestone bedrock outcrops occurred on steep slopes and erosion had stripped away topsoil in other areas so that regeneration was inhibited within the territories. It also breeds in unmowed orchards, Christmas tree plantations, and logged, burned, and grazed forests. It is predominantly an open-country bird breeding in areas with high ground cover and few trees. Ordination studies indicated that the Prairie Warbler was the terminal or extreme species at the xeric, upland, low-biomass, open-country end of the spectrum when all species were considered. In Missouri and other locations, it breeds in clear-cuts, predominantly those dominated by oak-hickory-pine communities. In mountainous areas, it breeds in dry open habitats such as brushy ridges where forest removal has created suitable habitat. It may occasionally inhabit natural woodland openings. In New England, it nests in pastures overgrown with white cedar and hillsides with an understorey of barberry. In Massachusetts, it nested in hazel shrubs along roadsides. It may use low growths of deciduous saplings, such as oak, maple, elm, tulip tree, black cherry, sassafras, red cedar, and ash, and these areas often contain clumps of shrubs, especially sumac, raspberries, sweet fern, and greenbrier. In South Carolina, number of observations per hour during the breeding season included 4.55 in dry thickets, 1.00 in pine-hardwoods, 0.59 in pine forest, 0.26 in wet thickets, 0.21 in floodplain forest, and 0 in beech and oak-hickory forests (Bent 1953; Brooks 1940; Chapman 1907; Graber et al. 1983; Harrison 1984; Lehnen and Rodewald 2009a; Nolan 1955, 1963, 1978; Nolan et al. 2020a; Noon et al. 1979; Parnell 1969; Wells 2007).

The Prairie Warbler nests in a variety of natural habitats in the United States. Pitch pine barrens on sandy soils are the most frequently used natural habitat and it is locally common in Massachusetts and New Jersey barrens. In these areas, pitch pine forms an open canopy with lesser numbers of black oak, white oak, and white pine. A dense shrub layer is present in occupied areas, predominantly of scrub oak and ericaceous species such as black huckleberry, sheep laurel, lowbush blueberry, wintergreen, and bearberry. In Massachusetts, there was a strong discrimination between occupied and unoccupied sites. It avoided areas with high coverage by oak trees and those with high coverage, height, and basal area of pitch pine. It decreased in abundance in a curvilinear fashion with increasing height of vegetation, percent cover and basal area of pitch pine, and vertical and horizontal heterogeneity (Brush 1987; Chapman 1907; Morimoto and Wasserman 1991a). In New Jersey, it was equally abundant in oak-pine forests and hardwood swamps, although it tended to be more common in oak-pine (Rich et al. 1994).

The Prairie Warbler uses 2 natural habitats in Michigan. The most important are Great Lakes sand dunes similar to those in Ontario. Less frequently, it may occupy habitat similar to that of the Kirtland's Warbler. This consists of young jack pines on acidic, nutrient-poor, well-drained sand. The pines are short with an open canopy and often clumped and may either be natural or planted. The Prairie Warbler rarely occurs in prime Kirtland's Warbler habitat, selecting areas with an admixture of deciduous shrubs that are unattractive to the Kirtland's Warbler (Nolan 1978).

In New York, the Prairie Warbler breeds on alvars where it is locally common. This habitat consists of calcareous pavement barrens mixed with limestone woodland communities characterized by open forests of small trees containing substantial amounts of red cedar interspersed with areas of exposed limestone bedrock and open grassy areas (G.A. Smith 1988).

The Prairie Warbler occasionally breeds in forests in the United States, notably in the Great Dismal Swamp in Virginia which has a closed canopy. It also nests in Hickory Point Swamp in Maryland and the Great Cypress Swamp that is predominantly in Delaware, but partially in Maryland and Virginia. In the latter swamp, it was associated with Atlantic white cedar stands where it nested in clear-cuts at the edge of the swamp. It did not occur in forest interior. In Rhode Island, it nests in red maple swamps surrounded by upland forest. In this habitat, it is associated mostly with shrub coverage in the interface between the upland and wetland forests. The Florida subspecies nests in mangrove forests where nests are often over water (Golet et al. 2001; Heckscher 2000; Nolan 1978; Nolan et al. 2020a; Prather and Cruz 1995).

In the mid-Atlantic states, the Prairie Warbler was positively correlated with percent canopy coverage by conifers and mean canopy height and negatively correlated with canopy closure. It preferred open coniferous stands with tall trees (Robbins et al. 1989). In Texas, its abundance was positively correlated with the number of shrub species, number of shrub stems, foliage density at 1 m, and percent coverage by pines 5-16 cm diameter at breast height (DBH). It was negatively correlated with vegetation height, canopy closure, foliage density at 12-15 m, percent coverage by pines 17-32 cm DBH, and the number of tree stems 17-32 cm DBH (Conner et al. 1983). Also in Texas, it built nests in dense areas with a few large trees, with more shrubs and vines and bigger trees (Novak et al. 2016). In Kentucky and Tennessee, its abundance was positively correlated with shrubs (Lituma and Buehler 2016). Nolan (1978) analyzed densities reported from a variety of breeding bird surveys and reached 7 conclusions. There was no difference in breeding densities between entirely deciduous and pine-deciduous communities. Density appeared to be positively correlated with the biomass of green vegetation above ground level and especially with density of the shrub layer, provided that the canopy was not closed. The most common characteristic of plots with densities of 75-100 pairs per km^2 was abundant foliage widely distributed on twigs and small branches that were considerably exposed to sunlight. Population density may be correlated with insect abundance. High density in the sparse scrub of Indiana dunes may be attributable to the ribbon-like configuration of territories. Xeric communities support higher densities than mesic communities. Numbers per tract and size of the total bird population are closely correlated. Populations appear to be unusually dense in Maryland and possibly Virginia and North Carolina. In North Carolina, the Prairie Warbler was negatively correlated with the amount of tree canopy within 200 m. As tree canopy increases, shrub coverage decreases (Gilbert and Ferguson 2019).

Shake et al. (2012) examined the effects of patch size and shape on occupancy by the Prairie Warbler. Patch area was a good predictor of occupancy and they considered it an area-sensitive species with low occupancy in the smallest patches. They estimated a minimum area requirement of 1.1 ha and an optimal area of 5.5 ha. Nonetheless, occupancy rate was approximately 40% in the smallest patches (0.3 ha), 50% at 1.1 ha, 90% at 5.5 ha, and 100% at approximately 13 ha. Because many occurred in patches smaller than average territory sizes, the Prairie Warbler cannot be

considered an area-sensitive species. There was no evidence for effects due to patch shape or the amount of forest cover within 1 km on site occupancy. In Ohio, annual survival and productivity were unrelated to patch size (Lehnen and Rodewald 2009a). Nolan (1978) demonstrated that it did not avoid edge. Females actively selected territory edges for nesting even when territories bordered on unsuitable habitat. Nests were occasionally a few metres into wooded areas. In Texas, all nests were within 100 m of edge and none were found in the core of woodlands (Novak et al. 2016). Rodewald and Vitz (2005) detected edge avoidance in 4-6-year-old clear-cuts in Ohio. Captures of both juveniles and older birds increased with distance from forest edge, with more than twice as many captures of both age classes 80 m from edge than at 20 m from edge. Although more were captured in large (13-16 ha) than small (4-8 ha) clear-cuts, the difference was not significant. In Missouri, Woodward et al. (2001) analyzed distance from forest edge of nests in shrub habitat. The Prairie Warbler avoided nesting within 20 m of forest; 29% of nests were within this distance category but it represented 45% of available habitat and was underutilized. It moderately preferred the 21-40-m distance-from-edge category, although this preference was not statistically significant. Nest predation rates were greatest within 20 m from edge, declined 21-40 m from edge, and increased further than 40 m from edge. Predation rates were lower more than 40 m from edge than within 20 m of edge. In Kentucky and Tennessee, its abundance was similar at roads and 300 m distant from roads, but was 40% greater 600 m from roads. This difference was not significant and evidence of road avoidance was weak (Lituma and Buehler 2016).

Nolan (1978) compared the habitat requirements of the Prairie Warbler with coexisting warbler species. Where it occurs with the Yellow Warbler, the Yellow Warbler is found in more moist areas, often willow shrubs, or less shrubby habitats. The Chestnut-sided Warbler has extremely similar ecology and the 2 species rarely occur together. Where they do, territories do not overlap. Where both these warblers are present, the Prairie Warbler is confined to hotter drier scrub in which there are often pines as well as deciduous trees. The Chestnut-sided Warbler occupies cooler, moister, more deciduous cover on north-facing slopes. The Pine and Prairie warblers frequently coexist, with the Pine Warbler foraging and nesting higher, preferring larger trees, and usually gleaning exclusively from conifers. The Common Yellowthroat and Yellow-breasted Chat often share habitat with the Prairie Warbler. Both prefer lower, denser, and possibly moister locations and rarely forage as high in open situations as the Prairie Warbler. The Blue-winged Warbler may occur with the Prairie Warbler, but invades regenerating fields much earlier and prefers denser growth than the Prairie Warbler.

During the breeding season in Indiana, the nocturnal roosts of 7 birds were at heights of 74-150 cm near the tops of small trees standing in herbaceous vegetation in open fields (Nolan 1978).

Nests reported to the Ontario Nest Records Scheme were typically in low shrubs, especially common juniper that supported 65.7% of nests. Other nest species included viburnums (including downy arrowwood and maple-leaved viburnum, 11.4% of nests), hazel (8.6%), white oak (5.7%), and 2.9% each in dogwood, sumac, and pin cherry. Nests were in crotches in the upper parts of the shrub or sapling or, less frequently, in the outer branches or between 2 branches. Nests were 0.24-1.5 m from the ground, with most 0.6-0.9 m up (Peck and James 1987, 1998a). Harrington (1922, 1924) reported 5 nests from Nottawasaga Bay on Georgian Bay. All were in common junipers with 4 about

30 cm from the ground and the other 60 cm up. All were about halfway up the stem on the outer portion of a branch. One nest was on an outer branch of a juniper on the edge of a large clump of this shrub. Another 4 Georgian Bay nests were in common juniper in open rock barrens within 100 m of shore (Matis and Squarek 2023). North of Parry Sound, Niskanen (1997) found a nest 0.8 m from the ground attached to 2 meadowsweet branches. It was hidden beneath sweet gale. It was only about 6 m from a cottage road. Curry (2006) reported a nest 1.8 m from the ground in a hawthorn near Campbellville.

The female prefers to select a nest site at the periphery of the territory; the central portion of the territory is avoided for nesting. Boundaries between territories are also avoided, presumably so the female is not disturbed by quarrelling males. Undisputed territory boundaries are selected for nest sites where available, and these usually abut unsuitable habitat. Nests may be at edges of woods or as far as 20 m into them. Nests have been found in branches overhanging mowed fields. In 1 year in Indiana, many nests were in tall trees of woods and fence lines at edges of territories after a late frost withered the leaves of many small trees and shrubs. Nests are in shrubby vegetation, including tree saplings. Most nests are in the third quarter of the plant, with the lowest quarter avoided. In Indiana, 1.9% of nests were in the lower quarter of the plant, 21.7% in the second quarter, 62.1% in the third quarter, and 14.3% in the top quarter. The lowest quarter usually consisted of a leafless stem or trunk that offered few forks and little concealment. Branches and forks of the right size were most numerous in the third quarter where shelter and concealment was also highest. Where nests were in dense clumps, these tended to be composed of trees of approximately the same size. In these cases, nests were almost invariably in branches projecting 0.1-1.0 m above the top of the clump, analogous to a nest in a low tree standing among forbs and grasses. The proximity of other habitats appeared to be of little or no importance in nest-site selection except that mature woods were usually avoided. In Indiana, 555 nests occurred in 7 different types of placement: 47% in an upright fork, 27% against the trunk on twigs, 18% on a horizontal or diagonal branch (12% on small branches, 4% on small arched trees, and 2% on large branches), 3% in vines, 2% wedged among small branches, 2% fastened to vertical branches, and 1% in broom-like growths. About half of Indiana nests were sheltered by Virginia creeper or fox grape vines, but very few nests were in deep shade: 14% were in direct sunlight much of the day, 6% were exposed no more than 1-2 hours, 52% were never exposed to direct sunlight but received flickering sunlight for several hours, and 28% were probably never touched by direct sunlight. Nests do not appear to be oriented in any particular direction. Conifers are seldom used for nesting in the remainder of its range, and this typically occurs prior to leaf-out of deciduous species. About 750 Indiana nests were in 40 species of plants. White elm was highly preferred and selected, supporting 50.8% of nests. Other nest-tree species included sugar maple (9.4% of nests), hawthorn and plum (7.1%), flowering dogwood (5.1%), sassafras (2.6%), blackberry (2.1%), pines (2.1%), red cedar (1.5%), and other species (17.6%). Other species it has nested in include black walnut, hackberry, black locust, black cherry, honey locust, apple, ash, red maple, sycamore, sumac, chinquapin oak, red mulberry, hophornbeam, tulip tree, red elm, black gum, shagbark hickory, smooth and shining sumac, Manitoba maple, rough-leaved dogwood, coralberry, Ohio buckeye, basswood, mangroves, sweet fern, poplar, laurel, sand cherry, and gray and silky dogwoods. Nests may be in vines of Virginia creeper, Japanese honeysuckle, and bittersweet; it also nests in barberry and hazel. In Indiana, white elm was the only species selected

more than its abundance. The many crooked branches and twigs of elm and frequent forking of upright branches offered favoured nest placement sites. The distribution of leaves and twigs appeared important in nest-site selection but shape and size of leaves were not important. Sugar maple and flowering dogwood were used in proportion to their availability and all other species were used less than their availability. Despite almost unlimited nest-site availability at an Indiana study area, at least 12 trees were selected more than once and 4 were used 3 times. Within the 12 trees, 10 nests were placed in the exact site of a previous nest. No reuse of a nest site occurred by the same female and in only 3 cases was the same male present. Nests have been reported at heights of 0.025-13.7 m, but the extreme heights are rare. Of 608 nests in Indiana, the median height was 1.74 m, the mean height was 2.29 m, 77% of nests were within 3 m of the ground, and 38% of nests were 1-2 m from the ground. Median nest height increases with the season. In 2 Illinois study areas, median height increased from 1.3 to 2.4 m on 1 study area and 1.7 to 4.8 m on the other. Increasing nest height was likely related to the probability of predation. Prior to leaf-out, branches and stems provided the most concealment and they were densest below 2 m, but nest height increased as leaves became available. In Virginia, the Prairie Warbler commonly nests at heights of 3-4.6 m in pitch pines, often as far as 3 m from the trunk on a horizontal branch. Nests are not reused by the same female, but 1 female used a nest that had been abandoned by another female. Old Prairie Warbler and American Goldfinch nests are occasionally dismantled to obtain nesting material (Bent 1953; Chapman 1907; Graber et al. 1983; Harrison 1984; Nolan 1955, 1978; Prather and Cruz 1995).

Some authors stated that the Prairie Warbler occurs in small colonies, but this is because birds congregate in what are often small patches of suitable habitat. Territories are vigorously defended and there is no evidence of any true coloniality. Nearest-neighbour distances in Massachusetts indicated that it was dispersed evenly in preferred habitat with no indication of clustering of territories. In spring, the earliest arriving males exhibit few signs of territoriality and may range over areas as large as 4 ha in a few minutes that cover part of 6 previous territories. As more males arrive, they become confined to progressively smaller areas until the arrangement of territories is finalized for the season. In Indiana, the closest nests on active adjoining territories were 55-95 m apart. Males with large territories spent most of their time in only the part of it where the nest was located. The activity centre shifts if a replacement nest is initiated. Many Indiana territories were in fields large enough to support only a single pair, and the boundaries of these remained constant from year to year. Territory boundaries are often zones about 10 m wide that both neighbours enter regularly. These may be treed fence lines or unvegetated strips that are rarely visited by any birds. Males preferred to sing and watch their territory from tall trees in fence lines and each male had the right to use them but not go beyond. Territory size was correlated with the number of large trees, possibly because males could defend more land from a tall tree. Individual males have similar-sized territories each year after they are yearlings. Old males had significantly larger territories (0.6-3.5 ha, mean 1.73 ha) than yearlings (0.5-2.8 ha, mean 1.37 ha). Territories were larger if they adjoined suitable unoccupied habitat. Territory size decreased significantly as the number of neighbours increased: 2.1 ha with no neighbours, 2.3 ha with 1 neighbour, 1.7 ha with 2 neighbours, 1.3 ha with 3 neighbours, and 1.1 ha with 4 neighbours. Mean size of territories and core areas in Indiana were 2.00 and 1.43 ha for polygynous males, 1.5 and 1.13 ha for males that were monogamous season

long, 1.46 and 1.03 ha for males that remained on territory all season and mated monogamously with more than 1 female, and 1.39 and 1.01 ha for males with short-term monogamous relationships that ended before 25 June. Territories of polygynous males were significantly larger than those of monogamous males; large territories were more likely to attract more than 1 female. As the population declined as a result of succession decreasing habitat quality, territory sizes increased. Indiana territories ranged from 0.4 to 3.5 ha (average 1.56 ha). In younger habitat, territories averaged 1.62 ha (range 0.5-3.5 ha) compared with 1.47 ha (range 0.4-2.4 ha) in older habitat with more and larger trees. In Georgia, 1 pair nested on a 0.24-ha island (Bent 1953; Lambert and Smith 1985; Morimoto and Wasserman 1991a; Nolan 1978; Nolan et al. 2020a).

Natal philopatry rates are low. The return rate of yearlings to their natal area was 1% of 166 banded nestlings (Schlossberg 2009). In Indiana, 10 of 272 fledglings (3.7%) returned, 2% of males and 5% of females. It was estimated that 11% of survivors returned, 7% of males and 16% of females. Two juvenile males that returned to breed did so 2.6-2.9 km from their natal site and 4 returning females nested 100-800 m from the natal site. Three of 10 returning fledglings never nested on the study area (Nolan 1978).

Schlossberg (2009) estimated an adult return rate of 29% based on 429 birds and 2 studies in Ohio and Indiana. In Ohio, 92.1% of returning adults exhibited site fidelity. There was some evidence that dispersing birds moved to younger patches but no evidence of their moving to areas with more shrubland habitat. The mean age of patches where birds were originally captured was 6.6 years compared with 5.6 years for dispersal patches. The latter estimate was for all shrub-nesting birds combined and was not specific to the Prairie Warbler (Lehnen and Rodewald 2009b). In Indiana, 65% of males that bred on the study area were seen in subsequent years and 60% returned the first year after banding. Essentially all surviving males returned to the most recent breeding site or its immediate vicinity. In the first year following banding, only 19% of females returned but there was a striking rise to a total of 55% the second year. If a female came back once, the probability that she would again was almost as high as it was for males. Virtually all survivors returned with 61% of females observed during the postfledging period returning. Significantly more successful breeding females (47%) returned than unsuccessful females (17%). Breeding success did not affect male return rates. Of 75 returning males, 55 (73.3%) reoccupied their former territory and small areas adjoining it. Four returned to their original territory, behaved territorially in other locations, then returned to the former territory to breed. The distance between permanent and temporary territories was 200-500 m (mean 350 m). In 90% of territory reoccupations, the latest territory overlapped the former one by at least 80%, but some males substantially shifted their centre of activity. Twenty males (26.7%) returned and relocated their territories, and 6 disappeared from the study area. All relocations occurred before the females arrived. Distances between nearest boundaries of old and new territories were 10-3,400 m (average 710 m). Only 5 males selected the nearest suitable habitat with the remainder passing over nearby habitat to chose sites further away. There were no perceptible differences in habitat of abandoned and selected territories and almost all abandoned territories were subsequently claimed by another male. Site fidelity was independent of male age. For females, selection of a breeding site also involves finding and selecting a mate. In only 14 of 137 cases (10.2%) did a female reoccupy and breed on her former territory; 3 females occupied sites in 3 consecutive years. Of the remaining cases, 73.3% of females were unbanded and

new to the area and 16.8% had been banded at a different location. Of returning females selecting new sites, 39.1% remained in the study area to nest 260-2,350 m from their previous year's nest. In 11 of 14 cases (78.6%) when a female returned but shifted territories, a male was present but already mated or no male had claimed the territory. In all cases when a female reoccupied her former territory, an unmated male was present. Both sexes may occasionally shift territories within the breeding season in response to predation or the loss of a mate. Two females bred on 2 separate territories within a year 125 m and 500 m distant from the study area. Many birds left the Indiana study area after nest failure, but may have nested elsewhere. New birds arrived in mid-season and these may have been failed breeders from other areas (Nolan 1978).

Jackson et al. (1989) studied within-season breeding dispersal in Indiana. For nests that failed after 10 June when females pass out of breeding condition, most females remained in the original territory without renesting. During this same period, females that nested elsewhere earlier in the season began to arrive and did not attempt to breed. Females were equally likely to leave their mate's territory and remate after unsuccessful (18%) and successful nests (17%). They hypothesized that females that lost nests due to predation would be more likely to move if predation was by an animal with a larger home range than a Prairie Warbler (larger mammals, snakes, and Brown-headed Cowbirds) than if it was by an animal with a smaller home range. In theory, it would have to move a longer distance to be outside the home range of the larger mammals whereas they could avoid chipmunk home ranges by relocating to another area within their own home range. This prediction was not substantiated with no difference in the rate of dispersal where depredation was by a species with a large home range (19%) or a small home range (6%). The authors regrouped the species and included the cowbird with the chipmunk as a species having a smaller home range than the Prairie Warbler. When these data were reanalyzed, significantly more females that suffered depredation due to animals with larger home ranges (22%) dispersed than those whose nests were depredated by chipmunks and cowbirds (8%). The reason for reclassifying the cowbird was that dispersal by the warbler would take it out of the range of that particular cowbird, but not outside the range of other cowbirds.

Limiting Factors

Nests have been reported in Ontario from mid-May until the second week of July, with most present 11-20 June (Peck and James 1998a).

Males usually acquire a territory on the day they arrive. Females sometimes move around before pairing, probably scouting the quality of habitat and potential mates. Females continue to arrive and mate throughout the season. Seventy percent of Indiana pair bonds were established within a few hours of the females' arrival. Thirty percent of older females settled 1-5 days on temporary territories before mating on their permanent territory. The period between the male's arrival in spring until pairing was 1-22 days (average 7.8 days). Several partial nests may be built before the final one is completed. These may be used for replacement or second nests. Early nests take 3-8 days to build, but mostly 3 or 4 days. Nests of pairs formed in mid-season were uniformly built in 3 days. Nest for second broods take 3-5 days to build, slightly longer because the female is interrupted by feeding the first brood. Nest building begins 0-15 days after pairing (average 5.0 days). Earlier-pairing females wait longer to build but also tend to initiate nest building earlier. Replacement nests are

initiated 0-14 days after loss (mean 1.7 days); 67% were begun the day after nest failure. Initiation of nests for second broods began 1-26 days after the first young fledged (mean 9.6 days). Females that renested after the second-brood nest failed did so 0-3 days after the loss (average 1.0 day). Development of vegetation in the spring was not related to the timing of nest initiation. Temperatures 2.5°C or more below normal retarded the initiation of first nests; 17.2°C was the lowest maximum daily temperature on which a first nest was started. Rain inhibited nest initiation during each phase of nesting. Females typically wait 1 day after the nest is complete before laying the first egg (range 0-8 days). One egg is laid per day. In only 5 cases of about 1,100 occasions did a female resume laying after skipping 1 or more days. It was more likely that a predator or a cowbird removed an egg than the female skipped a day laying. Most females begin roosting on the nest at night the day before they lay the final egg, but a few do not. Females spent 20-30% of their time on the nest the day the penultimate egg was laid, 3 times the amount of time spent the day the first egg was laid. In Indiana, the incubation period was 10.5-14.5 days (mean 12 days, mode 11.5-12.0 days). Cool weather prolonged incubation and therefore first nests took longer to incubate. Parasitism lengthens the incubation period and small clutches hatched quicker than larger clutches. The hatching interval ranged from 4 hours 45 minutes to more than 48 hours (average 13.5 hours). Young in Indiana left the nest when they were 8.00-11.25 days old (mean 9.34 days) and mostly when they were 9-10 days old. Those that left at age 8 days probably did so prematurely due to factors such as damage to the nest or ant infestations. Small broods tended to remain in the nest longer with young in larger broods probably feeling discomfort due to crowding. Nestling periods in Florida were longer and ranged from 10 to 14 days (Nolan 1955, 1978; Prather and Cruz 1985).

It is probable that only a single brood is raised in Ontario, but this has not been studied. In Indiana, 7% of pairs raised second broods. Renesting is common is a nest fails. Indiana females built 1-7 nests in a season (mean 3.2, mode 3). The numbers of nests built depended largely on success in escaping predation. In 1 case, the researcher took new nests from a female and she built 8 replacement nests. The mean distance between failed and replacement nests was 85 m (range 10-250 m), and the mean distance between successful nests and second-brood nests was 81 m (range 34-200 m). These distances did not differ from random. Clutch size appears to increase with latitude, although there are some exceptions. Ontario clutches contained 3-6 eggs, mostly 4-5 (mean 4.11 eggs, mode 4). In Indiana, clutches of 3-5 eggs occurred (mean 3.89 eggs, mode 4); only 7% of clutches contained 5 eggs. Data are sparse, but no 5-egg clutches have been reported from Tennessee or Kentucky, but some have been documented in Virginia, Oklahoma, North Carolina, and Georgia. In Florida, clutches consisted of 2-4 eggs (mean 2.86 eggs, mode 3). Ontario appears to be the only location where 6-egg clutches have been documented. In Indiana and probably elsewhere, clutch size declines with the season. Until 15 June, at least 75% of clutches contained 4 eggs with 5-egg clutches gradually disappearing and 3-egg clutches becoming more common. After 15 June, 3-egg clutches predominated. Larger clutches occurred in years when the first half of May was warmer. In Indiana, the mean clutch size of older females was 3.89 eggs compared with 3.73 eggs for yearlings. Older males and females were more productive than yearlings (Bent 1953; Nolan 1955, 1978; Peck and James 1998a; Prather and Cruz 1995).

Both sexes are capable of breeding when they are 1 year old. In Indiana, all males were mated in spring, but 6% were unmated on 1 June, 13% on 15 June, and 18% on 1 July. Few females were

unmated until early June, but by mid-June 13% were unmated and by 1 July 20% were unmated, when they were probably incapable of breeding. The instability of pair bonds in this population was probably caused in part by heavy nest losses due to predation. The mating system is predominantly monogamous but a small proportion of birds are polygynous. Only 5% of males were polygynous in mid-May but 10% were by 1 June. Most polygynous bonds were formed in mid-season when few unmated males were present. Females still selected superior males with larger territories and did not suffer any reproductive loss by mating with a polygynous male. When both females of a polygynous male nested on the same territory, their nests were separated by 50-300 m (mean 124 m). Only twice did a female build a nest within 60 m of her mate's other female's nest. Three males held 2 distinct territories with a female nesting on each of them. In 1 case, the territories were in different fields but contiguous at their corners. In another case, the territories were 100 m apart separated by a wooded ravine; in the final case, the territories were 1,300 m apart. Polygynous pair bonds involving a single territory were as stable as monogamous bonds. Seven categories of male pair bonds occurred in Indiana: season-long monogamy, short-term monogamy with 1 mate for less than a full season, successive monogamy without a location change, successive monogamy with a location change, polygyny on 1 territory, polygyny on 2 territories, and possibly polygyny with a location change. There were also 7 types of female bonds: season-long monogamy with a monogamous male, season-long monogamy with a polygynous male with 1 territory, seasonal monogamy with a polygynous male with 2 territories, short-term monogamy with a monogamous male, short-term monogamy with a polygynous male, successive monogamy with successively monogamous males, and successive monogamy with 1 or more polygynous males. The type of pair bond that an individual was involved in often changed as the season progressed, often repeatedly. Of 18 females raising second broods, 15 built and laid in second-brood nests without changing mates, 1 retained her mate but did not lay in her second-brood nest, and 2 changed mates before building and laying. Yearling females were more likely than older females to leave their first mate and pair again. In 13 cases, a female returned when her mate from the previous season was defending all or a part of that territory. Six of these remated and 5 did so at the beginning of the season. The other was courted by her former mate but paired with a neighbour and raised a brood and subsequently paired with her former mate and raised another brood. In the 7 cases of failure to reunite, 3 females reoccupied the site but paired with another male whose territory overlapped and 4 moved to different locations, probably because the male in their territory was already mated. It appeared as though females were attached to sites and not to mates (Ford 1995; Nolan 1978).

In Indiana, Nolan (1978) observed males 50 m to 1.2 km (mean 280 m) beyond their territory boundaries. Some, or all, males left their territory as often as once a day, especially when their mates were incubating. Most forays lasted 15-60 minutes (mean 30 minutes); 1 male was gone 3.5 hours. In unoccupied areas, roaming males sang repeatedly but were quiet and stealthy in occupied territories. The purpose of these forays appeared to be to establish another territory or to solicit extra-pair copulations (Morse 1989; Nolan et al. 2020a).

In Indiana, both sexes foraged from the ground to the tallest treetops and took food items from most or all vascular plants as well as from midair. The most common foraging technique was gleaning while perched followed (in order of frequency) by flycatching, hovering, clinging to vertical stems, hanging upside down, feeding on the ground, and seizing flying insects while perched.

Gleaning, flycatching, feeding on the ground, and feeding from bark were most common before leaves and most insects appeared. The Prairie Warbler specifically targets immature spittle bugs and is the only species known to do so. It relies on the froth to detect the insect's presence and may search for it with considerable persistence. Adults of both sexes fly plant to plant, probing into the masses of spittle and consuming the insect inside. In June, males foraged significantly higher (mean 6.1 m) than females (1.6 m). During the postfledging period, males foraged at an average height of 1.8 m compared with 1.6 m for females; these differences were not significant (Nolan 1956, 1978; Nolan et al. 2020a). Parnell (1969) summarized foraging strategies of the Prairie Warbler during the breeding season in South Carolina. Of the total time, 16.7% was spent in the canopy, 54.7% in low trees, 28.6% in shrubs, and 0% on the ground. In the canopy, 2.4% of foraging occurred in the top of the crown, 9.5% in the inner crown, 4.8% in the lower crown, and 0% on the bole. In low trees, 19.0% of foraging occurred in the top of the crown, 19.0% in the inner crown, 16.7% in the lower crown, and 0% on the bole. In shrubs, 2.4% of foraging occurred in the top of the crown, 9.5% in the middle crown, 4.8% in the lower crown, 9.5% in dense thickets, 2.4% in brush piles, and 0% in grass. In pitch pine barrens in Massachusetts, Morimoto and Wasserman (1991b) compared the foraging strategies of the Prairie Warbler and Common Yellowthroat. The Prairie Warbler foraged less in herbaceous plants and more in pines than the yellowthroat. Male Prairie Warblers differed significantly from yellowthroats in foraging height, use of plant species, foraging manoeuvres, and location in trees. There were no significant differences in these parameters for female Prairie Warblers and male yellowthroats. Both sexes of the Prairie Warbler foraged at heights of 0 to more than 6 m, but the female foraged lower. Yellowthroats and female Prairie Warblers exhibited a pronounced preference for foraging in scrub oak. Male Prairie Warblers divided their foraging more evenly between pines and oaks. Males spent 43% of their time foraging in pines, 46% in scrub oak, 7% in other deciduous species, 3% in ericaceous shrubs, and 1% in herbaceous plants. Females spent 67% of their time in oak, 23% in pine, 3% in other deciduous species, 3% in ericaceous shrubs, and 2% in herbaceous species. Prey was obtained most frequently from foliage, with males foraging distally more than females. Males selected higher (3-6 m) than lower song perches and preferred to sing and forage at heights above 3 m. Widely scattered trees in open habitat provided important song perches for males. Females foraged below 1.5 m near nest height where they remained fairly inconspicuous. Female Prairie Warblers were more similar to male yellowthroats in their foraging behaviour than they were to male Prairie Warblers.

When adults first arrive in spring, caterpillars large enough to eat may be rare. At this time, the Prairie Warbler spends much time in pine trees eating jumping plant lice. Males bring food to the nest 1-3 times per day during the incubation period. They do this even if the female is absent. This food is not fed to the female, although occasionally she eats it. This has been termed anticipatory food-bringing. The male is apparently unaware of hatching until he brings food and discovers young. Polygynous males fed nestlings at both nests equally, but none had 2 sets of nestlings simultaneously. Some had both nestlings and fledglings. The male may feed both fledglings and nestlings, terminate feeding the fledglings prematurely and feed nestlings, or abandon the fledglings and feed only the nestlings. When females attempted second broods, they usually did not feed their first brood, although 1 female did. Based on visual observations, 82% of the diet of nestlings consisted of caterpillars, 88.4% of which were green. These were mostly 20-25 mm in

length but some were as long as 50 mm. Sixteen percent of the nestling diet consisted of other insects (moths, flies, orthopterans, bugs, wasps, and a damselfly), and 2.2% of the diet was spiders; 1 millipede was consumed. During the breeding season, all but 0.3% of the diet of adults consisted of animal matter, including arthropods and fragments of a single snail shell. Spiders and 5 orders of insects (beetles, lepidopterans, flies, hymenopterans, and bugs) constituted 97% of the diet. It ate beetles in proportion to their availability and leaf beetles and weevils were prominent in the diet. It may take caterpillars more than their availability, perhaps because of their low mobility and high efficiency as a food item. Seventy-six percent of stomachs contained beetles, 35% contained lepidopterans, 34% contained flies, 30% contained hymenopterans, 24% contained spiders, 17% contained soft-winged bugs, and 6% contained true bugs. Volumes of food items ranked in approximately the same order. One ate a dobsonfly larva that was presumably captured in a stream while the bird was bathing. Other items consumed included crickets, jumping plant lice, aphids, green lacewings, and millipedes. Some birds consumed large quantities of insect eggs. In early spring, 1 female drank sap from a wound in a black locust (Nolan 1958, 1978; Nolan et al. 2020a). In Parry Sound District, both sexes at 1 nest fed on green larvae that they captured in red oaks and sweet gale (Niskanen 1997).

The Brown-headed Cowbird commonly parasitizes the Prairie Warbler. Rothstein (1975) artificially parasitized 2 nests and concluded that it was an acceptor of cowbird eggs. Bent (1953) stated that often a false bottom was built over the cowbird egg. Neither of these statements is strictly correct. In Indiana, desertion of parasitized nests was common, especially if the cowbird egg was laid at an inappropriate time in the warbler's nesting cycle. Seventy-four percent of nests that were being incubated when they were parasitized and 56% of nests when the cowbird egg was laid in an empty nest were deserted. Warblers always deserted nests when an egg punctured or broken by a cowbird leaked into the nest, but not necessarily when the egg dried out without leaking. Of several hundred Indiana nests, only 2 or possibly 3 cases of embedding cowbird eggs in the nest were observed. In all cases, the nest was still in the process of being built. Parasitism rates are highest early in the year. In May in Indiana, 29-40% of nests were parasitized annually, 25% of nests were parasitized 1-10 June, 20% were parasitized 11-20 June, and parasitism rates fell rapidly to 0% after then. Parasitism rates increased with increasing nest height, although not significantly. Presence of a cowbird egg did not significantly affect the hatching rate of warbler eggs: 95% of eggs hatched in unparasitized nests compared with 92% in parasitized nests. Parasitized nests produced few fledglings. Mean brood size in Indiana was 3.21 young warblers in unparasitized nests compared with 0.78 in parasitized nests. In this population, it was estimated that parasitism lowered production of young by 13.3% because fewer nests succeeded, female cowbirds removed warbler eggs, and presence of cowbird nestlings further reduced brood size. In Ontario, 10 of 37 nests (27.0%) were parasitized. In Indiana, 83 of 248 nests (33.5%) that contained warbler eggs on 10 June or earlier were parasitized. In Illinois, 2 of 9 nests (22.2%) were parasitized and another nest contained a punctured egg, possibly by a cowbird. In Michigan, 5 of 18 nests (27.8%) were parasitized; 0 of 6 were parasitized in Texas; 11 of 53 (20.8%) were parasitized in Missouri; and 7 of 30 (23.3%) were parasitized in Mississippi (Graber et al. 1983; Hackemack et al. 2016; Harrison 1984; Jackson et al. 1989; Nolan 1978; Novak et al. 2016; Peck and James 1998a; Roach et al. 2018).

Habitat loss and degradation are not significant issues in Ontario now, but affected the Prairie Warbler historically. The largest population south of the Canadian Shield was in the interdunal habitat at Wasaga Beach and Pinery Park. Habitat at Wasaga Beach, where an estimated 150 pairs once bred, was destroyed by cottage development by the late 1940s. Dune habitat has become unsuitable in some areas due to planting of pines that are now too mature to provide habitat, dune stabilization projects, and human disturbance. These were probably the greatest threats south of the Shield but, with the exception of a few pairs at Pinery Park, this population was extirpated decades ago. Pine plantations at St. Williams and Turkey Point formerly provided habitat but these have become too mature. Relict populations may be retained there if areas are set aside and managed to provide early successional habitat. Birds nesting on hydro rights-of-way may have their habitat abruptly destroyed by herbicides, but these can typically recolonize as other areas reach appropriate successional levels. Good habitat is often created by forest fires, so fire suppression may have negative effects. Natural succession in these types of habitat gradually makes the habitat unsuitable. A population in a burn in Frontenac County was most active for 30-40 years during the appropriate levels of succession, but small numbers of pairs persisted for 3-4 decades after optimum conditions prevailed. Most of Ontario's population breeds along the eastern shoreline of Georgian Bay. Habitat there is stable due to the bedrock outcrops, limited soil depth, and harsh microclimate adjacent to Lake Huron (Austen et al. 1994; James 1996c, 1999e; Lambert and Smith 1985).

Habitat loss is the most significant limiting factor for the Prairie Warbler in the United States, where it is mostly dependent on early successional habitats created by humans. This habitat has been declining since the 1970s, predominantly due to natural succession and tree planting, but also to development in some areas. Fire suppression also limits the amount of available open habitat. Populations waxed and waned in direct proportion to the amount of available shrubby habitat (Morse 1989; Nolan et al. 2020a; Wells 2007).

In North Carolina, the Prairie Warbler was significantly more abundant in burned than unburned areas, and exhibited the most positive response to fire of all species studied. It occurred more frequently only after high severity burns. It occurred less frequently as the time since the burn increased and was most frequent 5-10 years after burning. Large patches of severe burns should be beneficial to it (Rose and Simons 2016).

Harsh spring weather can affect reproductive success, particularly in the core of the Ontario range along the eastern shoreline of Georgian Bay. Late springs there can result in late melting of snow, retarded vegetation growth, and cold winds off the bay. Ice may remain piled up along the shoreline well into June (Harrington 1924). When this occurs, it is possible that some birds may not nest at all. Those that do initiate clutches later and are likely to have smaller clutches and be less likely to renest in the event of nest loss.

Alterman et al. (2005) examined the effects of forest management on the Prairie Warbler in Arkansas. The 2 harvest types investigated were seed-tree cutting, which consists of retaining 10-25 mature trees per ha in clear-cuts, and group selection, where 10% of the stand is cut every 10 years in patches 0.8 ha or smaller and allowed to regenerate. All 14 nests they found were in seed-tree cuts. Males were observed at 3 of 21 group-selection openings, but no females were present. They

concluded that group-selection openings were too small to support nesting Prairie Warblers, but seed-tree cuts provided suitable habitat.

In Indiana, 0.8% of nests failed due to blow fly infestations. In some nests that were infested with ants, the young fledged prematurely, but there was no indication that this was deleterious to the young (Nolan 1978).

Price (2004) predicted that the range of the Prairie Warbler might expand in southern Ontario if the average summer temperature increased by 2°C.

Status

The early status of the Prairie Warbler in Ontario is uncertain. In the United States, deforestation associated with European settlement resulted in creation of much new habitat and a marked population increase. It seems unlikely that this major event had any effect on Ontario populations if there were actually any in the province at that time. In Ontario, it is restricted predominantly to natural habitats and has not adapted to using the anthropogenic old fields in which it frequently occurs in the United States. It was first documented in Ontario in 1900 in Toronto and breeding on the Bruce Peninsula was suspected by 1906. Nesting was not confirmed until 1922 at Wasaga Beach. It has been suggested that the breeding population along Georgian Bay has been present for centuries or even millennia because of the stable habitat, and this theory appears to have been generally accepted. In the late 19th and early 20th centuries, the Prairie Warbler significantly expanded its range northward as a result of the abundance of newly created habitat. It became established in the northern states (Connecticut, Ohio, Indiana, Illinois, and Michigan) between 1870 and 1910. The rationale for the conclusion that the Georgian Bay area was always inhabited is based on larger numbers seen during spring migration on islands in Lake Erie in 1912 and on the Ohio Lake Erie shoreline in 1907 (Austen et al. 1994; James 1999e; Lambert and Smith 1985; Nolan 1978). These observations were made during the period when it was expanding its range northward, and are not conclusive evidence that the Georgian Bay population was always present. It seems unlikely that a small disjunct population would persist several hundred kilometres north of the core range even if suitable habitat were present.

Baillie and Harrington (1937) classified the Prairie Warbler as a local summer resident from Lake Erie north to Parry Sound District and Renfrew County and reported a single summer occurrence at Frank's Bay on Lake Nipissing in 1933. Within this broad range, they concluded that it bred fairly commonly along the shores of southern Georgian Bay and southern Lake Huron, but not elsewhere in the province. In 1914-15, it was common at Wasaga Beach and an estimated 200 pairs formerly nested there and in the Pinery and Ipperwash areas. By the late 1940s, the Wasaga Beach population had been extirpated due to cottage development and disturbance with only a few pairs persisting in the Pinery area. A population was present in Frontenac County as early as 1933 and peaked in the late 1940s and early 1950s at 35-40 pairs. Because of natural succession, this population declined to 6-7 pairs in 1963 but a few birds still persisted as late as 1989. Additional populations were subsequently found along the southern edge of the Canadian Shield in Frontenac and Peterborough counties. It bred many times on the Bruce Peninsula until the 1950s, but was not detected there during the first atlas. Small numbers formerly bred in the young plantations in the St. Williams–Turkey Point area but most of these disappeared by the late 1970s with only scattered

pairs persisting. By the mid-1980s, the population south of the Shield had all but disappeared except for isolated small populations. At that time, it was estimated that 90% of the Ontario population nested along the Georgian Bay coast in Muskoka and Parry Sound districts and along the southern Shield in Frontenac and Peterborough counties. Historically, the Prairie Warbler had been documented nesting in 10 upper-tier municipalities, but as of 1984, it bred regularly in only 6: Lambton, Simcoe, Muskoka, Parry Sound, Peterborough, and Frontenac. In 1985, 310-325 pairs were known to breed in the province, but numbers could have been as high as 462-702. It was estimated that about 500 pairs were present. Although the population and its habitat appeared to be stable at that time, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated it special concern because of the low population occurring in localized habitats (Austen et al. 1994; Bent 1953; James 1996c; Lambert and Smith 1984, 1985). Results of the first atlas were similar to what had been reported in the COSEWIC status report, primarily since most of the atlas data were available when it was written. The atlas documented about 10 pairs in the Pinery area and a few in the St. Williams area, with the bulk of the population along the eastern Georgian Bay coast and the southern Shield. Breeding along hydro rights-of-way was documented for the first time and isolated breeding records were obtained for the first time in Haliburton, Hastings, Lennox and Addington, Lanark, and Middlesex counties and the regions of Waterloo and York. The most northerly location where it was found nesting along the Georgian Bay coast was Pointe au Baril. Based upon the atlas results, Lambert (in Cadman et al. 1987) concluded that the breeding population could be somewhat less than 500 pairs. James (1991) concluded that the Prairie Warbler was a rare to locally uncommon summer resident in the south north to Parry Sound District and Frontenac County.

From 1990-94, a new population was discovered in pine plantations near Rockton. Only about 3 pairs were present and the Prairie Warbler later disappeared or became irregular once the trees grew taller. Breeding was also confirmed near Campbellville in 1982, so these 2 records provided breeding evidence for Hamilton and Halton for the first time (Curry 2006). In 1997, the Natural Heritage Information Centre conducted a systematic survey of the Georgian Bay shoreline for breeding Prairie Warblers. A total of 349 singing males were documented at 174 of the 420 sites (41.4%) investigated. The largest population occurred in the Honey Harbour to Cognashene area of Muskoka District where 108 males were present at 69 of the 107 (64.5%) sites visited. Other concentrations included 29 at Go Home Bay, 28 at San Souci, and 49 at Massasauga Provincial Park (Sutherland 1998). James (1999e) prepared an update COSEWIC status report on the Prairie Warbler and estimated that there were still about 500 pairs in the province, with about 20 pairs in Peterborough County and 65 in Frontenac County in addition to the Georgian Bay population. He concluded that any losses in the population were historical and that numbers and habitat had remained stable since the last report. He recommended that its status be maintained at special concern, but COSEWIC downgraded it to not at risk.

The second atlas confirmed that most of the population occurred along the shore of Georgian Bay between Pointe au Baril and Port Severn, with discontinuous populations along the southern edge of the Shield from Simcoe to Frontenac counties. It declined or disappeared from many areas in which it occurred during the first atlas and the small population (never more than 8 pairs) persisting in the St. Williams–Turkey Point area represented 2 of only 4 squares reporting breeding evidence south of the Shield. It was estimated that the total Ontario population did not exceed 320

breeding pairs, 270 of which occurred along the Georgian Bay coast (Sutherland and Harris in Cadman et al. 2007).

Hannah et al. (2024a) completed a detailed inventory of the Georgian Bay population in 2015 and detected 388 singing males. This was a considerable increase over the 1997 estimate of 270 singing males, but the 2015 survey checked locations that were previously missed. Even the later survey missed some sites due to inaccessibility, so the population may be around 427 singing males. Most suitable habitat appeared to be occupied.

The Breeding Bird Survey (BBS) indicates that the Prairie Warbler has been declining significantly in the United States since 1966. This survey is not relevant to Ontario as it is rarely detected by it so there are no trend data available. BBS data indicate a significant decline of 54%, or about 2% per year, from 1966 to 2005. Approximately 96% of the global population occurs in the southeastern United States and about 90% of the habitat is in the 4 southernmost counties of Florida (Austen et al. 1994; Nolan et al. 2020a; Wells 2007). Hanberry and Thompson (2019) compared BBS trends and forest composition over time in the eastern United States. They attributed the Prairie Warbler's decline in part to the reduction in the amount of early successional habitat and the increase in the amount of closed-canopy forest.

POSTFLEDGING PERIOD

In Georgian Bay, all Prairie Warblers left their breeding territories and travelled long distances, with one travelling as far as 40 km. They appeared to prefer outer edges of islands where common juniper was the dominant vegetation (Rusak 2025).

In old-field habitat in Indiana, brood division occurred shortly after young left the nest. Even when both sexes remained on the territory and a single brood was raised, fledglings remained with a single parent. In every case where the female attempted a second brood, the male took care of all independent young (Nolan 1978). The earliest that fledglings in Indiana could survive unassisted was 34-35 days, and young from first broods were often abandoned at this age. Extreme periods of fledging dependence were 34 to 55 days with a mean of 40.8 days (Nolan et al. 2020a).

The direction of first flight of fledglings was random and by the end of the first day young were scattered 30-35 m from the nest. Young produced on territories in low and open vegetation moved toward edges of woods or overgrown hedgerows and were often near the territory boundary. Before age 25 days, young averaged 45 m from where they had been the previous day, with a range of 12-110 m moved daily. Sometimes the daily movements were in the same direction but more frequently the movements cancelled each other out and the group remained within the territory. Birds whose parents were involved in a second brood tended to remain near the nest. After age 25 days, family units often travelled far and quickly (100-250 m in 10 minutes) and some moved 400-500 m per day. During this period, fledglings often had a preference for a particular thicket that they repeatedly moved to. Of males with fledglings 20 days old or less, 80% remained on the territory. The mean distance from the territory for those that left was 100-125 m (maximum 500 m). Sixty percent of females with young of the same age remained on the territory. The mean distance moved by those that left was 200-225 m (maximum 600 m). Groups led by females often began to move when they were quite young compared with those led by males. Of 50 family units, 38% rarely if ever left the breeding territory. Females that were moulting at the end of the reproductive cycle

tended to remain on or near the breeding territory. Brood home range sizes averaged 1.5 ha, similar to the breeding territory. Groups that moved appeared to set up similar-sized home ranges but some groups led by females did not establish fixed home ranges. Soon after independence, young left the site where they were last dependent and moved randomly in the region for several weeks. Fledglings probably remain near the hatching site for 20-30 days after independence. The distance between the last sighting of the year and the area where they were last dependent was 0-900 m for 26 young (mean 460 m). The final sighting was not always the furthest observation from the site of last dependence. Only 1 juvenile settled into what appeared to be a territory in September. Once young became fully independent at the age of 30-55 days, they left the study area (Nolan 1978).

After the young became independent, 49% of males were seen repeatedly within 200 m of the territory; 22% moved considerable distances, remained away for days or weeks, then returned in September; and 29% left the breeding territory and did not return. Only 13% of females remained within 100 m of the breeding site. A few left with young once they were independent, but most moved away permanently. A female moved 500 m to an area that she had occupied in 5 successive years during the postfledging period, even though she had no young. Fidelity to postfledging home ranges was not affected by reproductive success (Nolan 1978).

In addition to the old-field habitat used in Indiana, juveniles, adults, and family groups have inhabited clear-cuts, mostly in oak, hickory, or pine stands, during the postfledging period. Use of clear-cuts has been confirmed in Missouri, West Virginia, Virginia, and Ohio. In Missouri clear-cuts, where the Prairie Warbler also nested, numbers declined significantly with time after cutting. Numbers peaked at 19 birds per year 3 years after harvest and declined to 13 at 4 years and 12 at 5 years. No Prairie Warblers were captured 11-15 years after harvesting except for a single bird in year 14 (Marshall et al. 2003; Porneluzi et al. 2014; Vitz and Rodewald 2006).

On 1 night in Indiana, fledglings 25-29 days old roosted together 1 m up in a sumac thicket with the male, and 1 fledgling and the female roosted together in a flowering dogwood 1 m away. This roost was not used the following evening. Another group of 40-day-olds roosted together 1-2 m from the ground in a thicket (Nolan 1978).

MIGRATION

The migratory race of the Prairie Warbler winters in Florida and the West Indies. The Florida subspecies is largely sedentary. Collisions with tall structures indicate that much migration is nocturnal, but diurnal migration also occurs. Large daytime overwater movements toward Florida have been reported in spring. It is unknown if it migrates singly or in flocks at night, but it may fly with other warblers. Spring movement is associated with south winds. During the daytime, it often joins flocks of other warbler species. The maximum number of Prairie Warblers in a flock is 8 and 2-3 is normal (Nolan 1978; Nolan et al. 2020a). In Ontario, it would be exceptional to see 2 in a single flock.

In spring, older males arrive before older females and older birds arrive before yearlings. At a Florida television tower, the median date of death of old males was 6 April compared with 21 April for old females. The median date of death for yearling males was 21 April compared with 23 April for yearling females (Nolan and Mumford 1965). In Indiana, the mean date of the first arrival for males was 18.6 April (range 11-27 April) and the mean date of arrival for females was 23.4 April (range 19-

28 April). The earliest females never preceded the earliest males. The mean interval between the first male and female of the season was 5.1 days (range 1-9 days). When males were late arriving, the females were not similarly late and the gap between the arrival of the sexes was shorter. Birds arrived on the breeding grounds a few days before or after 30-50% of the dominant woody plants had leaves or were in flower. Many grasses and forbs began their annual growth at about the same time. Insects had emerged prior to the birds' arrival but were still far below their summer levels. Prairie Warblers appeared to arrive as early as sufficient food was available to sustain them. Most individual males consistently arrived early, late, or in the mid-period of arrival from year to year. Early arrival results in earlier nesting and opportunities for renesting and second broods. The beginning of egg laying was advanced by 1.4 days for each day that a male's arrival was accelerated and increased the length of period during which he had the opportunity to have a mate in reproductive condition by 3% (Nolan 1978). Spring migration south of the Shield in Ontario is throughout May, with some occurring in mid- to late April and others remaining into early or mid-June (Black and Roy 2010; Curry 2006; LaForest 1993; Lambert and Smith 1984; Weir 2008). The earliest that birds arrived at Go Home Bay in Muskoka District was 18 May (Mills 1981).

In autumn, young birds begin to migrate before adults and continue to do so as long as adults and consequently have a longer migration period. There appears to be no difference in the timing of migration of the sexes (Nolan 1978; Nolan and Mumford 1965). Migration probably begins in August in Ontario. In some breeding areas in Muskoka, it is seldom seen after the first week of August, but has been seen as late as 3 October at Go Home Bay (Lambert and Smith 1985; Mills 1981). In the south, autumn migration is typically from mid-August to mid-September, with some arriving in early August (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). Most birds have probably left the province by the end of September; there are very few October records (Lambert and Smith 1984, 1985).

During migration in Ontario, the Prairie Warbler occurs in slightly or very open habitats such as overgrown fields, forest edges, scrubby open areas at edges of pine-oak or beech–sugar maple forests, beach strands, open hawthorn thickets, wild plum thickets, mixed woodlands, and abandoned orchards (Lambert and Smith 1985). Eifrig (1909) observed one in alders prior to leaf-out along the shoreline of Lake Doré in Renfrew County. During spring and autumn migration in Illinois, most were found in shrubs and forest edges although a few occurred in mature upland forests (Graber et al. 1983). In pitch pine barrens in New Jersey, most spring migrants were seen in oaks (Brush 1987). During spring migration in South Carolina, numbers seen per hour were 7.58 in dry thickets, 1.09 in pine forests, 0.97 in pine-hardwood stands, 0.48 in wet thickets, 0.14 in floodplain forests, 0.13 in oak-hickory forests, and 0 in beech forests. It was significantly more abundant in dry thickets than other habitats and was the most abundant warbler in dry thickets (Parnell 1969).

Parnell (1969) studied the foraging habits of the Prairie Warbler during spring migration in South Carolina. The time spent foraging on different substrates was 15.8% in the canopy, 54.5% in low trees, 29.7% in shrubs, and 0% on the ground. In the canopy, 5.9% of foraging occurred at the top of the crown, 6.9% in the inner crown, 3.0% in the lower crown, and 0% on the bole. In low trees, 21.8% of foraging occurred at the top of the crown, 22.8% in the inner crown, 9.9% in the lower crown, and 0% on the bole. In shrubs, 9.9% of foraging was at the top of the crown, 6.9% was in the

inner crown, 4.0% in the lower crown, 7.9% in dense thickets, 1.0% in grasses, and 0% in brush piles. Singing males were recorded from the ground to over 15 m (mean 5.2 m). Nonsinging birds occurred at the same range of heights with a mean of 4 m.

In Florida, the Prairie Warbler is commonly killed during migration by striking television towers (Nolan 1965, 1978; Nolan and Mumford 1965). It undoubtedly strikes tall structures elsewhere, but this has seldom been documented. Graber et al. (1983) had no records of Prairie Warbler casualties at Illinois television towers. It has not been reported as a casualty at the Long Point Lighthouse, but 1 was killed at the Lennox generating station chimneys in 1981 (Lambert and Smith 1985; Weir 2008).

The Prairie Warbler is a rare migrant in Ontario, although there are records from every municipality from Algoma and Sudbury districts southward. An average of 2 per season annually is captured at Long Point. In the 20 years preceding 1984, 2.7 Prairie Warblers were captured at Long Point for every 10,000 warblers banded. The maximum number recorded during spring migration at Prince Edward Point is 3 (James 1991; Lambert and Smith 1984, 1985; Weir 2008).

Black-throated Green Warbler

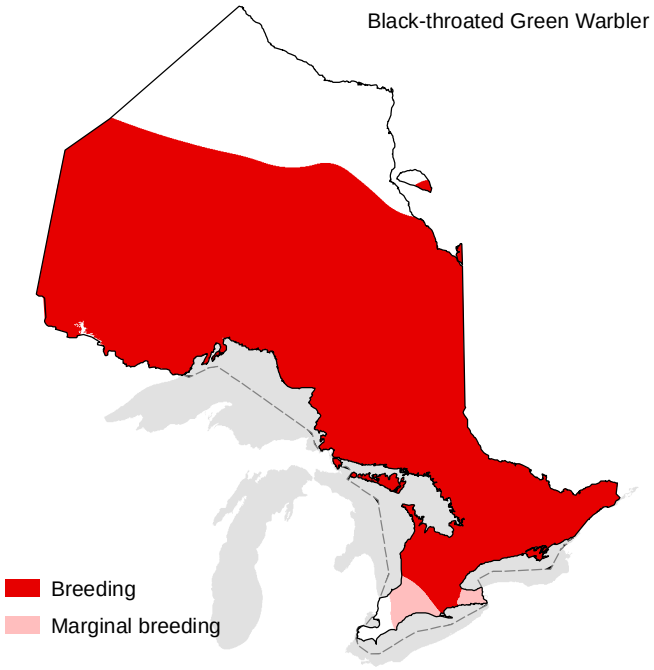
Setophaga virens

BREEDING SEASON

Habitat Requirements

Ontario Black-throated Green Warbler nests were within wooded areas: 51.7% of nests were in coniferous woods, 31.0% were in mixed woods, and 17.2% were in deciduous woods. Some were at forest edges near roads or water (Peck and James 1987). James (1984b) reported that it nested in coniferous or mixed forests where the trees were older second growth or mature. In mixed forests, it prefers hemlock. It prefers closed-canopy forests, especially those with some shrub growth.

In the Boreal Forest Region near Pickle Lake, the Black-throated Green Warbler occurred in low density in mixed forests and coniferous forests with an understorey. It was occasional in deciduous forests and absent in coniferous forests without an understorey, heath, tundra, and coniferous, mixed, and deciduous scrub (McLaren and McLaren 1981). James (1980) encountered it irregularly in small numbers in predominantly deciduous forests near Pickle Lake. In jack pine stands near White River, it was significantly more abundant in stands 40-100 years old with a large component of jack pine. It was a significant indicator of mature forest (Venier and Pearce 2005). Near Manitouwadge, it was more abundant in stands 60-223 years old than those 24-36 years old. It occurred at very low densities in stands 1-21 years old (Venier et al. 2009). Near Hearst, it was the most abundant species



in clear-cuts 13 and 19 years old in upland mixed forests. It was common in 24-year-old clear-cuts and uncommon in 11-year-old clear-cuts in upland mixed forests. It was not observed in lowland coniferous forests of any age (Welsh and Fillman 1980). In the Clay Belt, it was most abundant in trembling aspen stands followed by white cedar–tamarack, balsam poplar, and white spruce–white birch stands. It was least abundant in black spruce stands and not observed in jack pine stands. It occurred in very dry to wet areas and nutrient-poor to nutrient-rich sites (Welsh and Lougheed 1996). In the Boreal Forest Region, Erskine (1977) considered it one of the 3 most distinctive species of balsam fir stands. The Black-throated Green Warbler often attains much higher densities in pure hemlock stands than in any more boreal forest types. It is more common in mature coniferous stands. It is characteristic of the most fertile coniferous stands whether they are dominated by hemlock, balsam fir, or white spruce amidst poplar. It may use the richest white spruce stands if mature balsam fir or hemlock are unavailable. Higher densities are attained south of the boreal forest than in it.

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Black-throated Green Warbler occurred in both old-growth and mature white pine stands. It was more abundant in old-growth forests, but not significantly. Presence of supercanopy white pine with a diameter at breast height (DBH) of 60 cm or larger was a significant predictor of its abundance. Kirk et al. (2012) estimated that it required 23 supercanopy stems per ha. It was the fifth most abundant species in mature and old-growth white pine stands. In Quetico Park, it was most abundant in stands 112-370 year old, although it occurred in low density in 1-23-year-old stands. In 112-year-old stands, it was equally abundant as the Black-throated Blue Warbler and Red-eyed Vireo in heavier spruce–balsam fir cover (Apfelbaum and Haney 1985). In Muskoka and Parry Sound districts, the Black-throated Green Warbler was common in pine, hemlock, and hardwood forests and also in pastures with scattered spruce (Mills 1981). In young open jack pine stands mixed with deciduous species in Parry Sound District, James (1979a) reported it on 1 of 5 transects at low density. In northern hardwoods near Sault Ste. Marie, it was positively correlated with the basal area of small trees (Holmes and Pitt 2007). MacLulich (1938) concluded that it was abundant in both coniferous and deciduous stands in Algonquin Park. In the park, it nests in forests consisting of 85% sugar maple with the remainder mostly beech, hemlock, and yellow birch. It usually selects a territory that contains a group of hemlock and other conifers, with some territories containing only 1 or 2 canopy-sized conifers or none at all (Tozer 2008, 2012). Martin (1960) reported it in a variety of forest types in Algonquin Park. It was most abundant in hemlock stands where it was second in abundance. In these stands, it

ranged from the sapling layer to the top of the canopy. It was common in sugar maple–yellow birch stands where it was third in abundance and ranged from the middle of the shrub layer to midcanopy. It occurred in lower density in balsam fir–spruce-hardwood stands and in even lower density in poplar–white birch stands where it ranged from the mid-level of shrubs to the top of the canopy. It was absent in balsam fir–spruce stands, balsam fir and spruce mixed with poplar and white birch, and immature white pine stands. He considered it characteristic of hemlock but noted that it also occurred in hardwoods where hemlock was absent. In white pine stands in Algonquin Park, it was significantly negatively correlated with high percent coverage by conifers at heights of 2-5 and 5-10 m, and dense ground cover layer. These represented stands with a well-developed herbaceous layer and a well-developed coniferous subcanopy, features seen most frequently in recently cut areas (Kingsley and Nol 1999). In Haliburton County and Muskoka District, it was associated with high canopy volume, intermediate tree density, and above-average amount of understorey. Its habitat was indicative of undisturbed forest and it was associated with mature coniferous woods with considerable understorey (Clark et al. 1983).

In the Great Lakes–St. Lawrence Forest Region south of the Canadian Shield, McLeish and Robertson (1997) concluded that upland white cedar stands could provide quality habitat for the Black-throated Green Warbler. In Durham Region, it was common in a mature pine plantation and uncommon in a mature sugar maple–oak forest. Speirs and Orenstein (1975) considered it associated with pines.

In the Carolinian Forest Region in Elgin County, Lancaster et al. (2004) documented the Black-throated Green Warbler breeding in a mixed forest where hemlock was the dominant conifer. In the St. Williams Forest, it breeds in mature pine plantations that have evolved into naturally appearing forests of mixed pines and oaks; it also occurs there in sugar maple–beech forest with inclusions of hemlock (personal observation).

The Black-throated Green Warbler typically nests in forests, but may rarely nest in nonforested areas. It has nested in pastures and old fields containing scattered red cedars or pitch pine and possibly white cedars. There are rare reports of it nesting on a vine-covered pagoda on an open hillside some distance from forest and in a solitary spruce near a chapel with mixed woods nearby. It also nests in open pitch pine barrens (Bent 1953; Brewster 1895; Brown 1889; Chapman 1907; Morse and Poole 2020; Reading and Hayes 1933).

The Black-throated Green Warbler has been termed a wide-ranging habitat generalist that exhibits substantial geographic variation in its use of forested habitat, and particularly its requirement for conifers. Habitat selection differs among populations depending upon the forest type it inhabits (Robichaud and Villard 1999). It is most abundant in coniferous and mixed woods and tends to associate with conifers in mixed stands. It also occurs in pure deciduous stands. One subspecies breeds from southeastern Virginia and northeastern North Carolina in an exclusively deciduous area (Morse 1989, Morse and Poole 2020).

One habitat characteristic that is uniform throughout its range is that the Black-throated Green Warbler is most frequently associated with upland stands. There are some exceptions to this. In Michigan, it nested in bog communities treed with spruce (Pitelka 1940). In the northeast and New Jersey, it breeds in low to moderate densities in white cedar swamps (Brush 1987; Dawson 1979)

and it occasionally nests in red maple swamps in Rhode Island (Golet et al. 2001). In eastern Quebec and Labrador, its abundance was correlated with breeding-season precipitation, suggesting that it selected moister habitats (DesGranges and LeBlanc 2012).

Lanoue and Lafontaine (in Gauthier and Aubry 1996) provided an overview of the Black-throated Green Warbler's habitat preferences in different ecoregions of Quebec, and these closely match conditions in Ontario. It is infrequent in the black spruce zone of the northern Boreal Forest Region where it nests in intolerant hardwood stands. Further south, it becomes more abundant in the balsam fir ecosystem where it prefers mixed stands of balsam fir, white spruce, and poplar, or riparian habitat of white spruce and shrubs. It is most abundant in the south which contains mixed and deciduous forests, especially those dominated by sugar maple and yellow birch. Numbers are low in agricultural landscapes where it frequents rich, conifer-dominated sites, particularly those with hemlock, pine, balsam fir, white cedar, or white spruce.

Most authors consider the Black-throated Green Warbler a conifer specialist. It occurs in a wide range of coniferous and mixed forest types and focuses on conifers within mixed forests. Even in predominantly deciduous stands, territories may contain a few canopy-level conifers. In certain areas, it may exhibit a preference for 1 species of conifer over another, but these preferences are not consistent throughout its range. In Maine it prefers white and red spruce stands along the coast where red spruce is highly preferred to white spruce. Less than 10 km inland, it selects stands dominated by white pine (Morse 1976, 1989). It avoids black spruce, which occurs to the northern extent of its range and in boreal inclusions in the mixed-wood forest ecoregion (Kirk et al. 1996; Morse and Poole 2020; Whitaker and Montevecchi 1997). One constant is that it is strongly prefers hemlock. In certain areas of New Jersey, the Black-throated Green Warbler is considered an obligate hemlock species. Optimum habitat may not be pure hemlock stands but rather a combination of hemlock and hardwoods. The combined presence of hardwoods and hemlock results in layering of vegetation and a dense upper to mid-level concentration of foliage in the zone it prefers for foraging. The requirement for this layering may explain its absence or scarcity in spruce plantations and black spruce stands, because densely spaced spruce are self pruning leaving foliage concentrated in the upper canopy (Benzinger 1994; Brooks 1940; Keller et al. 2003). In New Jersey and Pennsylvania over a 15-year period, hemlock declined from representing 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. This warbler declined in response to the decline in hemlock (Toenies et al. 2019).

Coniferous forest types that the Black-throated Green Warbler has nested in include those dominated by pine (especially white, red, and pitch pine, less frequently in jack pine), spruce (especially red and white spruce, infrequently in black spruce), white cedar and Atlantic white cedar, balsam fir, hemlock, spruce–balsam fir, balsam fir–white cedar, and plantations dominated by pines (Bent 1953; Benzinger 1994; Bielefeldt and Rosenfield 1994; Brooks 1940, 1947b; Capen 1979; Chapman 1907; Collins 1983b; Crawford and Titterington 1979; Dawson 1979; Drolet et al. 1999; LaRue et al. 1995; Morse 1976; Pitelka 1940; Thompson et al. 1999; Titterington et al. 1979; Whitaker and Montevecchi 1997).

The Black-throated Green Warbler breeds in a variety of mixed forest habitats. In the northern portion of its range, these are usually a mix of intolerant hardwoods (poplar and white birch) and

white spruce and balsam fir. Either the conifers or the hardwoods may dominate. Further south, the mix is often sugar maple and yellow birch and miscellaneous hardwoods with hemlock, pine, or white spruce. Even further south, it may use oak-pine associations. Less frequently used mixed stands include white cedar and intolerant hardwoods (Beals 1960; Campbell et al. 2001; Kendeigh 1945; Pitelka 1940; Robichaud and Villard 1999; Schieck et al. 1995; Temple et al. 1979).

The Black-throated Green Warbler also nests in pure deciduous stands. These may either be intolerant hardwoods or tolerant hardwoods such as sugar maple, beech, and yellow birch. Other types of deciduous stands that it may nest in include those dominated by red maple, oak-hickory, and white birch–red oak (Back 1979; Beals 1960; Brooks 1940, 1947b; DeGraaf and Chadwick 1987; DeGraaf et al. 1998; Freedman and Johnson 1999; Freedman et al. 1981; Harrison 1984; Holmes and Sherry 2001; Noon et al. 1979).

Several studies examined forest type preferences of the Black-throated Green Warbler. In New Hampshire and Maine, it was most abundant in hemlock stands, followed by those dominated by white birch, northern hardwoods, and swamp hardwoods. It was present but in lower numbers in stands dominated by poplar, balsam fir, white pine, and spruce–balsam fir (DeGraaf et al. 1998). On Wisconsin islands, it was one of the most common forest species and occurred in all stand types. It was most abundant in white birch–yellow birch–white cedar stands followed by those dominated by pines (jack, white, and red), hemlock–yellow birch, white birch–red oak, and poplar. It was significantly associated with yellow birch and also correlated with spruce, balsam fir, white cedar, and hemlock. It exhibited a lack of preference for pines but occurred in moderate numbers where pine was mixed with white cedar or balsam fir. It also inhabited stands lacking conifers but was more common when at least a few conifers other than pine were present. In New Brunswick, forest types that were used more than their availability, in order of preference, included intolerant hardwoods, spruce–tolerant hardwoods, intolerant hardwoods–spruce, and intolerant hardwoods–tolerant hardwoods. Stand types used less than their availability, in order of avoidance included pine, spruce–intolerant hardwoods, and spruce–balsam fir (Parker et al. 1999). In British Columbia, it inhabited trembling aspen and balsam poplar stands only if they contained mature white spruce (Campbell et al. 2001). In Maine, it greatly preferred red spruce stands to white spruce stands. Morse (1976) concluded that red spruce provided a better foraging substrate. This was because the thinner red spruce boughs provided better access to resources than the thick white spruce boughs, the longer branches of red spruce facilitated its preferred radial movement pattern while foraging in trees, and red spruce needles lay flat whereas white spruce needles project nearly perpendicularly to the branch, possibly inhibiting movement of the warblers. It preferred red spruce despite the fact that insect numbers and biomass were higher on white spruce.

The Black-throated Green Warbler prefers mature forests but also occurs in younger stands at low densities (Benzinger 1994; Morse and Poole 2020). In New Hampshire and Maine, it was most abundant in large sawtimber sized stands (DBH 60 cm or greater), followed by sawtimber and poletimber stands. It was absent in sapling stands (DeGraaf et al. 1998; DeGraaf and Chadwick 1987). In New York clear-cuts, hemlock did not become prominent in the canopy and subcanopy until 55-75 years after cutting. The Black-throated Green Warbler was the dominant species in a guild that was the last to appear during succession, with numbers peaking in the oldest forest stands (Keller

et al. 2003). Also in New York, it was associated with second-growth and mature coniferous and mixed forests with more than 75% canopy cover and moderate ground and shrub cover (Litwin and Smith 1992). In northern hardwoods in the northeast, it was documented on 55% of surveys in mature undisturbed habitat and 40% of surveys in disturbed and successional habitats (Noon et al. 1979). In northeastern poplar–white birch communities, it occurred only in poletimber and mature stands and was absent in seedling-sapling and sapling-poletimber stands (Back 1979). Temple et al. (1979) reported that it was associated with mature mixed-wood stands in the northeast. In northern hardwoods in Nova Scotia, it was one of the most important species in stands 20 years old and older. It was usually absent in younger stands, but occurred in low density in stands 1-2 years old (Freedman and Johnson 1999; Morgan and Freedman 1986). In New Brunswick, Zitske et al. (2011) considered its habitat to be mature forest at least 60 years old. In balsam fir forests in Newfoundland, it was significantly more abundant in 40-year-old second-growth stands than in uncut mature stands at least 80 years old; abundance was intermediate in 60-year-old stands. Forty-year-old stands were characterized by a well-developed small-tree layer that had a high deciduous component, although deciduous stems constituted only 6% of the small trees. This deciduous component was mostly absent in older stands. The 2 most abundant deciduous trees, white birch and pin cherry, are short-lived and were mostly absent in 80-year-old stands. Thompson et al. (1999) concluded that this warbler may have declined with the decline of deciduous trees and leaf litter. Old stands also had fewer and shorter small trees. Other studies demonstrated that midcanopy vegetation is important to this warbler. In this study, it was significantly more abundant on nutrient-rich than nutrient-poor sites. In northern hardwoods in New Hampshire, Holmes and Sherry (2001) reported that the Black-throated Green Warbler increased over a 30-year period and attributed this to forest maturation. Although the forest was mature at the beginning of the study, it became more open due to treefalls and beech bark canker fungus. With the more open patchy canopy, a dense layer of tall shrubs and subcanopy developed and the low shrub layer became sparser. In spruce–balsam fir forests in Maine, it was one of the dominant species in older clear-cuts characterized by hardwood regeneration taller than 4.5 m with a DBH of 10-15 cm, and a slower-growing understorey of conifers. It was less than half as abundant in dense fir-spruce forests with an open understorey. It was uncommon in the early seral stages of succession (Titterington et al. 1979). In northern hardwood stands in Wisconsin, it does not appear until the average tree size is at least 23 cm DBH (Hoffman 1989a). In Pennsylvania, Haney (1999) documented it in 100% of old-growth mixed forests, 15.1% of forests statewide, and 31.5% of forests on the Appalachian Plateau. He considered it to have positive old-growth affinities. In poplar-dominated forests in Alberta, it was significantly more abundant in old-growth stands than in mature and young stands (where it was not detected). Old-growth stands had significantly more conifers than the other age classes (Schieck et al. 1995). In the Prairie Provinces, it was in a guild associated with conifers and was most prevalent in old stands on nutrient-rich sites (Kirk et al. 1996). In British Columbia, it is associated mainly with old-growth white spruce and balsam poplar on moist sites along major rivers. It may also use shrubbier habitat such as willows, white birch, alder, and trembling aspen thickets along edges of lakes, rivers, and ponds (Campbell et al. 2001).

Some studies examined landscape variables that may affect the distribution or abundance of the Black-throated Green Warbler. In southern Ontario, its abundance was significantly correlated

with the amount of forest cover within 2 km and the regional amount of forest cover (Austen et al. 2001). This appears to be consistent with the pattern of distribution identified by the second atlas. In the Carolinian Forest Region, the main area of concentration is on the heavily forested Norfolk Sand Plain and there is a clear concentration along the Niagara Escarpment (Crins in Cadman et al. 2007). Near Quebec City, Drolet et al. (1999) studied 100-ha landscapes in an area consisting of 3 general habitats: large tracts of coniferous forests, small (less than 30 ha) clear-cuts imbedded in a forest matrix, and large clear-cuts that delineated small coniferous patches. Forest cover within the 100-ha landscapes varied from a few to 90 ha. The Black-throated Green Warbler responded significantly to forest cover, edge, and core area combined, although it was not significantly correlated with any of these parameters individually. The authors concluded that it may avoid sparsely forested areas. In Michigan, Crozier and Niemi (2003) studied naturally heterogeneous landscapes and found that it was unaffected by landscape variables such as the proportion of habitat within the landscape.

In Alberta, Robichaud and Villard (1999) studied Black-throated Green Warbler territories in mixed-wood forests dominated by trembling aspen and balsam poplar with irregularly spaced mature white spruce. Conifer density was significantly higher in territories than it was over entire plots. It avoided areas without conifers, except that 3 territories occurred where conifers were sparse or absent. Trees with a large DBH and that were taller were more likely to be used for both singing and foraging than smaller trees. White spruce was significantly larger than other species and was used significantly more than trembling aspen. The preference for white spruce over balsam poplar was marginally nonsignificant; white birch was not avoided or preferred. For singing, the odds of usage increased 4-fold regardless of tree species for every 10 cm increase in DBH. In 1 plot, 97% of trees used were white spruce; 64% of trees used were spruce in the other plot. Spruce represented 36% of all trees in both plots. Despite its strong preference for large spruce, it still used deciduous trees for singing, foraging, and nesting.

Several studies examined microhabitat preferences of the Black-throated Green Warbler. Because of its usage of a wide variety of forest types, there is a great disparity in its habitat preferences. Habitat features that are selected in 1 geographic area may be avoided in another. There are 2 habitat components that are consistent throughout its range: a preference for large trees in the canopy in stands that are often fairly open, and a well-developed tall shrub or midcanopy level. Collins (1983b) compared its habitat preferences in Maine, New York, New Hampshire, and Minnesota. Six habitat variables were significantly different among the 4 sites and these were related to canopy height, the percentage of conifers in the canopy, and selection of different tree-size classes. Canopy height was greatest in Minnesota due to the presence of large red pines and white pines, and these also contributed to a higher percentage of conifers. More northern areas contained more trees in the smaller size classes. In some plots in other states, there were no conifers. The most consistent parameters were the number of trees 15-23 cm and 23-30 cm DBH. The presence of many small trees may be an essential feature of its habitat, or presence of small trees may simply be a consequence of forest structure. In these 4 states, there were gradients in habitat from tall to shorter canopies, large to smaller trees, and coniferous to deciduous forests. Collins (1983a) did another analysis of its habitat preferences in Minnesota and Maine. Habitat preferences varied significantly for 9 of the 11 parameters that were tested. These were related to percent ground cover, canopy

cover, canopy height, percent conifers, and tree size classes. In Minnesota, it was associated with large trees, more so than for any other warbler species, and fairly large conifers. In Maine, it was associated with large deciduous trees. Collins et al. (1982) characterized the habitat of the Black-throated Green Warbler in Minnesota, but Collins (1983a, 1983b) determined that results were significantly different in Maine, New York, and New Hampshire. Average habitat characteristics in Minnesota included 52.7% ground cover, 39.0% shrub cover, 84.3% canopy cover, 20.2 m canopy height, 50.3% coniferous cover, 5.7 tree species per 0.04-ha circle, 15.1 trees 7.5-15 cm DBH, 10.5 trees 15.1-23 cm DBH, 5.7 trees 23.1-30 cm DBH, 4.4 trees 30.1-38 cm DBH, 3.3 trees 38.1-53 cm DBH, 1.9 trees 53.1-68 cm DBH, and 0.9 tree larger than 68 cm DBH. It was associated with the highest number of trees larger than 68 cm DBH of all warblers studied. It was within a guild of warblers that occurred predominantly in undisturbed habitats containing conifers. Distinctive features of the habitat of this group consisted of moderate ground and shrub cover and more than 75% canopy closure. Territories of these species consistently contained more than 50% coniferous cover, mostly in the large tree categories. Conifers in territories of the Black-throated Green Warbler were typically white, red, or jack pine rather than spruce or balsam fir. In New Hampshire and Maine, it was positively correlated with coniferous trees 2-10 cm DBH, total foliage volume of both deciduous and coniferous trees larger than 10 cm DBH, and the total foliage volume of deciduous stems less than 2 cm DBH. It was negatively correlated with the number of conifers larger than 10 cm and the number of woody stems per ha (DeGraaf et al. 1998). In spruce–balsam fir forests in Maine, it was associated with deciduous trees 10-15 cm DBH and both deciduous and coniferous trees larger than 20 cm DBH (Titterington et al. 1979). In Maine and Vermont, its abundance was nearly proportional to the foliage volume above 6 m. Abundance fell off in 2 plots where very tall trees were present. It seldom used tall treetops for foraging so this foliage volume did not contribute to the usable habitat. In 1 area, the Bay-breasted Warbler was the most abundant species in spruce and the Black-throated Green Warbler occupied ridges forested with mixed hemlock and hardwoods (MacArthur 1958). Morse (1976) found no correlation between foliage volume and its abundance in Maine. In the mid-Atlantic states, it was positively correlated with the number of tree species, percent coverage by conifers, the number of trees larger than 38 cm DBH, and percent ground cover (Robbins et al. 1989). In northeastern mixed forests, it was associated with increasing coverage by yellow birch and sugar maple (Temple et al. 1979). In subalpine forests in New Hampshire, Sabo (1980) considered this warbler a lowland deciduous forest user. It was associated with lower-slope northern hardwoods and, to a lesser extent, mixed northern hardwoods, balsam fir, red spruce, white birch, and American mountain-ash. The main population was below mid-slope with average territory characteristics consisting of areas where some wet depressions were available, with a canopy height of 12.5 m, 79% canopy coverage, 37% coniferous coverage, 15 m^3 conifer foliage volume 0-2 m from the ground, 113 m^2 deciduous foliage volume above 5 m, and 13 cm DBH for living trees. In Vermont, the Black-throated Green Warbler was associated with closed-canopy mixed forests with a dense understorey. Average habitat parameters included 13.7% green ground cover, 13.6% ground cover slash, 88.4% canopy cover, 22.1 m canopy height, 12.5 m canopy depth, 13.3 m^2 BA of deciduous species, 12.7 cm DBH for deciduous species, and 17.0 cm DBH for conifers (Thompson and Capen 1988). In poplar-dominated forests in Alberta, it was positively correlated with tree species richness, downed woody material larger than 20 cm, canopy height, and trees larger than 20 cm DBH. It was negatively correlated with aspen density (Schieck et al. 1995).

Some studies identified other species that are in guilds with the Black-throated Green Warbler. In New Hampshire and Maine, it was in a guild associated with trees larger than 60 cm DBH (DeGraaf et al. 1998). In the northeast, Niemi and Pfannmuller (1979) placed it in a guild that was associated with moderate numbers of saplings and low shrubs, few tall shrubs, and increased numbers of trees and saplings. In Vermont, it was in a guild associated with closed-canopy mixed forest (Thompson and Capen 1988).

In Maine, Morse (1967) stated that the Black-throated Green Warbler typically occurred in the interior portion of the forest and Morse and Poole (2020) concluded that it was a forest-interior species. This was despite the work by Morse (1971b) on small islands in Maine where he documented breeding by this warbler. In no case did a part of an occupied forest lie more than 50 m from edge. Freemark and Collins (1992) considered the Black-throated Green Warbler a forest-interior species based upon a literature review. In southern Ontario, Austen et al. (2001) determined that its abundance was significantly correlated with the amount of forest cover 100 m or more from edge. Peck and James (1987) reported that some Ontario nests were found at forest edges near roads or water. In Maine, Stanwood (1910b) reported a nest at the edge of a woodlot. Chapman (1907) reported that it avoided deeply shaded forest interiors. Some studies specifically analyzed the response of the Black-throated Green Warbler to forest edge. In New Hampshire, King et al. (1997) examined the locations of territories in mature northern hardwoods adjacent to clear-cuts 6 years old and younger. There was no significant difference in the number of territories within 100 m of edge or within forest interior. Villard et al. (2007) conducted a similar experiment in Alberta. Experimental plots were 10 or 40 ha surrounded by clear-cuts at least 100 m wide. A significant edge avoidance response was exhibited by the Black-throated Green Warbler. The dominant pattern by all species combined was one of neutral short-term response to clear-cut edges, especially in the 10-ha fragments. The authors concluded that proximity to edge played a minor role in breeding site selection and questioned the validity of the forest-interior concept. In Quebec balsam fir stands, LaRue et al. (1995) found no difference in Black-throated Green Warbler density in forest interior and in riparian edge stands. In Newfoundland balsam fir stands, it was significantly more abundant in forest interior than in riparian edge stands. There was no significant difference in its abundance in forest interior and in forest–clear-cut edges. Riparian areas supported black spruce, a species not characteristically used by this warbler. The presence of black spruce in the riparian edges may have made this habitat less suitable and this may have been the cause of the apparent edge avoidance. It did not avoid clear-cut edges (Whitaker and Montevecchi 1997). In the same area, Whitaker and Montevecchi (1999) determined that the Black-throated Green Warbler was equally abundant in riparian buffers where adjacent upland forest had been retained and where it had been clear-cut. In Maryland, Gates and Giffen (1991) observed no edge effects for this warbler. The Black-throated Green Warbler is not a forest-interior species. In areas where it is more abundant in forest interior, it is likely that habitat along the edge is less than optimum and that birds are not responding to the edge itself.

Two studies examined the effects of gaps within forests on the Black-throated Green Warbler. In Michigan, Smith and Dallman (1996) compared usage of forest interior to gaps in canopy that were a minimum of 5 m in diameter extending through all vegetation layers down to an average height of 2 m above ground. Birds were considered to be using a gap if they were observed foraging

or singing within 1 m of it. Males used forest gaps significantly more (52.1% of all observations) and forest interior significantly less (30.9% of observations) than expected. Females demonstrated an even greater difference in use, using gaps 55.0% of the time and forest interior 25.0% of the time. Some males appeared to use gaps as territorial boundaries. Gaps may be important because they support more insects, have a warmer microclimate due to sun penetration thereby increasing insect activity, and males may have increased visibility and better song delivery in gaps. In Quebec balsam fir forests, Rail et al. (1997) studied how the Black-throated Green Warbler responded to treeless gaps 3-100 m wide. Five types of gaps were studied with all having similar habitat on both sides: trails 3-15 m wide, unpaved roads 4-35 m wide, clear-cuts 12-100 m wide, unpaved roads with clear-cuts on 1 or both sides 18-65 m wide, and hydro rights-of-way 38-55, 70-80, or 84-100 m wide. Broadcast calls were used to determine if warblers would cross gaps. Gap type had no effect on the probability of crossing. The probability of a Black-throated Green Warbler crossing a gap was 90% at 15 m width, 80% at 20 m, 70% at 35 m, 50% at 50 m, and 30% at 80 m.

Freemark and Collins (1992) concluded that it was uncertain if the Black-throated Green Warbler was area sensitive due to conflicting conclusions in the literature. In southern Ontario, Austen et al. (2001) determined that its abundance was significantly correlated with woodlot size. James (1984b) did not consider it area sensitive in Ontario whereas Coleman et al. (2000) did. In Michigan, its abundance was correlated with patch size (Crozier and Niemi 2003). In Connecticut, Askins et al. (1987) detected it in only 5 of 46 forests where it was restricted to larger tracts. The average patch area that it inhabited was 354 ha and the minimum patch size was 187 ha, significantly different from random woodlots. Robbins et al. (1989) found no relationship between its abundance and woodlot size in the mid-Atlantic states and did not consider it area sensitive. In Wisconsin, Beals (1960) reported that it was not confined to the larger islands that he studied. In Maine, it nested on islands that supported only 0.53-1.50 ha of forest cover, but was absent on islands with less than 0.35 ha of forest (Morse 1971b; Morse and Poole 2020). The disparity in the reported results may be related to the habitat requirements of the Black-throated Green Warbler. Its abundance appears to be depressed in landscapes that support limited suitable habitat. Within these landscapes, it may be restricted to larger high-quality forests and therefore be area sensitive. In highly forested landscapes, it is unlikely to be area sensitive. If this species is area sensitive in Ontario, it is likely to be so only south and west of the Niagara Escarpment, with the exception of the heavily forested portion of the Norfolk Sand Plain.

Nests reported to the Ontario Nest Records Scheme were in both small and large trees. Coniferous trees were much preferred to deciduous trees, with 82.9% of nests in 6 species of conifers and 17.1% in 4 deciduous species. Hemlock (11 nests), white cedar (10 nests), spruce (5 nests), and pine (5 nests) were used most frequently. Most nests were on a living, but rarely dead, horizontal branch (70.8% of nests) and were either saddled on the branch or supported by adjacent branches; 16.7% were in crotches of branches; and 12.5% were in crotches at the trunk. Most (73.9%) were distant from the trunk and the remainder were at or near the trunk. Distances from the trunk were 0.2-4.5 m, mostly 0.9-3.7 m. Nests were 0.5-15 m from the ground with most 2.3-7.6 m up (Peck and James 1987, 1998a). In Muskoka and Parry Sound districts, most nests were in hemlock but some were in birches and maples at heights of 3-15 m (Mills 1981). An Elgin County nest was 8.25 m from the ground in a fork of yellow birch (Lancaster et al. 2004). Bent (1925) reported 2 nests in deciduous

woods in Ontario. One was 12.2 m from the ground in a hophornbeam and the other was 6.1 m up in a small elm. Near Lake Nipigon, Kendeigh (1947) found a nest in a tangle of dead branches of a fallen tree 0.3 m from the ground. It rested on 1 branch and was supported around the sides by twigs and was partly concealed by beard lichen and fern leaves. It typically nested there in trees as high as 21.3 m from the ground. Of 6 nests that Tozer (2008) found in Algonquin Park, 4 were in tree cavities. Three were in Pileated Woodpecker foraging cavities and the fourth was at the bottom of a sugar maple borer scar. The scar had protruding bark at the bottom that supported and concealed the nest from above, below, and three quarters of the sides. These nests were at heights of 1.5-4.5 m in a balsam fir snag, a beech snag, a sugar maple snag, and a live sugar maple. There were at least 5 mature canopy-sized hemlocks within 75 m of each nest suggesting that lack of conifers was not a factor influencing birds to nest in cavities. Cavity nesting may be a regular but infrequent occurrence in Algonquin Park, but has not been reported elsewhere.

Most nests reported elsewhere were in trees, but there were a few exceptions. One was 3 m from the ground in a grapevine surrounding a small pagoda in Maine. It was on the main stem of the vine (Brown 1889). One Connecticut nest was on the ground among a large clump of ferns in a very low and damp site under a heavy growth of hemlock (Brewster 1895). A New Jersey nest was between the stems of a skunk cabbage and fastened to a greenbrier and the twigs of a dead shrub 0.36 m from the ground in a very wet location (Chapman 1907). A Massachusetts nest was 0.20 m from the ground in a red cedar in an old pasture. In Michigan, nests in northern hardwood forests were 0.6-0.9 m from the ground in American yew. One nest was in a barberry shrub 100 m from the nearest forest (Bent 1953). Typical nests are in trees, usually on a horizontal branch distant from the trunk but occasionally near the trunk. The Black-throated Green Warbler prefers conifers for nesting throughout its range, with hemlock highly selected. Other conifers it has nested in include Norway spruce, white spruce, red pine, balsam fir, pitch pine, and red cedar. Eighty percent of New York nests were in hemlock. Most Maine nests were in spruce or pine. The Black-throated Green Warbler nests much less frequently in deciduous species such as beech, yellow birch, balsam poplar, white birch, gray birch, sugar maple, white oak, American chestnut, alder, and elm. Nests have been reported 0-20 m from the ground, but most are 2-6 m up. Almost all of 58 Maine nests were in conifers at heights of 0.9-15.5 m, with most 3-6 m up (Bent 1953; Benzinger 1994; Brewster 1895; Brooks 1947b; Chapman 1907; Cruickshank 1956; Harrison 1984; Kotesovec 1994b, 1995; Morse and Poole 2020; Nice and Nice 1932; Philipp and Bowdish 1917; Pitelka 1940; Reading and Hayes 1933; Stanwood 1910b, 1914).

Males establish territories shortly after their arrival in spring and maintain them until the young fledge and leave the territories. Most activities are conducted within the territory, but birds occasionally wander outside them. Although interspecific territoriality does not occur, the Black-throated Green Warbler appears to be socially dominant to the Blackburnian Warbler, Yellow-rumped Warbler, American Redstart, and Northern Parula and may depress their populations where it is abundant. In turn, the Black-throated Green Warbler appears to be subordinate to Magnolia and Bay-breasted warblers. Territories tend to be smaller in coniferous forests than in mixed forests due to its preference for conifers. In Maine, it preferred red spruce and territories were smaller in red spruce than white spruce stands. There is an inverse relationship between territory size and food density, and territory sizes decrease as warbler density increases. When a Maine population declined,

remaining males trebled their territory boundaries. In Algonquin Park, territories averaged 0.26 ha (range 0.008-2.35 ha). Near Lake Nipigon, 5 territories averaged 0.49 ha (range 0.32-0.85 ha). In New York, 21 territories averaged 0.65 ha (range 0.24-1.01) in hemlock-beech forest. Territories in subalpine forests in New Hampshire averaged 1.2 ha. In Maine, average territory size was 0.25-0.28 ha in red spruce stands and 0.40-0.43 ha (range 0.35-0.55 ha) in white spruce stands (Kendeigh 1945; MacArthur 1958; Martin 1960; Morse 1976, 1977; Morse and Poole 2020; Sabo 1980). Near Quebec City, Bourque and Desrochers (2006) found no evidence of territorial aggregation at any scale.

No information is available on natal philopatry, but it is probably low. Limited data are available on adult site fidelity. Morse and Poole (2020) stated that, after first breeding at a site, individuals frequently return in subsequent years. One male returned to a Maine study area in 4 years. In New Brunswick, Zitske et al. (2011) banded 356 males over 7 years and reencountered 105 (29.5%) at least once. Five individuals moved 65-650 m from their original capture location. The apparent annual survival rate based on band recoveries was 34.1%, with experienced breeders having significantly higher survival rates. There was some evidence that survival, or return rates, increased as the amount of habitat at the 2,000-m scale increased. Survival was 12 times greater in landscapes with 85% habitat than those with 10% habitat. Areas supporting lower amounts of habitat had a lower number of individuals that had lower survival rates. The authors found evidence of long-term breeding dispersal away from original sightings and acknowledged that their survival estimates were low.

Limiting Factors

Eggs have been reported in Ontario nests from the beginning of June until mid-August, with most present in the last 3 weeks of June (Peck and James 1987, 1998a). In Algonquin Park, nests are under construction from mid-May to late June, eggs are present from late May to late June, nestlings are present early June to mid-July, and dependent fledglings have been observed mid-June to late August (Tozer 2012).

Pair formation occurs shortly after the females arrive and nest building commences soon thereafter. Nests typically take about 4 days to build. In 2 cases, the nest exterior was completed in 4 days and an additional 4 days were spent lining the nest. One day may elapse between completion of the nest and initiation of egg laying. The egg-laying rate is 1 per day. Incubation begins with the laying of the last egg. Two Ontario nests had incubation periods of approximately 11 days and eggs took 13 days to hatch in another nest. The incubation period has been reported to be 12 days elsewhere. The nestling period is 8-11 days, mostly 9-10 days (Bent 1953; Kotesovec 1994b, 1995; Morse and Poole 2020; Nice and Nice 1932; Peck and James 1987; Pitelka 1940; Stanwood 1910b).

Ontario egg dates suggest that second broods occur (Peck and James 1987). Nice and Nice (1932) thought that double broods were probable in Massachusetts due to the late dates that fledglings were observed. Double broods have never been confirmed for the Black-throated Green Warbler. It is a persistent renester if clutches are lost (Morse and Poole 2020). Clutches of 3-5 eggs have been reported in Ontario (average 3.64 eggs). Most clutches (17) contained 4 eggs but 16 contained 3 eggs (Peck and James 1987). Elsewhere, the clutch size is 3-5 eggs (mode 4 eggs). Mean clutch size in Vermont and Maine was 4.04 eggs. Clutch size does not vary with the abundance of spruce budworms (MacArthur 1958; Morse and Poole 2020).

The mating system is monogamous. Birds occasionally leave their territories suggesting that extra-pair copulations may be part of the mating strategy. Males can breed at the age of 1 year but it is unknown if yearling females are capable of breeding. Some yearling males remain unmated and do not breed (Morse and Poole 2020).

The Black-throated Green Warbler is a generalist, foraging in both deciduous and coniferous species. In specific locations, it exhibits preferences. Ninety percent of foraging is in conifers in coastal Maine, 60% in inland mixed forests, 43% in subalpine forests in New Hampshire, 26% in the Clay Belt of Ontario, 5-10% in New Hampshire in predominantly deciduous woods, and 0% in pure deciduous woods in West Virginia. In Alberta, males selected white spruce for foraging over trembling aspen. It used white birch according to its availability. It preferred conifers at both the territory and 25-ha scales. It was more likely to use larger-diameter trees for foraging, and most were spruce. Conifers have stronger branches and offer more support than deciduous trees, which also vary in their leaf morphology and attachment. White birch has shorter petioles than trembling aspen and balsam poplar, which gives foraging Black-throated Green Warblers easier access to prey. The 2 poplar species were significantly avoided for foraging but white birch was not and was slightly preferred. In Michigan, it used white cedar less than its availability during the breeding season and autumn migration. In New Hampshire, it foraged more frequently on tree species such as yellow birch that have foliage arrayed continuously and close to the branches. It tended not to forage in trees with a different foliage configuration. In an aviary experiment, warblers from Maine, where more than 90% of foraging occurs in conifers, and from New Hampshire, where 90-95% of foraging occurs in deciduous species, were tested for their substrate preferences. When prey was distributed equally among the types of vegetation, Maine birds spent 75% of their time in conifers and New Hampshire birds spent 80% of their time in deciduous vegetation. When prey densities were distributed away from the preferred substrate, Maine birds spent 68% of their time in conifers but captured 74% of prey in deciduous vegetation. New Hampshire birds spent 55% of their time in deciduous vegetation but captured 81% of their prey in conifers. Most birds captured all the available prey from their preferred substrate before beginning to forage in the less preferred vegetation (Greenberg et al. 1999; Morse 1989; Parrish 1995; Robichaud and Villard 1999; Robinson and Holmes 1982; Sabo 1980; Smith et al. 1998). In the Clay Belt of Ontario, 94.0% of foraging was on foliage, 46.3% by aerial attacks, 2.0% by hanging, 31.0% by hovering, and 22.1% by reaching at an average height of 11.3 m or 73.0% of tree height (Greenberg et al. 1999). In Parry Sound District during the breeding season, foraging by this warbler was restricted to northern hardwoods. In late summer, it foraged in hardwoods, intolerant hardwoods, and conifers. In autumn, it foraged predominantly in white birch. It foraged at heights of 5-16 m during the breeding season and 4-13.5 m in autumn. It was in a foraging guild that fed predominantly by gleaning on the under and upper surfaces of leaves (Mills 2007). MacArthur (1958) studied foraging strategies of the Black-throated Green Warbler in Maine and Vermont. He identified 6 vertical zones in conifers including the area beneath the tree and 5 equal zones within the tree. Three horizontal zones were also identified: the inner zone of bare or lichen-covered branches, the central zone of old needles, and the outer zone of new needles and buds. Most foraging time was spent in the outer portion of the middle zone of the tree (21.8%), followed by the central portion of the middle zone (14.1%), and the outer portion of the zone second from the top of the tree (17.3%). Usage of the outer top zone was 12.1%. At each

level, highest use was made of the outer zone. Least use was made of the inner zone, with a total of 2.6% for all horizontal zones combined. No foraging occurred beneath trees. It moved predominantly in a tangential direction within trees, significantly different from the other warbler species that were studied. It did not take long flights (7.6 m) between trees or hawk, but hovered significantly more than Cape May, Yellow-rumped, Blackburnian, and Bay-breasted warblers. The Black-throated Green Warbler was quite restricted in its feeding habits compared with the Yellow-rumped Warbler. Almost all foraging by the Black-throated Green Warbler was by rapid peering, hopping actively on thick foliage at ends of branches looking into the vegetation above, springing into the air, and hovering under a branch to capture prey. Although other warblers occasionally forage in this manner, it is characteristic of the Black-throated Green Warbler. It occasionally hawks for flying insects, missing a substantial portion of them, but this is atypical behaviour because it seldom sits motionless watching for insects. The 5 warbler species behaved in manners such that they would be exposed to different foods and the Black-throated Green Warbler was regulated by the amount of foliage volume at mid-height of trees. Cumming (2004) completed a similar study in Saskatchewan. Fifteen or more percent of foraging observations were in the outer portion of the top zone of conifers, 10-14.9% were in the central and outer portions of the central zone of the tree, 5-9.9% were in the central and outer portions of the second from the top zone, and 0-4.9% were in all other zones including the 2 lower vertical zones. In conifers, it was one of the least diverse foraging species along with the Blackburnian Warbler and Blue-headed Vireo. In deciduous trees, only 3 vertical zones were identified. Fifteen percent or more of foraging occurred in the outer portion of the top zone, 10-14.9% in the central portion of the top zone, 5-9.9% in the inner portion of the top zone, and 0-4.9% in all portions of the 2 lower zones. The mean foraging height of the Black-throated Green Warbler in conifers was 12.7 m, significantly lower than the Blackburnian Warbler and significantly higher than the Bay-breasted Warbler, Magnolia Warbler, and Blue-headed Vireo. The mean foraging height of 11.4 m in deciduous trees was not significantly different from the height in conifers. The Black-throated Green Warbler was seen in canopy-level trees in 77.3% of observations. Both it and the Blackburnian Warbler appeared to be specialized in a treetop niche and their foraging techniques overlapped by 85%, more than with any other species. There was no evidence that the Black-throated Green Warbler was socially dominant over any other species, possibly because it was the least abundant species. In Michigan during the breeding season, there were no significant differences between Lake Huron shoreline and inland habitats in its use of foraging manoeuvres, horizontal position, foraging height, and tree species used for foraging. In conifers, it favoured the top of trees more near the shoreline than inland (67.1% of foraging compared with 46.5%) and the bottom of the substrate more inland than at the shoreline (53.4% of foraging compared with 32.9%). There was no significant difference in deciduous species (Smith et al. 1998). In an aviary experiment, the Black-throated Green Warbler searched both sides of leaves and then focused on either the upper or lower leaf surface after the first capture. The contrasting foliage structure of sugar maple and yellow birch did not affect the ability of birds to learn about the distribution of prey (Whelan 1989). Morse (1968) compared the foraging strategies of the sexes in Maine. Males foraged significantly higher than females. Males foraged at heights of 0.3 m to more than 18 m and females foraged at 0.3-18 m. Males foraged at a lower height than they sang, but foraging areas were closer in height to singing perches than nests. Females usually foraged closer to the height of the nest. There were no significant differences in the foraging locations of the sexes:

78% on small limbs, 5-10% on large limbs, 3% at branch tips, and 5-8% on deciduous species. Males hawked significantly more than females; hovering was the dominant method of movement for both sexes. Most food was obtained by gleaning. In another Maine study, the Black-throated Green Warbler foraged at heights of 10.7 m to more than 19.8 m (mean 15.2 m). In spruce, 26.3% of foraging was at the tip of foliage (14.1% by gleaning, 1.3% by stretching, 10.9% by hovering, and 0% by hover-walking and hanging), 38.2% on live twigs 5 mm and smaller, 0.7% on dead twigs (all by gleaning), 8.2% on dead branches (7.5% by gleaning and 0.7% by hovering), 0.7% on beard-lichen-covered branches, 3.9% distally on branches, 14.4% proximally on branches, 0.7% on trunks, 2.0% by flycatching, 3.9% on deciduous growth, and 1.0% on the ground. The Black-throated Green Warbler and Northern Parula foraged at similar heights and in similar areas of the foliage, and hovered more than the other warblers (Morse 1967). On small islands in Maine, 65-80% of male foraging occurred on small limbs, 2-15% on large limbs, 2-10% on foliage tips, 2-8% on dead limbs, and 0-15% on deciduous growth. One female foraged 70% of the time on small limbs, 10% on large limbs, 10% on foliage tips, 6% on dead limbs, and 4% on deciduous vegetation. Both sexes foraged at heights of 0-21 m on 4 islands, with a different profile on each island. They generally foraged at the heights represented on each of the islands. The Black-throated Green Warbler appeared to be socially dominant to the Northern Parula and Yellow-rumped Warbler because these species altered their foraging behaviour in its absence (Morse 1971b). In subalpine areas of New Hampshire, its foraging techniques included 0.5% aerial flycatching, 38.8% leaf gleaning, 14.0% leaf hawking, 15.5% leaf hovering, 1.7% twig pecking, 18.5% twig gleaning, 7.8% twig hawking and hovering, 0.1% branch pecking, 1.9% branch gleaning, 0.1% bole pecking, 1.1% bole gleaning, and 0% litter pecking, litter gleaning, and fallen log manoeuvres. Foraging substrates included 57.0% distal to the trunk, 43.0% proximal to the trunk, 43.1% in coniferous foliage, 56.9% in deciduous foliage, and 0% in herbaceous foliage and on the ground. Foraging heights included 0% at 0.1-1.2 m, 23.8% in the midstorey at 2-5 m, 51.5% in the midcanopy at 5-8 m, and 24.8% above 8 m in the upper canopy. The Black-throated Green and Bay-breasted warblers foraged at greater heights than the other species that were present (Sabo 1980). In northern hardwoods in New Hampshire, 73.9% of prey attacks were on leaves and 13.6% were on bark. Most available prey consisted of adult and larval moths, adult flies, wasps, beetles, nymphal and adult leafhoppers and froghoppers, and spiders. Most of these were on leaves and not on twigs or small branches. Foraging techniques included 54.2% gleaning, 35.4% hovering, 6.6% flush-chasing, 2.0% hawking, 1.6% hanging, and 0% probing. Most hovers were directed vertically because most prey was on the underside of leaves. The Black-throated Green Warbler was in a foraging guild with the Black-throated Blue and Blackburnian warblers. These were near-surface searchers that predominantly gleaned small- to medium-sized, often cryptic, insects and made frequent short movements between perches. The Black-throated Blue Warbler was separated from the other 2 species by feeding exclusively in the understorey (Robinson and Holmes 1982). During wet periods, the Black-throated Green Warbler forages more frequently on bark and even on tree trunks and increases its frequency of hovering. Overall, more than 80% of foraging actions are by gleaning and another 10% consists of hovering at branch tips. Less frequent motions include hawking, chasing fallen food, and hanging upside down. Few items shorter than 2 mm in length are consumed although these dominate numerically (Morse and Poole 2020).

At an Ohio nest, caterpillars constituted 67.5% of the food items provided to nestlings and the remainder was predominantly tiny unidentified insects. At a Michigan nest, the male usually brought green caterpillars to the nestlings. The female provided small flies and various larvae. At a Maine nest, the nestling diet consisted of a large number of smooth green and brown caterpillars, flies, bee-like insects, beetles, and moths. In Massachusetts, young were fed green caterpillars and small insects. At a Connecticut nest, young were fed spiders, mayflies, green caterpillars, ants, small owlet moths, ichneumonid wasps, crane flies, and many smaller flies (Harrison 1984; Kotesovec 1994b; Nice and Nice 1932; Pitelka 1940; Reading and Hayes 1933; Stanwood 1914).

Stomachs of 5 adults near Lake Nipigon contained 45.0% lepidopterans, 27.5% spiders, 18.7% soft-winged bugs (mostly froghoppers with some planthoppers and seed bugs), 3.4% soldier beetles, 2.9% flies (house flies and 1 march fly), and 2.5% hymenopterans (Kendeigh 1947). Stomachs of 23 New Hampshire Black-throated Green Warblers contained 47.8% caterpillars, 34.8% soft-winged bugs (mostly leafhoppers), 13.1% beetles, and 4.3% adult lepidopterans. The diet determined by visual observations consisted of 82.8% caterpillars, 8.6% adult lepidopterans, 6.9% beetles, and 1.7% adult flies plus unidentified items (Robinson and Holmes 1982). In Maine, males actively selected large prey items and caterpillars. The number of caterpillars in stomachs was 15.1-61.3 times that expected based upon the proportion of caterpillars in sample collections. Caterpillars were the only food item taken more than expected. Foliage samples were dominated by aphids but few were eaten (Morse 1976). One bird collected in Maine during a spruce budworm outbreak had consumed 35% budworm larvae and pupae by volume (Mitchell 1952). A warbler in an orchard infested with cankerworms had eaten 70% cankerworms, 15% beetles, 5% true bugs, and 10% hymenopterans, gnats, beetle larvae, and mites. Other food items this warbler has consumed include locusts, leafroller moths, aphids, tent caterpillars, budworm larvae, and juniper and poison ivy berries (Bent 1953). In an aviary study, gypsy moth larvae were presented to Black-throated Green Warblers. Eight of 9 second-instar offerings and 3 of 5 third- to sixth-instar offerings were accepted. Warblers were simultaneously offered gypsy moth larvae (11 of 30 accepted), tussock moth larvae (4 of 20 accepted), cabbage loopers (all 30 accepted), and mealworms (all 18 accepted). It exhibited a preference for hairless larvae. Whelan et al. (1989) concluded that it was likely to eat gypsy moth larvae only when no alternative prey was available.

The Black-throated Green Warbler may respond positively, neutrally, or negatively to insect outbreaks. In Maine, Morse (1976) found a direct correlation between both the numbers and biomass of caterpillars and numbers of this warbler. In New Hampshire, it fluctuated irregularly but appeared to be more abundant during an outbreak of the saddled prominent (Holmes and Sturges 1975). Near Manitouwadge, it did not respond numerically to increasing spruce budworm populations (Venier et al. 2009). During a spruce budworm outbreak in New Hampshire and Maine, Crawford and Jennings (1989) found an average of 1.0 budworm per stomach. This rate of consumption was low to moderate compared with other species. Black-throated Green Warbler populations were unaffected by budworm numbers. In New Brunswick, Gage et al. (1970) concluded that its density was not related to the population size of the black-headed budworm. No first-instar budworms were consumed even through this invertebrate was most abundant at this stage. Consumption increased to a maximum as prey size increased and then declined to 0 as prey density also declined to 0. Few pupae were eaten when they first entered the population but consumption

increased to a maximum when pupa density peaked, followed by a decline in consumption as pupa density decreased. In New Brunswick, the population of the Black-throated Green Warbler decreased when spruce budworm populations increased (Morris et al. 1958). Declines during spruce budworm outbreaks may be due to competition from the abnormally high populations of the budworm specialist warblers or it is possible that its preferred prey decreases in abundance or availability in the presence of abundant budworms (Morse 1989).

Morse and Poole (2020) considered the Black-throated Green Warbler an infrequent host of the Brown-headed Cowbird. The effects of parasitism on the reproductive success of this warbler are unknown. Tate (1967) observed a female cowbird removing a warbler nestling from a nest that contained 3 warbler and 1 cowbird nestlings. In Ontario, 11 of 42 nests (26.2%) were parasitized, suggesting that it may be more than an infrequent host, at least south of the Canadian Shield (Peck and James 1998a). Two of 18 nests (11.1%) in Maine were parasitized (Harrison 1984).

The Black-throated Green Warbler appears to be vulnerable to habitat fragmentation at the landscape level. It has been documented disappearing from several woodlands smaller than 100 ha that became isolated from similar habitat, although the habitat did not noticeably change within these woodlands (Benzinger 1994; Morse and Poole 2020). This lends credence to the hypothesis that it may be area sensitive in landscapes with low amounts of forest cover.

In many areas, the Black-throated Green Warbler is highly dependent upon hemlock. This tree is being threatened by the introduced hemlock woolly adelgid, and the balsam woolly adelgid is threatening other conifers. Major declines of this warbler occurred following habitat changes caused by the death of conifers. This has resulted in major declines or disappearances in southern non-montane areas and in high-elevation populations of Fraser-fir (Benzinger 1994; Morse and Poole 2020).

The Black-throated Green Warbler appears to be adversely affected by even low-intensity housing or cottage lot development. In North Carolina, its abundance was negatively correlated with the number of houses and buildings within 200 m (Lumpkin and Pearson 2013). In Michigan, it was significantly more abundant on the forested side of shoreline access roads than on the other side of the roads where cottages had been built. Higher abundance of coarse woody debris, canopy cover, and understorey density 0-1 m above ground in the undeveloped areas may have influenced its abundance (Ford and Flaspohler 2010).

The Black-throated Green Warbler is often unaffected by single-tree selection cuts or low-intensity group selection cuts, but occasionally even this level of forest management has negative effects. It is adversely affected by more intensive cuts. In Algonquin Park, it was not affected by single-tree selection or typical or intensive group selection harvesting (Jobes et al. 2004; Tozer et al. 2010). Kingsley and Nol (1999) examined the effects of shelterwood cuts in white pine stands in Algonquin Park. It was observed on 42.9-53.3% of plots in stands with no recent history of logging, 20-45.4% of plots in 10-16 year-old cuts, and 8.3% of plots in 2-9 year-old cuts. Kirk et al. (2012) cautioned that it may be vulnerable to forest harvesting practices in central Ontario that reduce the number of supercanopy white pines. The shelterwood harvest prescription has a short rotation period that would not allow the development of supercanopy pines. In northern hardwoods near Sault Ste. Marie, it was associated predominantly with controls and unharvested plots rather than

areas where single-tree selection occurred (Holmes and Pitt 2007). In the Canadian Shield of Ontario, there was no difference in its abundance in early successional and mid-successional clear-cuts and burns in the same seral stages. It was significantly less abundant in early successional and mid-successional stands than in mature stands (Zimmerling et al. 2017). Haché et al. (2013) studied the effects of selection harvesting in New Brunswick. This treatment removes 30-40% of basal area of all stems 10 cm DBH and larger over a 20-25-year rotation period. It also reduces canopy cover by about 20% but there was no significant reduction in density or basal area of conifers. Density of the Black-throated Green Warbler was significantly lower in treated plots 2-5 years postharvest. In Pennsylvania, Stribling et al. (1990) compared abundance of the Black-throated Green Warbler in woodlots where timber stand improvements had been undertaken. Snags were removed in some plots and retained in others. It was significantly more abundant in woodlots where snags were removed. There were fewer trees in snag retention plots and they had a more patchy and open canopy and more low-growing vegetation. In Ontario, it exhibited a stronger negative response at a given harvest level in the Boreal Forest Region than elsewhere. It declined when 30% or 50% of trees were removed and became extirpated when 70% of trees were removed. It was expected to decline by 25% when 20% of trees were removed, decline by 50% when 35% of trees were removed, and decline by 75% when 55% of trees were removed (Vanderwel et al. 2007, 2009). Webb et al. (1977) examined its response when 25%, 50%, 75%, and 100% of merchantable trees were removed from northern hardwood stands in New York. It appeared to be unaffected by lower logging intensities but exhibited a decline in population with increasing intensity of harvest. Harrison et al. (2005) examined the effects of partial forest harvest on the Black-throated Green Warbler in Alberta. In mixed forests, it increased with removal of 25% of trees, decreased at 50% removal, and became extirpated when 90-100% of trees were removed. In coniferous forests, it became extirpated with 25% tree removal, colonized stands with 50% tree removal, decreased with 80% tree removal, and became extirpated when 90-100% of trees were removed. In Minnesota, it responded negatively to all types of forest management prescriptions, including in uncut buffers adjacent to clear-cuts, although buffers as narrow as 30 m were sufficient to support the species. It was among the species that responded most negatively to forest harvesting. Negative effects disappeared 4 years after harvest (Hanowski et al. 2003, 2005). In Alberta, it was not more abundant in clear-cuts where some residual trees had been retained. Tittler et al. (2001) established that it would be necessary to retain more than 40% of the trees and 46% of the basal area to maintain habitat for it. In Minnesota, Niemi and Hanowski (1984a) found it in only 1 of 8 clear-cuts. The plot that supported it had the highest density of living trees and low shrub density. In New Brunswick, Zitske et al. (2011) noted that intensive forestry activities had reduced the amount of mature forest to 12-50% of the landscape. The amount of mature mixed woods was declining at a rate of approximately 1.5% per year due to short-rotation clear-cutting. This did not appear to have an impact on the Black-throated Green Warbler population. In British Columbia, its primary habitat of mature spruce and mature spruce–trembling aspen–balsam poplar stands has high timber value and is being harvested rapidly. These stands tend to be converted to agricultural uses or pure deciduous or spruce stands due to short rotation periods, so some habitat may be permanently lost.

In Alberta, the Black-throated Green Warbler was significantly less abundant at seismic lines than in adjacent forest interior. There was no difference in its abundance at pipelines or well pads than in

forest interior adjacent to these habitats (Bayne et al. 2016). Farwell et al. (2019) conducted a similar study regarding shale gas infrastructure (well pads, access roads, and pipelines) in contiguous forest in West Virginia. It avoided all types of infrastructure and was significantly more abundant distant from them than close to them.

Numbers of the Black-throated Green Warbler are thought to have decreased during the period of usage of pesticides such as DDT and fenitrothian. It may also decline in response to current spraying practices for the spruce budworm (Morse and Poole 2020).

Blake et al. (1992) demonstrated that this warbler responded negatively to drought in Michigan and Wisconsin. Drought was accompanied by hotter than average temperatures. This may have caused poor reproductive success that in turn affected populations.

Nestlings may die of exposure or starvation during cold rainy weather or thunderstorms. Late spring snow storms may cause heavy mortality, depressing populations for years. Extensive rainy periods in late June and early July of both 1972 and 1973 decreased fledging success and severely reduced the 1974 Maine coastal population (Morse and Poole 2020).

Price (2004) predicted that the Black-throated Green Warbler could disappear as a breeding species in southern Ontario if the average summer temperature increased by 2°C.

Status

McIlwraith (1894) did not identify the Black-throated Green Warbler as a breeding species in Ontario, but most of his observations were in the Hamilton area. Baillie and Harrington (1937) considered it a common summer resident from the southern boundary of the province north to Lac Seul and Moose Factory. Summer records at that time extended north to the intercontinental railway and they concluded that it likely bred throughout its observed range. The first atlas confirmed that it bred from the shorelines of Lakes Erie and Ontario north to Little Sachigo Lake and to slightly north of Moosonee. It was largely absent in agricultural southwestern Ontario except in more heavily forested areas such as Rondeau, Long Point, the Niagara Escarpment, northern Grey and Bruce counties, and the eastern shoreline of Lake Huron. It was most abundant in Haliburton County and Parry Sound and Manitoulin districts (Crins in Cadman et al. 1987). James (1991) stated that it was a common summer resident across the province, north to Sandy Lake and Moosonee, becoming rare south of the Canadian Shield to Norfolk County and Rondeau.

The second atlas revealed that there had been no significant changes in the distribution of the Black-throated Green Warbler. It was found somewhat further north than during the first atlas to the Ekwan River in the east, but it was not documented in some of the northern blocks where it had been recorded previously. The range south of the Shield was similar, but it was much more widespread in this area. It continued to be absent in Essex County with only scattered records in Chatham-Kent, Lambton County, and Niagara Region. Its probability of observation increased significantly since the first atlas province-wide and in all atlas regions except the Hudson Bay Lowland where it experienced a nonsignificant decline. It is rare within this region where it was documented in only 22 squares during the first atlas and 11 during the second atlas. Highest densities occurred along the northern and eastern shores of Lake Superior east to Georgian Bay and Algonquin Provincial Park, as well as on the Bruce Peninsula and the southern shore of Manitoulin

Island. These areas support extensive mixed forests with high coverage by coniferous species, especially white pine and hemlock (Crins in Cadman et al. 2007).

The Black-throated Green Warbler was probably much more common in southern Ontario and in much of its range prior to deforestation by European settlers. Breeding Bird Survey data indicate that it decreased at annual rates of 0.793% in Canada and 0.482% in Ontario 1970-2021. The trends 2011-21 were annual decreases of 2.48% in Canada and 3.93% in Ontario. All results were of medium reliability except that the long-term Canadian trend was highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Brood division may occur once young leave the nest. Young often wander from the natal territory as soon as they can fly and do not return (Morse and Poole 2020).

Both adults and juveniles may inhabit clear-cuts 2-10 years old during the postfledging period. In Minnesota, 14 adults and 5 juveniles were caught in clear-cuts during the postfledging period but none were caught during the breeding season. During the postfledging period in Pennsylvania, 24 adults and 15 juveniles were captured in clear-cuts compared with 2 adults and 0 juvenile in adjacent mature forests. The percent shrub coverage was equal in the 2 habitats. Raspberries and cherry seedlings dominated the shrub layer in clear-cuts. Beech and red maple seedlings dominated in forests (Stoleson 2013; Streby et al. 2011b).

In Maine spruce forests, the Black-throated Green Warbler often occurs in 0.1-5-ha white birch stands generated from logging or windthrow. Leafrollers and other caterpillars are abundant in birch at this time (Morse and Poole 2020).

In Alberta, shrubs are an important substrate for foraging by fledglings (Robichaud and Villard 1999).

MIGRATION

The Black-throated Green Warbler is predominantly a nocturnal migrant. It is likely to be seen migrating in the day only over large bodies of water, typically returning to land. During the day while on migration, it often joins mixed-species flocks, especially in autumn, consisting of chickadees, nuthatches, kinglets, and other warblers. Autumn migration is often precipitated by high-pressure cells that generate favourable strong northwesterly winds. A bird banded in extreme western Quebec just east of Ontario was recovered in Guatemala (Bent 1953; Brewer et al. 2018; Graber et al. 1983; Morse and Poole 2020).

In spring, males arrive before females and adults arrive before juveniles. At Prince Edward Point, the mean arrival date of males (20.0 May) was 4 days earlier than for females (24.0 May). Mean capture dates for males at Long Point were 10.5 May for adults, 17.2 May for yearlings, and 11.5 May for those of undetermined age. Mean capture dates for females were 18.0 May for adults, 22.8 May for yearlings, and 10.3 May for those of undetermined age. The Black-throated Green Warbler exhibited the greatest intervals in arrival dates between adult and yearling birds for all species studied. All differences at both sites were significant (Francis and Cooke 1986; Stewart et al. 2002). In southern Ontario, spring migrants first appear in late April or early May and are often found into early or mid-June (Black and Roy 2010; Curry 2006; Fleming 1907; Flinn 2003; Keast 1980; LaForest 1993; Lancaster et al. 2004; Weir 2008). In the southern Shield, average arrival is early to mid-May, with

some arriving in mid-April (Mills 1981; Tozer 2012). Kendeigh (1947) first saw this warbler on 22 May near Lake Nipigon.

In Virginia and West Virginia, Stewart (1986) found no differences in timing of autumn migration between sexes and age classes. Most Black-throated Green Warblers pass through the southern Shield in September. Most are gone by the end of September with a few remaining until early October (Mills 1981; Tozer 2012). In southern Ontario, migrants are observed by mid-August. Most are gone by early to mid-October, with rare stragglers until early November (Black and Roy 2010; Curry 2006; Fleming 1907; Keast 1980; LaForest 1993; Lancaster et al. 2004; Weir 2008).

In British Columbia, habitat used during migration is similar to breeding habitat (Campbell et al. 2001). McIlwraith (1894) noted that the Black-throated Green Warbler used all types of trees during migration, but appeared to prefer pines for foraging. In most areas, it may be found anywhere that there are trees, including woodlands, roadside trees and shrubbery, gardens, and parks. It is also common where there are no conifers and may not exhibit a preference for conifers even where they are available. During migration in Maine, it occurs on treeless islands where it forages in herbaceous vegetation and along the shoreline. In Illinois, highest densities during both spring and autumn migration were in forest edges and shrubs, but it was well represented in all woody habitats (Bent 1953; Chapman 1907; Graber et al. 1983; Morse and Poole 2020). During spring migration in Pennsylvania, Smith and Hatch (2008) detected it on transects significantly more in forested habitat than in shrubs, but the capture rate in mist nets was significantly higher in shrubs than in forests. Invertebrate numbers and biomass were significantly higher in shrubs. During spring migration in Ohio, it was significantly more abundant in mature upland forests than in mature riparian forests. Upland forests had less canopy cover (74% compared with 83%) and more shrub coverage (39% compared with 19%; Rodewald and Matthews 2005). Rodewald and Brittingham (2002, 2004) determined relative abundance of this warbler in different forested habitats. In the first study, it was equally abundant in all habitats examined. In the second study, it was significantly more abundant in forest edges than in forest interior, shrub-sapling-stage forests, suburban forests, pole-stage forests, and forest-agricultural edges. During spring migration in Pennsylvania, its abundance was positively correlated with woodlot size, but no such relationship existed in autumn (Keller and Yahner 2007).

Keast (1980) studied the foraging behaviour of the Black-throated Green Warbler at Prince Edward Point. Foraging height was 1.5-18 m, with a peak around 7 m. It fed part of the day at 17-18 m, then in the tops of saplings and subsequently descended for short periods into shrubbery only 1.0-1.5 m tall. Forty-six percent of foraging occurred on outer leaves, 29% on sapling foliage, 10% on twigs and inner leaves, 10% on outer branches, and 0% in the air, outer and inner branches, sapling branches, low shrubs, and the ground. Occasionally it made aerial pursuits after flying insects. He also reported on its foraging behaviour at Point Pelee when several were grounded by adverse weather. Sixty percent of foraging occurred on bare twigs, 20% on branches, and 20% on sapling trunks; some aerial foraging also occurred. It foraged on bare trunks and branches along with the Black-and-white Warbler. Foraging heights were 0% at 17 m or higher, 50% at 13 m, 20% at 10 m, 10% at 7.5 m, 10% at 3 m, and 0% at 0.6-1.8 m and on the ground. During autumn migration, Lebbin et al. (2007) observed nocturnal foraging by the Black-throated Green Warbler in an area illuminated

by football stadium lights. It made aerial sallies after insects and appeared to glean arthropods from foliage. R.J. Smith et al. (1998, 2007) examined the foraging of the Black-throated Green Warbler during migration in Michigan. They compared foraging along the Lake Huron shoreline with areas more than 0.4 km from the lake. There was no significant difference in foraging in autumn except for foraging height, with an average of 9.34 m inland and 8.34 m at the shorelines. This difference was attributable to shrub use. It did not vary in foraging heights in any of the 5 most frequently used trees. During spring migration, inland birds gleaned significantly less (56.6%) than shoreline birds (69.1%) and sally-hovered more (23.0% inland, 14.1% shoreline) and sally-struck more (26.5% inland, 16.8% shoreline). There were no significant differences in where birds foraged within trees at the 2 sites. Inland birds used white cedar less and balsam fir, trembling aspen, white birch, and white spruce more relative to birds foraging near the shoreline. The most pronounced difference was the use of white cedar along the shoreline. It foraged substantially more in cedars than in other tree species along the shoreline. In early spring, the biomass of midges, spiders, and total arthropods was higher in shoreline habitat. In late spring, midge and spider biomass was higher in shoreline habitat. The arthropod biomass, excluding spiders and midges, was higher inland. Large hatches of midges occur within 0.4 km of the lake in early spring and their abundance attracts large numbers of spiders. The phenology of leaf development was inhibited near the lake which probably explained the preference for foraging on cedars. Due to retarded leaf-out near the shore, caterpillars were scarce and it is likely that warblers were foraging on the abundant midges. Emergent aquatic insects such as midges may be an important source of prey for spring migrants. Climatic influences from the lake affected vegetation development, invertebrate activity, and warbler foraging behaviour.

The diet during migration consists almost entirely of arthropods, predominantly insects but spiders are often consumed. Along the Great Lakes shorelines, midges and spiders may be locally important in the diet. Stomachs of Illinois migrants contained 70% caterpillars, 15% beetles, and 5% bugs, with the remainder comprised of a wide range of insects and spiders. Autumn migrants occasionally eat small amounts of fruit, such as poison ivy and juniper berries (Bent 1953; Morse and Poole 2020; R.J. Smith et al. 2007).

The Black-throated Green Warbler is commonly killed at television towers and other tall structures during migration (Graber et al. 1983; Morse and Poole 2020). A total of 435 were killed at the Lennox generating station chimneys 1972-82 (Weir 2008).

Strode (2003) studied the effects of climate change on the migration of the Black-throated Green Warbler in Illinois and North Dakota. Over 100 years, there was no significant spring temperature change in Illinois but spring had advanced an average of 8.6 days in North Dakota since 1961. Spring had also advanced north of Illinois. The Black-throated Green Warbler exhibited no response to changing temperature patterns and now has as many as 20 fewer days to travel between southern Illinois and northern Minnesota.

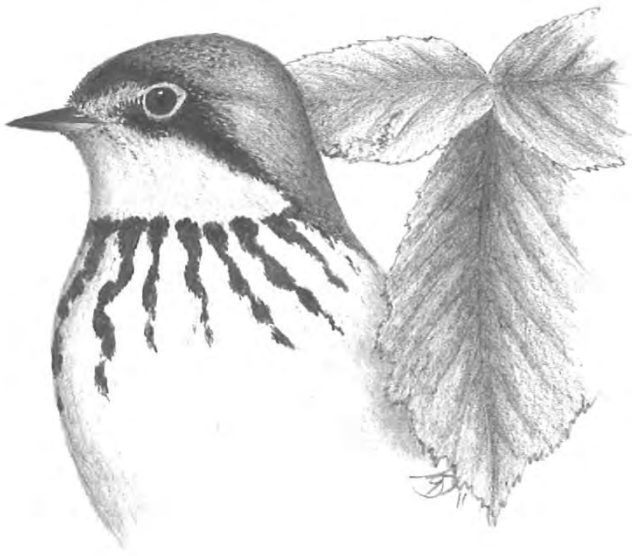
James (1991) considered the Black-throated Green Warbler a common migrant in Ontario. Flinn (2003) concluded that it was one of the more abundant migrants in Toronto.

At Long Point Bird Observatory (LPBO), Hussell et al. (1992) reported a nonsignificant decrease of 1.5% per year 1961-88. Trends by period were: 1961-70, −1.3%; 1970-79, +4.2%; and 1979-88, −8.2%. It demonstrated a similar but less pronounced change in population indices as the budworm

specialists suggesting that it might be affected to some degree by spruce budworm outbreaks. A more recent analysis of LPBO data revealed that it increased significantly at a rate of 1.4% per year 1961-2001. A significant increase of 5.6% per year was experienced at Prince Edward Point 1998-2002 and a nonsignificant decline of 2.8% per year occurred 1996-2002 at Selkirk Provincial Park. In the Toronto area, numbers were highest in the 1970s followed by a decline in the 1980s and an increase in the 1990s, a trend similar to that at LPBO. There appears to have been a decline over time in the Toronto area (Flinn 2003).

Canada Warbler

Cardellina canadensis



BREEDING SEASON

Habitat Requirements

Most Ontario Canada Warbler nests were in forests (86.7% of nests). Equal numbers of nests were found in deciduous and mixed forests, but only one was in a coniferous forest. One nest was in a swamp thicket and another was in a sphagnum bog. Although some wooded areas supporting nests were dense, most nests were in open stands, in clearings, or at woodland edges. It slightly favoured dry sites over those that were wet or swampy. Five nests were on slopes and knolls and another 5 were in rocky areas. Many nests were in areas with a heavy undergrowth of bracken fern, blueberry, poison ivy, clubmoss, hazel, alder, or other plants, shrubs, or saplings. Others were in or near brush piles and fallen logs (Peck and James 1987). James (1984b) reported that it nested in deciduous, mixed, and coniferous forests, often in swampy and riparian areas. Trees may be short in breeding habitat, but it prefers taller trees and requires a dense layer of shrubs under an open forest canopy, or areas at edges or in clearings.

In the Boreal Forest Region near Pickle Lake, McLaren and McLaren (1981) detected the Canada Warbler only in mixed scrub habitat. In the same area, James (1980) observed it only in alders at margins of lakes. Near Lake Nipigon, it was one of the most abundant species in overmature

trembling aspen stands, but it was rare to absent in spruce–balsam fir stands with no budworms (Sanders 1970). Near Manitouwadge, it was equally abundant in stands 1-21, 24-36, and 60-223 years old (Venier et al. 2009). Welsh (1993) considered it a species that nested in all ages of stands in the Boreal Forest Region. He detected it in stands 6-220 years old. Near Hearst, it nested in upland mixed clear-cuts 3-24 years old and in uncut upland mixed stands. It reached its greatest abundance in a 6-year-old stand and was not observed in lower-slope mixed or lowland coniferous stands (Welsh and Fillman 1980). In the Clay Belt of Ontario, it was most abundant in trembling aspen and balsam poplar stands, followed by those dominated by black spruce, white cedar, white birch–white spruce, and jack pine. It reached maximum density in nutrient-rich vegetation that contained at least some deciduous trees. It was found in both wet and dry forests (Welsh and Lougheed 1996).

In the Great Lakes–St. Lawrence Forest Region in the Canadian Shield, the Canada Warbler nested in mature and old-growth white pine stands. It was slightly more common in old-growth stands but not significantly (Kirk et al. 2012). In Algonquin Park white pine stands, it occurred in shelterwood cuts. It was observed in 14.3-20% of stands with no recent history of logging, in 10-18.2% of cuts 10-16 years old, and in 25% of cuts 2-9 years old (Kingsley and Nol 1999). Tozer (2012) noted that white pine stands logged in Algonquin Park from 1970 to 1978 had significantly more understorey than those logged in other years, creating ideal habitat for the Canada Warbler. In jack pine stands near Gogama, it was not specifically associated with pines. It was rare and occurred only in an area of dense deciduous shrubs with moist depressions (James and Peck 1995a). Near Parry Sound, it was absent in pure jack pine stands but occurred in low density in open jack pine stands mixed with a variety of deciduous species (James 1979a). It bred in areas of dense deciduous undergrowth in Parry Sound and Muskoka districts (Mills 1981). In Algonquin Park, Martin (1960) considered the Canada Warbler characteristic of pioneer deciduous forest. Highest densities occurred in balsam fir–spruce-hardwood stands where it was third in abundance. Moderate densities occurred in stands dominated by white birch–poplar, white birch–poplar–balsam fir–spruce, black spruce–white cedar, and in plots at edges of forest stands. It was rare in black spruce stands and absent in bogs, immature white pine stands, hardwood stands, and hemlock stands. In all types of stands, it confined its activities from the ground to the lower tree branches. MacLulich (1938) stated that it was distributed throughout Algonquin Park where there was shrubbery and mixed forest. Tozer (2012) noted that it bred in Algonquin Park in cedar woods, swampy forests, sphagnum bogs, moist forest clearings, woodland edges, spruce-tamarack bogs, poplar and moist

spruce–white birch forests, alder and willow along stream banks, and in cut-over forests. Back (1979) reported it nesting in Ontario in pole-sized to mature poplar–white birch stands but not in younger stands of similar species composition.

In Durham Region in the Great Lakes–St. Lawrence Forest Region south of the Shield, Speirs and Orenstein (1975) considered the Canada Warbler associated with balsam fir. It occurred in moderate density in a young open-canopy forest with poor drainage. It supported many balsam fir thickets and this is where it reached its greatest abundance. It also occurred in a hilltop covered with sugar maple sloping down to a stream bordered by white cedar, balsam fir, spruce, and dense deciduous shrubs, and presumably was found in the lowland habitat. These researchers also reported it in a black spruce bog bordered by a red maple–poplar swamp with an understorey of black ash. McIlwraith (1894) reported that it bred in low damp woodlands near Listowel. Near Kingston, all nesting areas were near wet areas or along streams within forests (Weir 2008). At Luther Marsh, it nested at edges of mixed swamps (Sandilands 1984). In Richmond Hill, territorial males were observed in the interior of an old-growth white cedar–yellow birch swamp (personal observation).

Black and Roy (2010) reported a number of breeding records in Wainfleet bog in the Carolinian Forest Region. Lancaster et al. (2004) reported 18 territories at 8 different sites in Elgin County, including in a white cedar swamp. It also nested at the Chesney bog in Oxford County in the surrounding swamp of red maple and white pine, with lesser amounts of white cedar and yellow birch (personal observation).

The Canada Warbler breeds in a wide range of forest types, including coniferous, mixed, and deciduous forests that may be either wet or dry. It occurs mostly in nutrient-rich sites but also uses nutrient-poor stands. In the east, mixed stands appear to be preferred to pure deciduous or coniferous stands. In the west, it often occurs in deciduous stands where conifers are completely lacking. In Quebec, it is less abundant in the north where the proportion of conifers is too high and declines in the south where the proportion of deciduous trees is too high. It occurs mostly in mixed stands dominated by deciduous species. In New Brunswick and Nova Scotia, it nests predominantly in northern hardwoods, mixed stands of intolerant and tolerant hardwoods, and spruce stands mixed with tolerant hardwoods. It selects these forest types more than their availability for breeding. Stand types used less than their availability, in order of greatest avoidance, included intolerant hardwoods, pine, spruce–intolerant hardwoods, intolerant hardwoods–spruce, and spruce–balsam fir. In the Prairie Provinces, it is usually absent in black spruce and species-poor jack pine stands and is associated mainly with mixed or deciduous stands. It tends to occur in drier, nutrient-rich sites. In British Columbia and areas of the Prairie Provinces, it prefers pure trembling aspen forests. At 103 occupied sites in British Columbia, 78 (75.7%) were composed of 80-100% hardwoods, 17 (18.4%) had 60-79% hardwoods, and 6 (5.8%) had 40-59% hardwoods. Trembling aspen occurred at every site, balsam poplar at 42.7% of sites, and white birch was present at 32.0% of sites. Trembling aspen was the dominant canopy species at 102 sites (99.0%) with a mean diameter at breast height (DBH) of 24.7 cm. White spruce was the dominant conifer at occupied sites; it occurred at 81.6% of sites. Where spruce was present, it was typically a secondary species and always had a smaller DBH (19.6 cm) and lower crown height than trembling aspen. There were only 4 sites dominated by white spruce, suggesting that as it becomes dominant a site gradually becomes less suitable for the

Canada Warbler. In the Yukon, it breeds in white spruce forests or white spruce stands mixed with trembling aspen or balsam poplar. At a site in Minnesota, it was most abundant in mixed forests followed by lowland conifers and upland deciduous stands. At another site, it was most abundant in lowland conifers and upland conifers. It was most common in wet mixed deciduous-coniferous forests with a well-developed shrub layer. In Vermont, it nested in northern hardwood forests, lowland spruce-fir forests, oak-hickory forests, white cedar–balsam fir swamps, and red maple–white cedar swamps. In New Hampshire, it nested in a 20-year-old clear-cut and a red maple swamp. In West Virginia, it was most likely to occupy northern hardwood forests and least likely to occupy oak-pine forests. The Canada Warbler has nested in several other forest types. These include upland red maple, upland and swamp white cedar, tamarack swamp and bog, willow-poplar, hemlock with a rhododendron understorey, American chestnut stands with many snags and dense regenerating chestnut, hemlock–white pine–red pine, sugar maple–yellow birch–beech, white pine–red oak, beech-oak, oak, and hemlock–yellow birch. In the Boreal Forest Region, it is one of the dominant and characteristic species in poplar and birch stands (Beals 1960; Brooks 1940, 1947b; Brush 1987; Campbell et al. 2001, 2007; Capen 1979; Chace et al. 2009; Crawford and Titterington 1979; DeGraaf and Chadwick 1987; Dimmig et al. 2022; Erskine 1977; Faanes and Andrew 1983; Gates and Giffen 1991; Golet et al. 2001; Grinde and Niemi 2016; Hallworth et al. 2008a; Hobson and Bayne 2000; Kirk et al. 1996; Krause 1965; LaRue et al. 1995; Morse 1989; Parker et al. 1999; Perreault and Tardif in Gauthier and Aubry 1996; Reitsma et al. 2020; Savignac 2008; Sinclair et al. 2003).

Many authors considered the Canada Warbler a species associated with mature or old-growth stands. Others classified it as a mid-successional or early successional species. In trembling aspen forests in Alberta, it was significantly more abundant in stands older than 120 years than those 51-63 years old. It was not detected in stands 23-26 years old (Schieck et al. 1995). Ball et al. (2016) examined results of point counts conducted throughout Alberta and found that it had a strong association with older deciduous, and to a lesser extent, older mixed forests compared with younger age classes and other forest types. Swamps and shrubby lowland areas were of intermediate suitability. Open and shrubby upland habitats and all types of human footprint areas were of low suitability. Young forests were unsuitable regardless of whether they had been modified by fire or forest management. Older forests were predicted to support 31.9% of the population. Kirk et al. (1996) considered it an old-forest species in the Prairie Provinces, although it occurred in low density in stands 1-20 years old. In the Yukon, it nests predominantly in old-growth spruce and spruce-poplar stands (Sinclair et al. 2003). In northeastern poplar–white birch stands, Back (1979) reported it only from pole-sized and mature stands. It was not detected in seedling-sized or sapling-sized forests. In northeastern mixed stands, Temple et al. (1979) considered it a late-succession species but not an associate of mature forests. In Quebec, Perreault and Tardif (in Gauthier and Aubry 1996) concluded that it frequented predominantly mid-successional forests. In Maine and Vermont, highest numbers occurred in intermediate-aged mixed woods 20-60 years old, more than in late successional forests. Lowest numbers occurred in intermediate-aged to mature hardwood stands 60-100 years old. In British Columbia, it nested predominantly in mature stands. The youngest occupied sites were 20-25 years old (Campbell et al. 2007). The Canada Warbler may be locally abundant in regenerating forests following fires or clear-cutting activities. Regenerating forests 6-20 years old are occupied in the east and those 20-30 years old are occupied in the west (Reitsma et al.

2020; Savignac 2008). Chace et al. (2009) stated that, in upland habitats, it appeared to specialize in disturbed areas where windthrow, ice damage, or timber removal created suitable habitat. In Manitoba, forest age significantly affected the probability of site abandonment, or local extinction. Probability of extinction was lower in stands older than 80 years. In upland deciduous stands, the probability of occurrence was higher in younger stands (average age 41 years, range 5-89 years), but these stands were more likely to be abandoned than older stands (Grinde and Niemi 2016).

Shrubs or saplings in the understorey are an essential habitat component and this, as well as forest structure, is more important than forest type or age. The Canada Warbler may also nest in wet, treeless alder or willow thickets but those with scattered trees are superior because they provide singing perches for males. If shrubs or saplings are absent, the habitat is unsuitable. It inhabits forests with an open canopy where light penetrates to the forest floor, promoting shrub growth. In British Columbia, occupied sites were moderately open, with 15-40% canopy cover, to moderately closed, with 60-80% canopy closure. The mean canopy closure was 62.0%. Stands with patchy canopies were used more than stands with uniform canopies. Average shrub coverage was 79% (range 20-95%, median 80%) with 80% of sites having shrub heights of 2.5-3.5 m. The space between the lower leafy branches of trees and the upper shrub understorey appears to be important for singing males. When viewed from the side, stands often had a well-developed shrub layer that was distinctly separate from the upper canopy. Herbaceous plants less than 50 cm tall were abundant in territories, with average coverage of 73% (Campbell et al. 2007). In mature and old-growth forests, the Canada Warbler may be restricted to areas where treefalls have created gaps in the canopy and allowed shrub growth to occur (Campbell et al. 2001; Reitsma et al. 2020). Almost all studies have identified that the Canada Warbler requires shrubs (Beals 1960; Bent 1953; Golet et al. 2001; Hallworth et al. 2008b; Harrison 1984; Litwin and Smith 1992; Perreault and Tardif in Gauthier and Aubry 1996; Reitsma et al. 2020; Savignac 2008; Sinclair et al. 2003; Stewart et al. 2009). In West Virginia, it was most likely to occur in areas with high rhododendron density in the understorey and those that were close to riparian areas (Dimmig et al. 2022). In Minnesota, Niemi and Hanowski (1984a) found this warbler in 1 of 8 clear-cuts they examined. This site was characterized by high foliage density and moderate shrub density. In New York clear-cuts, it was in a guild associated with homogenous patches of dense sprouts and shrubs. The density of this guild was highly correlated with leaf area and it increased significantly over a 4-year period postharvest. These species were absent during later stages of succession, except for the Canada and Black-throated Blue warblers that persisted in forest openings. The Canada Warbler was associated with low dense seedlings and shrubs as tall as 3 m (Keller et al. 2003). In spruce–balsam fir stands in Maine, it was absent in the earliest stages of clear-cuts and in mature closed-canopy forests. It was common in stands with hardwood regeneration taller than 2 m with a well-developed but slower-growing coniferous layer, and in hardwood regeneration taller than 4.5 m with trees 10-15 cm DBH (Titterington et al. 1979). In New Brunswick, it was positively correlated with the density of saplings 3-8 cm DBH, and preferred coniferous saplings (Parker et al. 1999). In the mid-Atlantic states, its abundance was correlated with foliage density 0.3-1.0 m from the ground (Robbins et al. 1989). In northeastern northern hardwoods, Noon et al. (1979) reported it on 3% of plots in mature and undisturbed habitats and 27% of plots in disturbed and successional plots, which presumably would have higher shrub densities. Crawford and Titterington (1979) stated that it bred and foraged in the shrub-sapling stratum in northeastern

upland spruce–balsam fir stands. In northeastern mixed stands, Temple et al. (1979) concluded that it was associated with increasing density of the understorey. In balsam fir–white cedar stands in Quebec, it was more common, but not significantly, in riparian plots where there was an edge community of alders and reed grass (LaRue et al. 1995). In Maine and Minnesota, the Canada Warbler was a shrub-forest edge species. It was in a guild of warblers that inhabited forests with high coverage of shrubs, moderate canopy cover, and low coverage by conifers in the canopy (Collins 1983a). In New Hampshire, Reitsma et al. (2008) compared habitat in territories of adult and yearling males. Territories of older males had lower canopy height, which provided more song perches, and higher shrub stem density than territories of yearlings (42.05 compared with 26.60 in a 5-m radius). In a red maple swamp, adult males occupied most of the dense deciduous thickets where stems were mostly smaller than 2.5 cm DBH. Yearlings occupied peripheral areas that had larger-stemmed shrubs (10.13 stems larger than 2.5 cm DBH in a 5-m radius for yearlings compared with 2.29 for adults). Shrubs were an integral component of the habitat and small-diameter stems appeared to provide superior habitat. In the same area, Hallworth et al. (2008b) compared habitats at sites settled first in spring to those settled later, at successful and unsuccessful nests, and on and off territories. Males that arrived within the first week of the breeding season held territories with greater shrub-stem density (48.76 in a 5-m radius) than late-arriving birds (39.74). Males that were successful in fledging at least 1 young had a greater total shrub density (42.98 within 5 m) than unsuccessful males (40.34) and higher densities of shrub stems smaller than 2.5 cm DBH (36.48 compared with 25.0). Compared with nonterritories, territories contained denser shrub foliage 2.0-2.5 m above ground, lower canopies, and a greater number of perch sites. Females appeared to select males whose territories contained high densities of shrubs. Birds in the red maple swamp had territories 40-50% smaller than those in an adjacent regenerating clear-cut, suggesting that the swamp was of higher quality. Density of shrubs was 2 times higher in the swamp, and it also had more moss coverage. Dufour-Pelletier et al. (2025) analyzed breeding habitat selection by the Canada Warbler in Quebec in 3 habitats: mixed boreal forest, agroforest, and riverine deciduous forest. The mixed boreal forest was dominated by balsam fir, trembling aspen, and white birch. The agroforest was characterized by sugar maple–basswood and sugar maple–bitternut hickory communities. The riverine deciduous forest was dominated by sugar maple–yellow birch and sugar maple–basswood. In the mixed boreal forest, stands dominated by deciduous species had a higher probability of Canada Warbler occurrence than those dominated by coniferous species. In the agroforest, it had a higher probability of occurrence in mixed stands than in coniferous stands. Presence of small saplings had a slightly positive effect in both these regions. Mountain maple, beaked hazel, and pin cherry were positively associated with its presence in the mixed boreal forest; it was negatively associated with saplings of trembling aspen, white spruce, and black spruce as well as large balsam fir saplings. In the agroforest, it was associated with small saplings of balsam fir, rhododendrons, viburnums, and blueberries, and large red maple saplings. In the riverine forest, it was positively associated with beech. Most of the species associated with the Canada Warbler's occurrence were shrubs. In New Hampshire, Goodnow and Reitsma (2011) examined nest-site selection by the Canada Warbler. Nest sites had significantly more concealment (86.7%) than mock nest sites on territories (39.8%). Mock nest sites on and off territories were not significantly different. Successful nests had higher stem density and greater nest concealment than failed nests. Densities of smaller stems (less than 1 m tall and 1 cm DBH) were particularly high around nests when compared with

either category of mock nest sites. Emergent trees above the understorey were also important for singing perches.

Coarse woody debris in the form of fallen trees and logs, woody detritus, and logging debris may be an important habitat component. The Canada Warbler uses fallen logs for foraging and occasionally as singing perches. In British Columbia, coarse woody debris was observed at every site supporting the Canada Warbler, with a mean of 7 pieces per 10 m^2 (range 2-24; Campbell et al. 2007). In New Hampshire, nest sites included high amounts of coarse woody debris, ferns, and moss as components of the ground cover. Coarse woody debris, including stumps and downed logs, contribute to ground substrate complexity and often provide highly concealed nest sites and shelter from the weather (Goodnow and Reitsma 2011).

Many authors concluded that the Canada Warbler occurs mostly in cool, moist forests and some stated that it is confined to these habitats (Baker et al. 2016b; Bent 1953; Chapman 1907; Harrison 1984; Reitsma et al. 2020). In Rhode Island, it is restricted to breeding in red maple swamps and in the mid-Atlantic states its abundance was significantly correlated with moisture (Robbins et al. 1989). In most areas, it is as likely to occur in dry as wet habitats. Adults are equally likely to home to nesting sites in wet and dry habitats (Campbell et al. 2001, 2007; Goodnow and Reitsma 2011; Hallworth et al. 2008a, 2008b; Niemi and Pfannmuller 1979; Reitsma et al. 2008; Welsh and Fillman 1980). Reitsma et al. (2020) stated that the Canada Warbler often breeds near water and is often associated with areas with abundant sphagnum moss. He concluded that suitable habitat often has a well-developed layer of moss on an uneven forest floor. It also frequently breeds where there is no water or moss, so these are not essential habitat components. Abundance of shrubs is a more significant habitat component than moisture and presence of water or mosses.

The Canada Warbler often nests in gullies and on slopes (Campbell et al. 2001, 2007; Reitsma et al. 2020; Savignac 2008). It also nests in wetlands and other areas where slopes are lacking. In British Columbia, the mean slope at 103 sites was 17° with a range of 0° (43 sites, 41.7% of sites) to 75° at 1 site. Most sites had gentle slopes of 1-5°. It is unlikely that the slope itself is important, but conditions created by slopes may create important microhabitats: moist areas, nutrient-rich spots, breaks in the canopy, and lush understorey growth (Campbell et al. 2007). Ball et al. (2016) determined that it was associated with locations near incised streams in Alberta rather than broad wet areas. Westwood et al. (2019) modelled factors affecting its abundance in Nova Scotia and New Brunswick. Highest densities were predicted in stands with a high proportion of balsam fir, alders, spruce species, and black spruce. Lowest densities occurred in stands dominated by maples, tamarack, white spruce, and pine species. Highest densities occurred in areas defined as wet with a depth to water table of 1 m or less; larger effects occurred at the territory scale of 250 m. High population densities were associated with medium values of standard deviation of canopy closure and height and mean canopy height. Higher complexity and connectivity of landscapes were predicted to support higher densities. It was less abundant near roads and in landscapes with more human disturbance.

Some studies determined Canada Warbler habitat requirements at the landscape level. In southern Ontario, there was no relationship between its abundance and the amount of forest cover in the region. It was negatively correlated with the amount of forest cover within 2 km, but not significantly (Austen et al. 2001). In Saskatchewan, it was randomly distributed within fragmented

landscapes and there were no significant relationships between its abundance and forest size, the amount of forest cover within 5 km, or forest type. It was significantly more common than expected in contiguous woodlands than in fragmented woodlots (Hobson and Bayne 2000). In Rhode Island, the only variable that made a contribution to its abundance in red maple swamps was the amount of upland forest within 1 km (Golet et al. 2001). In Alberta, the availability of deciduous and mixed forests at the 1-km scale was important in determining occupancy of stands, regardless of forest size (Ball et al. 2016). In Nova Scotia, its presence was positively correlated with canopy height heterogeneity and landscape complexity. It was negatively correlated with depth to water table, distance to a coniferous or deciduous stand, and distance to a stand with dead material. Presence of a high water table was the most important factor (Bale et al. 2020).

Several studies examined macrohabitat and microhabitat requirements of the Canada Warbler. In northwestern Ontario in and near Quetico Park, its occurrence was higher where shrub coverage was greater than 55%. Shrub coverage was the top predictor of its presence. The dominant shrubs present were mountain maple and beaked hazel. Canopy height and cover were also important. Canopy height averaged 12.3-13.0 m where it was present and canopy cover was 55.6-57.9%. The dominant trees were white birch and white spruce. Seventy-three percent of sites where 2 or more individuals were present were in landscapes that were 20-70% harvested. Sixty-nine percent of locations where only a single bird was detected were where no tree harvesting had occurred. Recently harvested sites supported higher levels of social aggregation, probably due to the increase in shrub growth (Cupiche-Herrera et al. 2024a). In Minnesota lowland coniferous stands, its probability of extinction was lower in older stands and stands with greater percent coverage by conifers within 100 m and 500 m. In deciduous stands, its probability of extinction was lower in older stands and stands with greater coverage by deciduous species within 500 m. Its probability of extinction in upland deciduous stands decreased with increasing open land within 500 m. In lowland conifers, its probability of occupancy decreased as the amount of open habitat increased within 500 m (Grinde and Niemi 2016). In New Hampshire and Maine, it was most strongly associated with sapling stands followed by poletimber stands, large sawtimber stands, and sawtimber stands. Its abundance was correlated with both coniferous and deciduous trees larger than 10 cm DBH, deciduous trees 2-10 cm DBH, the number of woody stems per ha, and the foliage volume of conifers 2-10 cm DBH. It was negatively correlated with conifers 2-10 cm DBH, snags larger than 10 cm DBH and taller than 5 m, and the foliage volume of deciduous trees smaller than 2 cm DBH and 2-10 cm DBH (DeGraaf et al. 1998). In trembling aspen forests in Alberta, it was associated with large sparse trees, snags and trees larger than 20 cm DBH, shrub richness, and canopy height (Schieck et al. 1995). In Minnesota, average habitat characteristics consisted of 88.3% ground cover, 73.3% shrub cover, 56.7% canopy cover, 18.8 m canopy height, 33.3% coniferous cover, 5.3 trees 7.5-15 cm DBH in a 0.04-ha circle, 9.7 trees 15.1-23 cm DBH, 8.0 trees 23.1-30 cm DBH, 3.7 trees 30.1-38 cm DBH, 4.3 trees 38.1-53 cm DBH, 0 tree 53.1-68 cm DBH, and 0.3 tree larger than 68 cm DBH. It was associated with medium-sized to larger trees and was in a guild of warblers that represented second growth and forest edge habitats with a high percentage of ground cover (Collins et al. 1982). In subalpine areas of New Hampshire, average territories contained wet depressions, had a canopy height of 10.4 m, 76% canopy coverage, 44% total coniferous foliage volume, 27% coniferous foliage volume 0-2 m from the ground, 68% deciduous foliage volume above 5 m, and trees with a DBH of

11 cm (Sabo 1980). In northern hardwoods in Vermont, its abundance was correlated with a lower canopy height and higher percent cover of shrubs and ferns than areas where it was not detected. These conditions were created naturally by windthrow, ice storms, and insect damage, and also by forest management (Chace et al. 2009). In West Virginia, successful nests had more low cover, less vertical diversity, more woody debris, more saplings, and greater edge density than failed nests (Becker et al. 2012). In New Brunswick, it was associated with the density of large deciduous trees, suggesting selection for mature forest (Parker et al. 1999). In the mid-Atlantic states, the Canada Warbler was correlated with foliage density 0.3-1.0 m from the ground, moisture gradient, basal area, and forest size. It was negatively correlated with canopy height and percent ground cover (Robbins et al. 1989).

Freemark and Collins (1992) considered the Canada Warbler a forest-interior species. Most studies demonstrated that it occurs in edge habitats as well as deep within forests. In the Yukon, it is found in the interior of forests in small openings in the forest canopy that encourage shrub growth. It also occurs rarely along edges created by roads or logging (Sinclair et al. 2003). In British Columbia, it is common in forest interior, but often occurs along roadsides where forest stands are fragmented. It often nests at edges between forest cover, shrubby areas along roads, hydro transmission line corridors, and ski hills (Campbell et al. 2001, 2007). In Alberta, its abundance at roads was 79% of that at off-road counts (Ball et al. 2016). In Maryland, it was more abundant in hemlock stands near an edge created by a stream than in forest interior. No edge effect was exhibited by this warbler and habitat type was more important than distance from edges (Gates and Giffen 1991). In Illinois, 1 pair nested in a clearing in an oak-hickory forest in an urban park (Graber et al. 1983). Reitsma et al. (2020) stated that it nested in forest edge habitats. In southern Ontario, its abundance was negatively correlated with the amount of forest cover 100 m or more from edge, but not significantly (Austen et al. 2001). The Canada Warbler occurs in both edge and forest-interior habitats. In forest interior, it is often restricted to gaps in canopy, especially if the forest cover is mature.

Based upon a literature review, Freemark and Collins (1992) concluded that the Canada Warbler was area sensitive. Field studies have demonstrated that it is area sensitive in some areas and not in others. Robbins et al. (1989) were the only researchers to document area sensitivity in this species. In the mid-Atlantic states, its abundance was strongly correlated with forest size. Its probability of occurrence was at a maximum in woodlands larger than 3,000 ha, probability of occurrence was reduced to 50% of the maximum at 400 ha, and the 3 smallest woodlots it was detected in at least twice were 883, 883, and 187 ha. In Wisconsin, it was not restricted to the larger islands studied by Beals (1960). In red maple swamps in Rhode Island, it was equally abundant in stands smaller than 1 ha and those 11-20 ha in size. These swamps were surrounded by upland forest, so this may not have been a true test of area sensitivity. In southern Ontario, its abundance was negatively correlated with forest size, although this relationship was not significant (Austen et al. 2001). Coleman et al. (2000) concluded that the Canada Warbler was area sensitive in the province. They listed Bent (1953) as their source of information but he made no mention of area sensitivity. The results for Ontario are equivocal and warrant more research to determine if this warbler is area sensitive within the province. Its distribution in the extreme southwestern portion of the province suggests that factors

such as area sensitivity or low forest cover at the landscape level may be preventing apparently suitable habitat from being occupied.

Ontario nests were on or near the ground. Ground nests (64.7% of nests) were in grass clumps (29.4%), at the base of stumps or beside fallen logs (23.5%), and in rock cavities (11.8%). Five other nests were elevated in recessed pockets of upturned tree roots (23.5% of nests) or in a brush pile (5.9%). One nest (5.9% of nests) was 0.9 m from the ground in the crotch of a maple sapling. This may be the only documented record of this species nesting in a tree or shrub (Peck and James 1987). McIlwraith (1894) reported that nests near Listowel were in cavities of upturned roots of trees and in depressions in banks near pools of water. In Elgin County, a nest was in a steep bank along a stream (Lancaster et al. 2004).

Throughout its range, the Canada Warbler builds its nest on the ground and in cavities in roots of upturned trees. Less frequently, nests are in steep overhanging banks along watercourses. Ground nests tend to be in the middle of dense shrub thickets, well concealed by the surrounding vegetation. They are often among woody debris and at the base of a shrub, occasionally concealed under dead grass. Many are sunken into moss hummocks where they are very cryptic and difficult to find. Nests may also be in clumps of ferns or grasses, under fallen trees, in rotted stumps, on top of mossy logs where they are usually concealed by additional overhead logs, under leaves on the forest floor, or in brush piles. Nests in upturned roots may be over standing water. One nest was built on top of an old nest and occasionally old nests are refurbished and used again (Bent 1953; Campbell et al. 2007; Chapman 1907; Goodnow and Reitsma 2011; Harrison 1984; Krause 1965; Mousley 1916a; Reitsma et al. 2008, 2020; Stewart et al. 2009).

Birds may pack into areas of suitable habitat where the habitat is heterogeneous such that territories are clustered into neighbourhoods. Territories may overlap to some degree, but such boundaries frequently remain in dispute. Nests are often within 30 m of each other. In Algonquin Park, territory size averaged 0.22 ha (range 0.03-0.74 ha). In New York, 1 male initially defended a territory of 0.24 ha but wandered over 0.8 ha after nesting. Another male with a nest roamed over 1.2 ha or more, an expansion of an earlier singing area. In both cases, a larger area was used once nesting began, and the entire larger area was defended. A territory in a hemlock stand in Quebec was 0.40 ha. In subalpine areas of New Hampshire, average territory size was 0.7 ha. In another area of New Hampshire over a 7-year period, the mean territory size of older males was 0.67-1.16 ha and 1.16-1.36 ha for yearlings. Over 4 years, average territory sizes were 0.88 ha in red maple swamp and 1.5 ha in early to mid-successional mixed forest, suggesting that the swamp was superior habitat. Mean territory size was 0.97 ha (range 0.15-3.36 ha) and the mean core area, where 50% of activity occurred, was 0.17 ha (range 0.02-0.77 ha). Mean core areas of adults (0.19 ha) and yearlings (0.23 ha) did not differ. In Vermont, average territory size was 0.38 ha and average home range size was 2.0 ha. Average territory size near Fort Liard, Northwest Territories, was 0.75 ha; territories averaged 0.31 ha in British Columbia. In Vermont, an unpaired male ranged over 7 ha in a single day. In Alberta, home ranges of males covered 0.18-9.87 ha. Males may occasionally travel as far as 1 km from their territories. In Alberta, mean territory size of 40 males was 0.47 ha. Territory size decreased as percent shrub coverage increased and was smaller where red squirrels were present. Territories tended to be smaller at shoreline sites than interior sites, and territory sizes were also more variable at shoreline

sites. There was a weak negative correlation between density and territory size. Insect abundance appeared to have no effect on territory size. There was a direct effect of territory size on breeding success, with success increasing with territory size. Breeding success declined with warbler density, and when squirrels were present in territories with dense shrub cover near shorelines. Warblers with larger territories are likely to have higher breeding success because they have greater access to resources, have higher quality mates, or are of higher quality themselves. Another Alberta study determined that home range sizes averaged 0.94 ha: 1.27 ha in harvested stands and 0.72 ha in unharvested stands (Baker et al. 2016b; Campbell et al. 2007; Flockhart et al. 2016; Hallworth et al. 2008a, 2008b; Hunt et al. 2017; Kendeigh 1945; Martin 1960; Perreault and Tardif in Gauthier and Aubry 1996; Reitsma et al. 2008, 2020; Sabo 1980; Savignac 2008).

Natal philopatry rates are uncertain but are probably low. In New Hampshire, 3 male and 3 female fledglings returned, but the number of young that were banded was not specified. Some returned late, presumably as nonbreeding floaters. One male nested as a yearling 5 km from its natal site. In Massachusetts, 2 juveniles returned to the same location (Reitsma et al. 2020).

Adult site fidelity rates are high. Return rates of 48.2% in Alaska and boreal Canada and 37.4% in the northeastern United States were reported. In New Hampshire, return rates of males over 3 years were 57%, 50%, and 47% (average 52%). Twenty-five percent returned in 2 years and 10% returned in all 3 years. The mean distances of territory shifts over the 3 years were 27.6, 36.9, and 31.1 m. Distance that a territory shifted was not influenced by pairing or fledging success the previous year. There were no significant differences in return rates in a clear-cut (44%) and a red maple swamp (53%). In New York, a female returned to the same general area to breed 2 years later and was recovered 5 years later during spring migration in Ohio, approximately 800 km west of the original capture site. Adult females exhibited site fidelity in New Hampshire, settling 0.5-1.0 km from their previous year's territory. In North Carolina, 12 of 109 adult males (11.0%) returned the following year. All were recaptured within 200 m of their original capture locations and all were seen at only 1 of 9 study areas. This was a declining population near the southern extent of this warbler's range (Chandler et al. 2018; Hallworth et al. 2008a, 2008b; Reitsma et al. 2020; Savignac 2008).

Limiting Factors

Eggs have been reported in Ontario nests from the last week of May until the end of June, with most present in the first 3 weeks of June (Peck and James 1987). In Algonquin Park, eggs are present from early to mid-June, nestlings are present in early July, and dependent fledglings have been seen from mid- to late July (Tozer 2012).

Males establish a territory as soon as they arrive. Upon arrival and pairing, the female assesses potential nest sites and selects one in an area of dense shrubs as large as 5 cm DBH. In New Hampshire, a male and female arrived on the same day and the female began lining the previous year's nest later that day. Nests typically take 3-5 days to build. When an old nest is reused, nest construction may take less than 2 days. Eggs are laid at the rate of 1 a day and incubation begins with the laying of the last egg. The incubation period is 11-12 days and all eggs usually hatch within 24 hours. The average nestling period is 8.1 days, but young may be as old as 10 days when they leave the nest (Campbell et al. 2007; Krause 1965; Reitsma et al. 2020).

A single brood is raised annually. It has been suggested that 2 broods are raised in Pennsylvania, but late nests are probably replacement nests and not second broods. No second broods have been positively confirmed. Renesting may occur until late June. Clutches of 3-6 eggs have been reported in Ontario (mean 4.43 eggs, mode 4 eggs). North American clutch sizes range from 2 to 6 eggs and most nests contain either 4 or 5 eggs. Mean clutch sizes reported elsewhere include 4.45 eggs in unparasitized nests reported to 5 nest record schemes, 4.8 and 4.36 in Michigan, and 4.13 for North America (Bent 1953; Campbell et al. 2007; Chapman 1907; Peck and James 1987; Reitsma et al. 2020).

Both sexes are capable of breeding when they are yearlings. In New Hampshire, adults paired at significantly higher rates (96%) than yearlings (64%) but there was no significant difference in the proportion of adult males (76.7%) and yearlings (67%) that successfully fledged young. Proportionately fewer yearlings persisted throughout the breeding season than older birds. Some yearlings were successful in rearing young in the same year that adults were unsuccessful. Differences in pairing success may occur because adult males secure territories in areas that females find more attractive or adults may be more attractive to females because of their brighter and bolder necklaces. Adults may arrive on the breeding grounds paired or, if the females arrive later, pairing occurs shortly after their arrival. Some New Hampshire females paired with a male that was a neighbour the previous year, even if she was successful in fledging young that year. The Canada Warbler is typically socially monogamous. In 1 territory in New Hampshire, there were 2 active nests 32 m apart, suggesting polygyny (Campbell et al. 2007; Reitsma et al. 2008, 2020).

Extra-pair fertilizations occur but there is limited information on the incidence of this. In New Hampshire, Reitsma et al. (2018) determined that 35 of 61 nests (57.4%) had at least 1 extra-pair young and 77 of 185 nestlings (41.6%) were extra-pair. Males were equally likely to be cuckolded by neighbours and non-neighbours. The probability of siring extra-pair young declined significantly with distance from the male's nest, but 1 male sired extra-pair young in a nest 2 km from his own and 5 extra-pair young were sired by a male at nests more than 1 km from his own. There was no difference in the cuckold rate of nests of yearling and older males, but older males accounted for 83% of extra-pair young. Males that sired more extra-pair young sired fewer of their own young compared with males that did not sire extra-pair young, or sired few. Males that sired extra-pair young in multiple nests sired the least of their own nestlings.

The Canada Warbler typically feeds in shrubs and low tree branches at heights of 3-5 m. In northern British Columbia, it foraged mostly in red-osier dogwood and young white birch. It also forages aerially and occasionally on the ground. In New Hampshire, the mean foraging height was 3.8 m (range 2.6-5.2 m). In Wisconsin, it always foraged in the shade. It uses a variety of foraging techniques, including flycatching, sallying, hover gleaning, foliage gleaning, and ground gleaning. Its flycatching ability is comparable to that of the American Redstart. In some areas, the Canada Warbler forages mostly by flycatching but prefers to glean and hover in other areas (Bent 1953; Chapman 1907; Hallworth et al. 2008a; Savignac 2008). In the Clay Belt of Ontario, 15.0% of foraging occurred in conifers, 92.0% in foliage, 82.1% by aerial attacks, 0% by hanging, 30.7% by hovering, and 0% by reaching at an average height of 4.3 m, which represented 58.0% of tree height (Greenberg et al. 1999). In subalpine New Hampshire, foraging techniques included 0.9% aerial flycatching, 29.0% leaf gleaning, 9.9% leaf hawking, 8.6% leaf hovering, 2.5% twig perching, 36.0%

twig gleaning, 10.4% twig hawking and hovering, 0.3% branch pecking, 1.8% branch gleaning, 0.1% bole pecking, 0.5% bole gleaning, and 0% litter pecking and gleaning and fallen log manoeuvres. Most (56.3%) foraging occurred proximal to the trunk and 43.7% was distal. Only 36.3% of foraging occurred in conifers, 63.4% was in deciduous foliage, 0.2% was in herbaceous foliage, and 0% was on the ground. Foraging heights included 4.3% at 0.1-2 m, 71.7% at 2-5 m, 22.4% at 5-8 m in the midcanopy, and 1.8% above 8 m in the upper canopy. It preferred to forage at low heights in deciduous vegetation (Sabo 1980). In Wisconsin, Sodhi and Paszkowski (1995) compared the foraging behaviours of the Canada Warbler to those of the Nashville, Mourning, and Chestnut-sided warblers. All species used young disturbed forests characterized by high light penetration and a well-developed layer of shrubs and herbaceous plants. This habitat was quite heterogeneous, but warblers did not use a particularly wide variety of the tree and shrub species present. The Canada Warbler was the most distinctive of these warblers because it foraged in coniferous trees scattered through a forest dominated by deciduous species. Of the other species, the foraging techniques of the Chestnut-sided Warbler were most similar to those of the Canada Warbler. Male Canada Warblers foraged more frequently in aspen, spending 38% of their time in aspens, 18% in hardwoods, 20% in shrubs, and 24% in conifers. Females spent 34% of their time in aspens, 15% in hardwoods, 21% in shrubs, and 31% in conifers. Both sexes foraged more in conifers than the other species. The mean foraging height for males was 4.06 m (range 0.3-23.0 m). Mean foraging height of females was 3.18 m (range 1.0-8.3 m). Canada Warblers foraged lower than Nashville and Chestnut-sided warblers and higher than Mourning Warblers. Male Canada Warbler foraging substrates included 59% on branches, 19% on twigs and leaves, 18% in the air, and 4% on limbs and trunks. Females foraged 61% of the time on branches, 22% on twigs and leaves, 8% in the air, and 7% on limbs and trunks. Males foraged by hovering 40% of the time, 31% by gleaning, 25% by sallying, and 4% by pouncing. Female foraging techniques included 58% gleaning, 20% hovering, 20% sallying, and 2% pouncing.

Young were fed 45.4% adult flies and 34.0% caterpillars in New Hampshire. Nestlings have been documented consuming crane flies, yellow grubs, mosquitoes, caterpillars, and adult moths. Adults eat some spiders but mostly insects including mosquitoes, flies, moths, adult and larval beetles, hairless caterpillars, ants, bees, other hymenopterans, scale insects, and insect eggs (Bent 1953; Harrison 1984; Krause 1965; Reitsma et al. 2020). The Canada Warbler also eats spruce budworms, although its consumption of them was low compared with other species in New Hampshire and Maine. In these 2 states, its population increased significantly with increasing budworm numbers, but the reason for this was uncertain given its low dependence on budworms (Crawford and Jennings 1989). Near Manitouwadge, it exhibited no significant response to budworm populations, although the trend was a decline with increasing numbers of budworms (Venier et al. 2009). Although it is not a budworm specialist, Savignac (2008) and Stewart et al. (2009) concluded that its population may correlate with budworm numbers and that current budworm management and the resulting decline in budworm outbreaks may be contributing to its decline. Sleep et al. (2009) used Breeding Bird Survey (BBS) data for the Canada Warbler and compared these abundance estimates with the area defoliated each year by the spruce budworm. They concluded that the Canada Warbler may be even more closely associated with the spruce budworm than known budworm-associated species. Venier et al. (2012) examined this conclusion using 60 years of BBS

data rather than the 30 years used in the first analysis. They determined that there were insufficient observations in Alberta and Manitoba to support the conclusions because most Canada Warbler observations occurred more than 100 km from any budworm defoliation. They concluded that there was little evidence to support the theory that the Canada Warbler decline was a function of spruce budworm decline. In an aviary experiment, Whelan et al. (1989) offered a Canada Warbler a second-instar gypsy moth larva and it was refused; no older larvae were offered. When different food items were offered simultaneously, 3 of 6 gypsy moth larvae were accepted, 0 of 4 tussock moth larvae were accepted, 5 of 6 cabbage loopers were accepted, and 4 of 4 mealworms were accepted. All the cabbage loopers and mealworms were eaten before any gypsy moth larvae were consumed. It demonstrated a clear preference for hairless larvae. In Maine, Mitchell (1952) examined the contents of 1 Canada Warbler stomach in 1949 and 3 in 1950; spruce budworms were abundant in the latter year. In the first year, the stomach contained 0% budworms and 100% other insects and invertebrates. In the second year, 3% of the volume of food consumed consisted of spruce budworms and 97% were other insects and invertebrates.

The Canada Warbler is a moderately common host of the Brown-headed Cowbird where the ranges of the 2 species overlap. The warbler appears to accept cowbird eggs and frequently fledges cowbirds. Mean warbler clutch size in parasitized nests was 2.5 eggs (range 1-4 eggs). Parasitism results in the loss of an average of 1.5 warbler eggs per clutch; effects on warbler fledging success are unknown. In Ontario, 5 of 25 nests (20.0%) were parasitized. In British Columbia, 5 of 34 breeding records (14.7%) involved parasitism, mostly of adults feeding cowbird fledglings. In Michigan, 21.4% of 14 nests and 54.5% of 11 nests were parasitized; 0 of 72 New Hampshire nests were parasitized (Campbell et al. 2007; Peck and James 1987; Reitsma et al. 2020).

Habitat loss and fragmentation may be limiting factors in agricultural landscapes but do not appear to be an issue in forested landscapes. Reduction in forest size or in the amount of forest cover within agricultural areas have the potential to make otherwise suitable habitat less attractive. Most large woodlands south of the Canadian Shield are designated significant woodlands and these areas are usually protected from development. Forest clearing can still occur for agricultural purposes and treed swamps may also be drained. These 2 activities combined have resulted in extensive habitat loss in the east. Most of this occurred from the 1950s to 1980s, but losses are still occurring due to agriculture and development (Reitsma et al. 2020; Savignac 2008; Stewart et al. 2009; Wells 2007). Even the construction of a single house within a woodlot inhabited by this warbler may have adverse effects. In North Carolina, its abundance was negatively correlated with the number of buildings within 200 m (Lumpkin and Pearson 2013). In Rhode Island, it was negatively affected by the proximity and length of roads in forested habitat (Savignac 2008).

Forest management practices that maintain or enhance the shrub layer are beneficial to the Canada Warbler. In northwestern Ontario, its probability of occurrence was 70% in unharvested forests but was 60% within 6 years of forest management indicating that it talks advantage of regenerating forests. Cupiche-Herrera et al. (2024b) recommended retention of tall trees and managing logged areas to retain shrub and riparian habitat. Clear-cuts provide good habitat 6-20 years after harvesting as long as they are allowed to regenerate naturally. Clear-cuts have the potential to create habitat where none previously existed or enhance habitat where the existing

forest had a full canopy with limited understorey. In Quebec and Minnesota, its abundance was lower in landscapes where forests were managed than in natural landscapes. In Alberta, the more extensively harvested a stand was and the more recently it had been harvested, the less likely that males were to use it. Over 50% of males' home ranges did not include any postharvest habitat and the average proportion of postharvest habitat in home ranges was only 14%. Males were more likely to use postharvest stands in areas supporting high densities, suggesting that usage of postharvest stands was more dependent upon conspecific attraction than the suitability of the habitat. Another Alberta study concluded that loss of older forests due to forest harvesting may be contributing to the decline of the Canada Warbler. In British Columbia, retained trees in clear-cuts provided important habitat in the form of singing perches. Retained residual trees had no effect on it in Alberta. In this study, the residual trees were used for perches by birds of prey and the retained trees were inadequate to provide cover from predators. In the Boreal Forest Region of Ontario, it increased when 30% or 50% of trees were removed from stands and decreased when 70% of trees were removed. In New York, it exhibited no response when 0-75% of merchantable trees were removed, but increased when 100% were removed. This still left a forest community, but one with many canopy openings that would favour shrub growth. In Quebec, it responded positively to strip-cuts and increased with the amount of deciduous regrowth in the strip. It bred at higher densities in old (14-15 years) cuts than in young cuts. In Minnesota, the Canada Warbler did not exhibit a significant response to harvesting in riparian buffer strips. In deciduous forests in Alberta, it declined significantly when 25% of trees were removed and became locally extirpated when 50% or more of trees were harvested. The effects of forest harvesting are variable and largely a function of what impact the management has on shrubs. Activities that decrease the amount of shrubs are detrimental; those that encourage shrub growth are beneficial. Excessive tree loss may be detrimental even where shrub growth increases. The amount of tree cover that can be removed may vary geographically and by stand type. Removal of a high proportion of trees may be beneficial in northern hardwoods. The same intensity of logging in intolerant hardwoods may be detrimental. In Ontario, removal of as many as 50% of the trees in a stand may be beneficial to the Canada Warbler. Clear-cuts are occasionally sprayed with herbicides to kill deciduous woody regeneration and release conifer species; this practice is detrimental. Short rotations may also be detrimental where it prefers mature or old-growth forest (Baker et al. 2016b; Ball et al. 2016; Becker et al. 2012; Campbell et al. 2007; Falardeau et al. 1999; Hallworth et al. 2008a; Hanowski et al. 2005; Harrison et al. 2005; Hunt 2016; Reitsma et al. 2020; Savignac 2008; Stewart et al. 2009; Tittler et al. 2001; Vanderwel et al. 2009; Webb et al. 1977). In Ontario in the Boreal Forest Region, there was no difference in its abundance in early successional and mid-successional clear-cuts than in burns of the same successional stage. There was no difference in its abundance in young clear-cuts and mature forests, but it was significantly less abundant in mid-successional than mature stands (Zimmerling et al. 2017). In Alberta, Hunt et al. (2017) examined the effects of forest harvesting and male density on reproduction in the Canada Warbler. They surveyed 132 plots 17.3 ha in area within aspen-dominated stands with a gradient of 0-100% of the plot harvested and 1-30 years postharvest. Male density was 86% lower in harvested than unharvested stands. Males were 16.6 times more likely to place their home ranges in harvested stands within 100 m of unharvested stands than 300 m into harvested stands. Males were also 3 times more likely to place their home ranges 100 m from conspecifics than 300 m from them. The mean size of home ranges that included harvested areas

was significantly larger (1.27 ha) than those that had not been harvested (0.72 ha). In harvested portions of home ranges, use of space was 1.1 times greater within 50 m of conspecifics than 350 m from conspecifics, but space use in unharvested stands was unrelated to proximity of conspecifics. Pairing success was higher for males at low and mid-densities than at high densities. Forestry impacts may be greater in western boreal forests where it prefers deciduous stands older than 125 years. In clear-cuts, territories were near the edge and retention of unharvested fragments 5 ha or smaller did not mitigate the effects of forest harvesting. There was no evidence that harvesting had an effect on pairing or fledging success. The authors concluded that forest harvesting seems to constitute a threat to Canada Warbler breeding habitat in this area because it results in lower use and density of birds. Postharvest stands are more likely to be used if they are near unharvested stands. Territories were clustered, so large tracts of unharvested forest should be retained.

Populations of the Canada Warbler respond to any factor that affects the abundance of shrubs. These factors may affect regional (forest maturation and grazing) and local (forest fires, insect invasions, diseases, and windthrow) populations. In eastern North America, much farmland was abandoned from the 1950s to early to mid-1990s. These areas initially provided good habitat, but continued forest maturation resulted in a reduction in understorey and amount of suitable habitat. Natural openings in the forest canopy do not occur again until later in succession when overmature trees die. Forest maturation in Algonquin Park has probably reduced the understorey and the Canada Warbler population. Two long-term studies in New York concluded that it declined due to forest maturation and the loss of understorey (Keller et al. 2003; Litwin and Smith 1992; Reitsma et al. 2020; Tozer 2012; Wells 2007). Overbrowsing by white-tailed deer has been cited as a significant problem in many areas and may be a limiting factor to the Canada Warbler south of the Canadian Shield. It has been identified as an issue in Algonquin Park. In some areas, cattle-grazing in woodlots is an issue, but this is not much of a problem in Ontario now (Baker et al. 2016b; Campbell et al. 2007; Gates and Giffen 1991; Reitsma et al. 2020; Savignac 2008; Stewart et al. 2009; Tozer 2012; Wells 2007). Forest fires have varying effects depending upon the severity of the burn. Severe burns may damage soils to the extent that regeneration is greatly inhibited. An Ontario forest fire in a mixed-coniferous forest caused a decline in the Canada Warbler. In New York, it was more abundant in old regenerating burns than in unburned forest. It appears to decrease initially after fire due to the loss of understorey vegetation, but eventually benefits once regeneration becomes established (Reitsma et al. 2020). Defoliating insects do not appear to have an adverse effect provided that understorey vegetation is not killed (Campbell et al. 2007). It is possible that it will benefit from the emerald ash borer because the loss of these trees in the forest canopy may promote the growth of shrubs. The Canada Warbler benefits from windstorm damage in woodlands. The fallen trees provide excellent cover and open up the canopy and create a dense shrub layer. In an aspen forest in Manitoba, populations increased 400% due to blowdowns (Reitsma et al. 2020).

In Alberta, the Canada Warbler was more abundant along pipelines and seismic lines than in undisturbed forest. It is probable that the disturbed habitats supported more shrub cover than the undisturbed forests (Bayne et al. 2016).

Probably the greatest limiting factor to the Canada Warbler is habitat loss in the wintering grounds. It winters in the dense undergrowth of Colombia's forests in the northern Andes and in

the lower slopes of the Andes in Ecuador and Peru. Approximately 90% of the forest in the northern Andes has been removed (Baker et al. 2016b; Stewart et al. 2009; Wells 2007).

Other potential threats have been suggested, but these are all currently of minor concern and some have not been documented as actually occurring. These include reduced availability of insects, acid precipitation that may affect abundance of aquatic insects and result in bioaccumulation of toxins such as mercury, habitat shifting and alteration due to climate change, changes in the timing of insect abundance due to climate change, temperature extremes and storms, and pesticides (Baker et al. 2016b; Wells 2007).

Price (2004) predicted that the Canada Warbler might disappear as a breeding species in southern Ontario if the average summer temperature increased by 2°C. In North Carolina near the southern extent of its range, Chandler et al. (2018) determined that it was most abundant at the highest elevations and absent in low areas. They considered the distribution shift to higher elevations a response to climate change and predicted that it may only persist at high-elevation sites in future.

Status

McIlwraith (1894) reported that a few Canada Warblers remained in the Hamilton area to breed. Baillie and Harrington (1937) concluded that it was well distributed but not very common. They had breeding season records from the southern portion of the province north to southern Kenora District and James Bay and it had also been reported along the Ontario-Manitoba boundary between latitudes 53°N and 54°N. It was known to breed north at least to the transcontinental railway. MacLulich (1938) stated that it was not very abundant in Algonquin Park. The first atlas confirmed that it bred from the southern boundary of the province north to the Wetiko Hills in the west and Attawapiskat in the east. It was not documented in many blocks in the central Boreal Forest Region. It was concluded that this may have been due to inaccessibility combined with scarcity of areas with deciduous undergrowth. Distribution south of the Shield was spotty. No breeding records were obtained in Essex County and the western portions of Lambton and Chatham-Kent. It was suspected that it was overlooked in some areas south of the Shield (McLaren in Cadman et al. 1987). James (1991) considered it a common breeder across central Ontario north to Sandy Lake and Attawapiskat, rare in southern agricultural areas, and absent in the extreme southwest.

The second atlas confirmed that there had been no change in the distribution of the Canada Warbler since the first atlas. There were no significant changes in its probability of observation province-wide, but significant declines occurred in the Carolinian Forest Region and the Great Lakes–St. Lawrence Forest Region in the Canadian Shield; trends in other regions were negative (McLaren in Cadman et al. 2007). There was a province-wide decline of 0.8% per year between atlases, a 16% decrease (Baker et al. 2016b). It was most abundant in the Boreal Forest Region and in the Great Lakes–St. Lawrence Forest Region in the Canadian Shield. Areas of higher densities occurred in a band from Rainy River to Cochrane, along the eastern shoreline of Lake Superior, and from Georgian Bay through Algonquin Park (McLaren in Cadman et al. 2007).

BBS data indicate that the Canada Warbler is declining rangewide and in Canada and Ontario. Rangewide, it declined at a rate of 2.3% per year 1966-2007. The BBS is not effective in monitoring this warbler. Much of its range is outside the area covered by this survey, its habitat is patchy in

distribution and this survey is best for widespread species, and the roadside survey is not well suited to detecting it. South of the Canadian Shield, Forest Bird Monitoring Program data for Ontario indicated an annual decline of 6.3% (Baker et al. 2016b; Campbell et al. 2007; Reitsma et al. 2020; Savignac 2008). BBS results indicate that it decreased at annual rates of 2.09% in Canada and 1.8% in Ontario 1970-2021. Trends for 2011-21 were annual decreases of 2% in Canada and 1% in Ontario. All results were of medium reliability (A.C. Smith et al. 2023).

Based predominantly on BBS results, the Committee on the Status of Endangered Wildlife in Canada designated the Canada Warbler threatened nationally. It was designated special concern in Ontario. The recovery strategy acknowledged that there was uncertainty in estimating its population size and trends using the BBS, and the strategy includes approaches to improve monitoring Canada Warbler populations. The short-term objective of the recovery strategy is to halt its decline by 2025 while ensuring that the population does not decline more than 10% over this time. The long-term objective is to ensure a positive 10-year trend after 2025 (Baker et al. 2016b).

POSTFLEDGING PERIOD

Brood division may occur once the nestlings fledge. Fledglings remain near the nest for a few days, usually close to the ground in thick cover such as bracken ferns, clumps of balsam fir, or small dense shrubs. There is high variation in the distances initially dispersed by fledglings. One was found 370 m from the male's territory 6 days after fledging and another stayed within 50 m of the nest for at least 18 days. Young are fully independent by age 2 weeks (Reitsma et al. 2020).

Young, adults, and family groups have been captured in clear-cuts 1-10 years old during the postfledging period in West Virginia, Virginia, Minnesota, and Pennsylvania. It is probable that widespread use of regenerating areas occurs after fledging, but limited study has been done on this. Although some Canada Warblers breed in this habitat, many move to early successional areas after breeding in forested habitat. In Minnesota clear-cuts, 43 adults and 16 juveniles were captured during the postfledging period over 4 years. In a single breeding season, only one was captured. In Pennsylvania, 5 adults and 6 juveniles were captured in clear-cuts and none were captured in adjacent mature forests (Marshall et al. 2003; McDermott and Wood 2010; Stoleson 2013; Streby et al. 2011b).

In West Virginia clear-cuts, caterpillar biomass was a positive predictor of captures of adult Canada Warblers. Juvenile abundance was significantly negatively correlated with basal area, arthropod density, stem density, and vertical complexity of vegetation. Although adults were correlated with arthropod biomass, juveniles were negatively correlated with food abundance. It is likely that juveniles are too inexperienced to recognize food-availability cues (McDermott and Wood 2010).

Adults and juveniles also inhabit forested habitat during the postfledging period. In 100 net-hours, 0.3 Canada Warblers were captured in upland forests and 1.4 were captured in riparian forests; 75% of juveniles captured were in riparian habitat. Upland forests consisted of 100-year-old trembling aspen and large-toothed aspen. Riparian forests were a mix of alder, honeysuckle, and trembling aspen. It is likely that the higher shrub abundance in the riparian stands was attractive to this warbler (Akresh et al. 2009).

MIGRATION

The Canada Warbler is a nocturnal migrant that often spends its diurnal stopovers in flocks of other warblers and small passerines, particularly in autumn. Some arrive on the breeding grounds paired so these presumably migrate together (Campbell et al. 2007; Reitsma et al. 2020; Tozer 2012).

Males usually arrive in spring before females but occasionally pairs arrive simultaneously, apparently already mated; adults arrive before yearlings. At Prince Edward Point, the mean capture date of males (24.4 May) was 3.2 days earlier than for females (27.6 May), a significant difference. At Long Point, the mean capture dates of males were 21.0 May for adults, 24.3 May for yearlings, and 22.1 May for males of undetermined age. Mean capture dates of females were 24.3 May for adults, 27.9 May for yearlings, and 26 May for females of undetermined age. All differences between age classes and sexes were significant. In Alberta, adult males arrived an average of 3.5 days earlier than adult females. Mean arrival dates were 30.5 May for adult males, 1.5 June for yearling males, 3 June for adult females, and 3.5 June for yearling females. Males may occasionally precede females by as much as 5 days and males arrived an average of 4 days earlier than females in Maine (Campbell et al. 2007; Flockhart 2007, 2010; Francis and Cooke 1986; Reitsma et al. 2020; Stewart et al. 2002).

In southern Ontario, the Canada Warbler typically arrives in mid-May, with some arriving in early May or very late April. Most are gone by the end of May but a few remain into June (Black and Roy 2010; Curry 2006; Fleming 1907; Keast 1980; LaForest 1993; Lancaster et al. 2004; Weir 2008). Average arrival in the southern Shield is mid-May with the earliest records in the second week of May (Mills 1981; Tozer 2012).

Autumn migration timing of adults appears to be linked to the timing of the moult, with birds initiating southward movement approximately 2 days after the moult is complete. In Alberta, old females departed on 3 August, juvenile females and juveniles of unknown sex departed on 5 August, juvenile males departed on 6 August, and adult males departed on 9.5 August. It has been confirmed in other areas that females and juveniles migrate earlier than adult males. In western Pennsylvania, the peak for adults was 5 days after the peak for juveniles. Males spent 72 days on the breeding grounds, significantly more than the 62 days spent by females. The Canada Warbler spends the least amount of time on the breeding grounds of any warbler. This inhibits its ability to renest and have second broods (Flockhart 2007, 2010; Graber et al. 1983; Reitsma et al. 2020). In Maine, autumn stopover times averaged 3.4 days (range 1-10 days), longer than in spring (Reitsma et al. 2020).

In the southern Shield, the Canada Warbler is fairly common through August and into September, with the latest records in late September (Mills 1981; Tozer 2012). In the south, average arrival is in mid-August and average departure is in mid-September, but migrants may be present from early August with stragglers to mid-October or rarely November (Black and Roy 2010; Curry 2006; Fleming 1907; Keast 1980; LaForest 1993; Lancaster et al. 2004; Weir 2008).

During migration, the Canada Warbler occurs in habitats similar to those used during the breeding season. These include shrubby edges of wooded areas, forests with a shrubby understorey, floodplains and riparian habitats, utility and railway corridors, and occasionally sloughs and marshes with some shrubby cover. It may also occur almost anywhere that there are trees, shrubs, or tangles of vines including in urban parks, villages, rural residential lots, and margins of beaver ponds. Presence of shrubs appears to be essential in areas where it stops over for a day or more (Campbell

et al. 2001, 2007; Leighton et al. 2002; Reitsma et al. 2020; Stewart et al. 2002). During autumn migration in Pennsylvania, it was equally abundant in forest interior, forest edges, forest-agricultural edges, suburban forests, pole-stage forests, and shrub-sapling-stage forests (Rodewald and Brittingham 2002). In Illinois, it was most abundant in both spring and autumn in bottomland forests and also occurred in forest edges and shrub habitats. In spring, it occurred in mature upland forests but numbers were consistently low in this habitat in autumn (Graber et al. 1983). In spring in North Carolina, it was most abundant in floodplain forests followed by wet thickets. It was not observed in dry thickets or upland forests dominated by pine-hardwoods, pine, beech, or oak-hickory (Parnell 1969). During spring migration in Ohio, it was most prevalent in lower portions of swampy woods or in dense undergrowth and preferred swamps with an understorey of spicebush (Bent 1953). During spring migration in Pennsylvania, it was significantly more abundant in shrub habitat than in forested habitat. The number of captures per 1,000 mist-net hours was 1.8 in shrubs and 0.1 in forests (Smith and Hatch 2008). Suomala et al. (2010) compared usage of 2 islands in the Gulf of Maine during migration over 2 years. During spring, there was no significant difference in island usage in 1 year, but in the other year it was significantly more abundant on the island with greater tree density and canopy cover and with high density of shrubs taller than 3 m. In autumn, more birds used this same island, but the differences between the 2 islands were not significant. During autumn migration in South Dakota, twice as many Canada Warblers were captured in a 3.5-ha woodland than in a contiguously forested riparian corridor (Dean et al. 2004).

During migration at Prince Edward Point, the Canada Warbler fed at heights of 1.5-7 m, mostly around 3 m. It foraged consistently in the lower parts of branches of saplings and spent much time in low shrubs. Foraging substrates included 5% on outer leaves, 10% on outer branches, 25% on inner branches, 13% on sapling branches, 25% on low shrubs, and 0% in the air and on twigs, inner leaves, trunks, and the ground (Keast 1980). During spring migration in North Carolina, Parnell (1969) considered it a low-tree user in floodplain forests. Foraging occurred 13.3% of the time in the canopy, 80.1% in low trees, 6.7% in shrubs, and 0% on the ground. In the canopy, 13.3% of foraging occurred in the lower crown and 0% occurred at the top of the crown, in the inner crown, or on the bole. In low trees, 0% of foraging occurred at the top of the crown, 46.7% in the inner crown, 26.7% in the lower crown, and 6.7% on the bole. In shrubs, 6.7% of foraging occurred in the inner crown and 0% at the top of the crown, in the lower crown, in dense thickets, in brush piles, and in grasses. During autumn migration, it has eaten fruit, locusts, and other insects (Reitsma et al. 2020).

Graber et al. (1983) stated that the Canada Warbler was an uncommon victim at Illinois television towers during migration. Other reports indicate that it is highly vulnerable to striking tall structures and this is considered a high threat to the population. It has been estimated that approximately 20,600 are killed annually in central and eastern North America at communication towers. Thirty-four were killed in 5 of 7 years at the Barrie television tower. From 1972 to 1982, 325 were killed at the Lennox generating station chimneys near Kingston; 131 were killed on 5 September 1981 (Baker et al. 2016b; Devitt 1967; Reitsma et al. 2020; Weir 2008). Loss et al. (2014) examined bird-building collision data for the United States and determined that the Canada Warbler was highly vulnerable to being killed at buildings. It was 17.9 times more likely to strike buildings of all types than the average for birds. It was 46.7 times more likely to strike low-rises and 25.8 times more likely to hit high-rises than average. It was not on the top 20 list of birds striking residences 1-3 storeys tall.

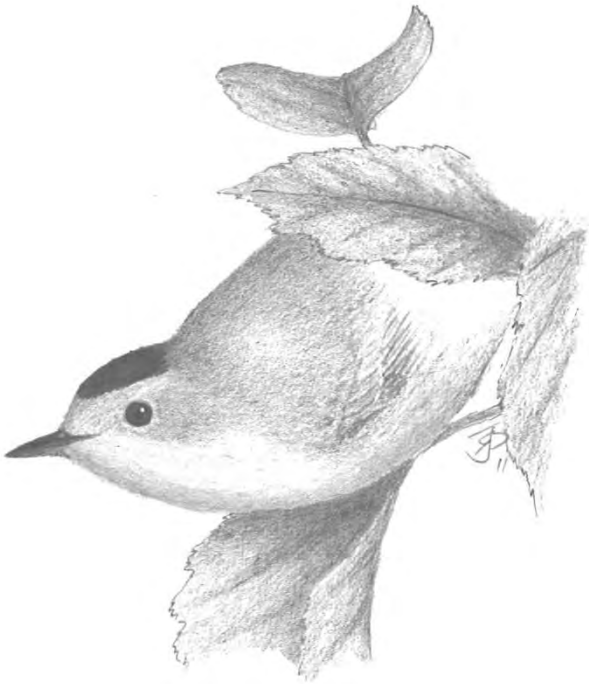
The Canada Warbler may be vulnerable to predation by cats while it is on migration. Birds nesting in agricultural landscapes are also vulnerable to predation and depredation of nests by cats (Baker et al. 2016b).

James (1991) considered the Canada Warbler an uncommon migrant, but it may be locally common in southeastern Ontario (LaForest 1993; Weir 2008).

At Long Point Bird Observatory from 1961 to 1988, captures of the Canada Warbler decreased significantly by 3.7% annually. Trends by periods included: 1961-70, –7.3%; 1970-79, +5.6%; and 1979-88, –8.3% (Hussell et al. (1992). More recent data for Long Point indicate that it decreased at a nonsignificant rate of 0.2% per year 1967-2005. During 1995-2005, it decreased significantly at a rate of 8.5% annually at Thunder Cape (Savignac 2008).

Wilson's Warbler

Cardellina pusilla



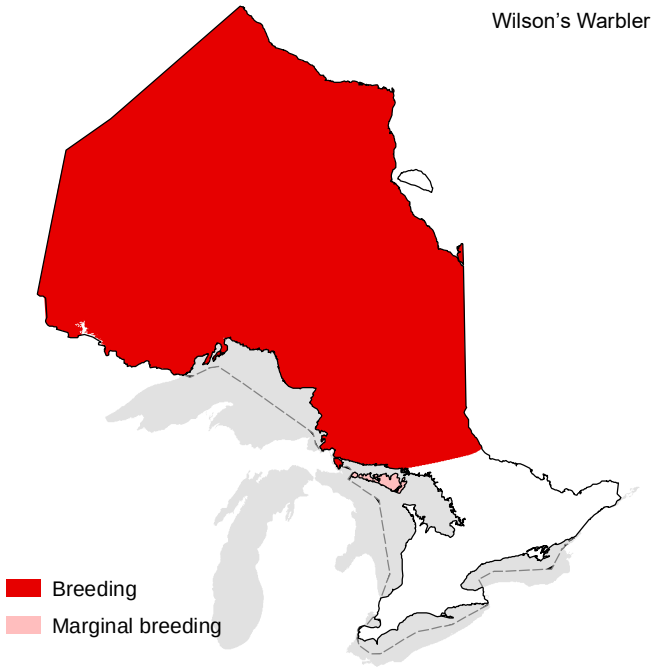
BREEDING SEASON

Habitat Requirements

There are 3 subspecies of the Wilson's Warbler, 2 in western North America and 1 in the east. The range of the eastern subspecies extends from Newfoundland and the Maritime Provinces west to central Alberta and the south-central District of Mackenzie, with a small proportion of its range in northern New England (Ammon and Gilbert 2020). Genetic analyses determined that the eastern subspecies is strongly differentiated from the western group. The eastern and western groups winter in different areas, are different morphologically, the eastern subspecies occupies a narrower ecological niche than the western group, and there is no evidence of breeding between the eastern and western groups. It has been suggested that the Wilson's Warbler may be treated as 2 separate species, with the eastern subspecies comprising one of the species and the western subspecies comprising the other (Ruiz-Sánchez et al. 2015). Information on both groups is provided in this species account, but in a manner such that it can be determined which group it pertains to.

Ontario nests were all in wet areas. Sixty percent of nests were in alder or willow thicket swamps with associated growths of black spruce, tamarack, dwarf birch, and Labrador tea; 30% were in grass, herbaceous plants, or raspberry thickets near streams or ponds; and 10% were in a drained area with dead cedars (Peck and James 1987).

In the Tundra Region and Hudson Bay Lowland, Wilson and McRae (1993) documented the Wilson's Warbler breeding in riparian willow thickets. Manning (1981) reported that it probably bred in willow thickets on the Twin Islands in James Bay.



In the Boreal Forest Region from Pickle Lake north to the Wetiko Hills, the Wilson's Warbler was most abundant in deciduous scrub followed by mixed scrub. It occurred in much lower densities in deciduous forests, coniferous forests with and without an understorey, and mixed forests. It was absent in heath and tundra habitat (McLaren and McLaren 1981). Near Pickle Lake, James (1980) found it only in shrub habitat at edges of forests. Near Hearst, it was fairly common in clear-cuts in lowland coniferous forests 3-19 years old, with highest densities in 11-13-year-old stands. It was absent in upland or lower-slope mixed forests and uncut coniferous lowland stands (Welsh and Fillman 1980). Near Manitouwadge, it was most abundant in mixed-wood stands 1-21 years old, but was still uncommon in these areas. Its abundance declined with forest age. Its abundance in 24-36-year-old stands was 14.6% of that in young stands and its abundance in 60-223-year-old stands was 6.25% of that in young stands (Venier et al. 2009). In the Clay Belt, it was most abundant in jack pine stands followed by those dominated by balsam poplar, black spruce, white cedar, and white birch–spruce. It occurred in wet to dry sites, but was most common in wet areas. It was present in stands at both extremes of the nutrient-richness scale, but occurred mostly in nutrient-poor sites (Welsh and Lougheed 1996).

Although the Wilson's Warbler has nested in a variety of forest types, it is usually confined to shrub thickets or wetland pockets within a forested matrix. Forest type is not significant to it and the general habitat descriptions of these stands may not be representative of the area that it actually inhabits. Its typical habitat includes shrub thickets that are in moist or wet habitat in nutrient-poor areas. Willow and alder swamps are prime habitat and these are often along streams, rivers, or lake shorelines, or in open wet depressions within forests. Bogs and fens with scattered conifers such as black spruce, tamarack, and white cedar provide suitable habitat in Ontario. Clear-cuts with patches of willows, alders, or regenerating saplings provide temporary habitat until the site reverts to forest-like conditions.

Limited information is available from other locations on the habitat requirements of the eastern Wilson's Warbler. In Newfoundland balsam fir–spruce stands, it was absent in undisturbed forests but occurred in low density in riparian buffer strips within 30 m of water. The riparian vegetation mostly consisted of alders and other tall shrubs, often in dense thickets. Whitaker and Montevecchi (1999) classified it as a riparian species. In New Brunswick, it nested in a bog surrounded by forest, with considerable growths of small white cedar, tamarack, spruce, and balsam fir saplings (Philipp and Bowdish 1917). In Maine, several inhabited a wet alder swale adjacent to a highway. The nest was on a dry slope above the swale vegetated with raspberries. In Maine, it nests in sphagnum bogs, and in willow thickets and shrubby pastures bordering young growth (Chapman 1907; Harrison 1951, 1984; Tyler in Bent 1953). On Anticosti Island, the Wilson's Warbler nested in clear-cuts 6-7 years old. Cardinal et al. (2012) considered it strongly dependent on the shrub layer for foraging and nesting. Near Quebec City, it occurred in very low density in a recent burn. It was not detected in clear-cuts, older burns, or uncut forests (Imbeau et al. 1999). In Quebec, it is uncommon in deciduous forests but becomes more abundant as conifers predominate and latitude and altitude increase. It is most numerous in the boreal spruce forest and in montane balsam fir–spruce forests. In the boreal forest, it does not nest within the forest itself, but in wet habitats with tall shrubs or short deciduous trees, mostly alders and willows. Boggy areas with nearby tamarack or stunted spruce are typical habitat and there is often a stream near occupied areas. Highest densities in the south occurred in balsam fir–spruce–white birch stands and abandoned fields overgrown with willow and alder thickets. In the north, highest densities were associated with shoreline shrub thickets. It frequently inhabited burns and ecotones between burns and coniferous forest (Alvo in Gauthier and Aubry 1996). In Quebec, extensive logging of mature boreal forests produced habitats with a patchy structure similar to that found in alder and other wet scrubland. The water table can rise in the 5 years following clear-cutting creating favourable mesic conditions and promoting growth of alders. The clear-cuts were less than 15 years old and regenerating with balsam fir, white birch, white spruce, raspberries, elderberries, and alder. Usage of clear-cuts was compared with usage of natural alder thickets 0.2-4.8 ha in area. There was similar use of clear-cuts and alder thickets, with 34% of 39 alder sites and 40% of 97 clear-cuts used. In both habitat types, it was more abundant in larger patches. In clear-cuts, it was more abundant in older cuts. This warbler is more abundant in landscapes affected by forest management than in natural landscapes. Occupancy of a given area increased with the amount of alder or clear-cut within 400 m of point-count stations. Desrochers et al. (2012) considered the Wilson's Warbler area sensitive because its probability of occupancy increased with patch size. It is not truly area sensitive because many of the smallest patches were inhabited. Even when very small amounts of habitat occurred within 400 m of a point-count station, the occupancy rate was 60% for alders and 64% for clear-cuts. This study demonstrated that clear-cuts, at least up to 100 ha, are beneficial and provide good habitat. In lowland coniferous stands in the northeast, Dawson (1979) reported it in low densities in shrubs with scattered conifers and in young or low black spruce, but stated that it was locally common. Near Churchill, it nests in tall willow thickets (Jehl 2004). In the Prairie Provinces, it was in a guild concentrated in young aspen stands, but it also occurred in wet marshy or bog habitats. It was observed in stands 0-20 years old but not in those 40 years old or older. It was associated with nutrient-poor wet sites and younger stands (Kirk et al. 1996). In the Boreal Forest Region, Erskine (1977) considered the Wilson's Warbler characteristic of tundra and alpine ecotones with boreal forest. Ammon and Gilbert (2020)

summarized the habitat of the eastern subspecies as clearings or bogs in moist early successional forests or stunted conifers, and in alders, sphagnum moss, and Labrador tea. In eastern Canada and the United States, occurrence of vegetation at 20 nests consisted of 60% alder, 45% grasses, 25% conifers (spruce and balsam fir), 25% mosses, and 15% Labrador tea. Other species at nests included willows, shrubby cinquefoil, pine, blackberry, nettles, ferns, and huckleberries. Seventy-nine percent of nests were adjacent to bogs and 21% were in drier cleared areas. Nest sites were near streams, on shrubby hillsides, in tundra, in moist meadows, in willow thickets, by lakes, in shrub thickets other than willow, in woods or swamps, and at edges of marshes. Its abundance was positively correlated with deciduous tree and shrub cover.

Much more research has been conducted on the western subspecies of the Wilson's Warbler. Western populations breed in mesic shrub thickets at edges of beaver ponds, lakes, and bogs and in clear-cuts. It also may breed within forests, particularly deciduous forests with sparse canopy closure. It is less abundant in young clear-cuts than in uncut forests but is more abundant in 10-20-year-old clear-cuts than in uncut forests. In the Yukon, it inhabits shrubby draws and wetlands interspersed within extensive black spruce forests. It is also found at the treeline, in shrubby areas along rivers, and at high elevations. It is uncommon to rare in lowland areas. It also occurs in streamside thickets in uplands and shrubby riparian forests, particularly those dominated by balsam poplar. In British Columbia, it breeds in dense low shrubby vegetation. It is characteristic of willow shrub thickets, but uses a variety of other shrubs. It may use clear-cuts for nesting but it is much more common in trembling aspen forests. Most nests were in forests where the cover was predominantly deciduous and the moisture level encouraged growth of a ground cover of mosses or grasses. It tends to avoid British Columbia coniferous forests for nesting but riparian shrub thickets at edges of coniferous forests provide suitable habitat. In many regions, particularly in alpine areas, the Wilson's Warbler nests almost exclusively in willow thickets. Alder thickets are also important and it may use thickets of bog birch, shrubby cinquefoil, rhododendrons, raspberries, young conifers, and maple seedlings. In most areas, it is a forest edge species but in California it nested throughout coniferous forests. In South Dakota, it nested in green ash woodlands with an understorey of chokecherry. It may nest in dry shrubby meadows. The most consistent habitat requirement for all subspecies of the Wilson's Warbler is dense growths of deciduous shrubs. For the most part, these are in wet areas and are mostly dominated by willows or alders (Ammon and Gilbert 2020; Bent 1953; Brand and George 2001; Campbell et al. 2001; Douglas et al. 1992; Finch 1989b, 1991a; Harrison 1951; Hutto 1981; Matsuoka et al. 2001; Michaud et al. 2004; Morrison 1981; Raley and Anderson 1990; Rumble and Gobeille 1998; Sinclair et al. 2003; R.M. Stewart 1973; Stewart et al. 1977; Whitmore 1977; Wiebe and Martin 1998).

All Ontario nests were on the ground sunken in grass or moss hummocks or in clumps of grass or herbaceous species. One nest was under the edge of a small bank in a low area. Four were at the bases of small trees (willow, white cedar, and tamarack; Peck and James 1987).

All reported nests of the eastern subspecies were on the ground or slightly below ground in a small depression. They were frequently sunk into mounds of sphagnum moss in bogs or at the bases of shrubs or small trees. Nests are usually well concealed under grasses, sedges, Labrador tea, low branches of shrubs, or other ground vegetation. Nests are not reused, but nest depressions are

frequently reused, often by birds other than the original breeder. One nest depression was used 10 years (Alvo in Gauthier and Aubry 1996; Ammon and Gilbert 2020; Harrison 1951; Phillip and Bowdish 1917; Tyler in Bent 1953). Nests of the western subspecies are similar, except along the Pacific coast where they may be elevated in shrubs. In California and Oregon, 7 nests were on the ground and 274 (97.5%) were elevated at a mean height of 1.7 m (maximum 10.0 m). Almost all nests are less than 2 m from the ground. A variety of plants may be used to support the nest, but blackberries, alders, willows, and ferns are favoured. Unusual nest sites include in a cavity under the root of a stump, in sparsely vegetated areas, on top of an old Barn Swallow nest under a bridge, and in an axe notch in an old stump (Ammon and Gilbert 2020; Bent 1953; Campbell et al. 2001; Michaud et al. 2004; Sinclair et al. 2003; R.M. Stewart 1973; Stewart et al. 1977).

The Wilson's Warbler is territorial, with boundary conflicts occurring 0.5-1.5 m from the ground in dense tangles. In Quebec, its occurrence was strongly clustered at scales of 240-420 m, which corresponded to the size of territorial neighbourhoods. The tendency to form clusters of territories may explain why it was more abundant in larger patches. Birds may wander from their territories. In California, males were seen 125-300 m from their territories and a pair was seen 135 m from the territory in the extreme edge of the adjacent territory. Nonetheless, most foraging and other activities occur within the territory. During the breeding season in California, groups of 3-8 birds may remain in an area of 10 m^2 or less for several minutes, eventually moving through the underbrush slowly or departing with 1 individual in the lead. These groups pass through the territories of mated pairs without invoking any agonistic reactions. The composition of these groups is uncertain and they may be nonbreeding floaters. This population was very high and contained many nonbreeders. Territory sizes have not been determined for any eastern populations. In Colorado, mean territory size was 0.19 ha (range 0.06-0.31 ha). In California, mean territory size in high altitude areas of the Sierra Nevada was 1.17 ha (range 0.7-2.0 ha) compared with coastal populations with a mean of 0.57 ha (range 0.2-1.3 ha) in oak-mixed forest and 0.48 ha (range 0.3-1.0 ha) in willows (Ammon and Gilbert 2020; Desrochers et al. 2012; R.M. Stewart 1973; Stewart et al. 1977).

All information on natal philopatry and adult site fidelity is for the western subspecies. In California, the annual return rate of juveniles to the natal area ranged from 0% to 11.1% and averaged 2.1% (49 of 2,289). In Colorado, 3% of 214 fledglings returned to the natal area (Ammon and Gilbert 2020; Chase et al. 1997).

In coastal California, at least 6 males returned to breed, mostly in their previous territories, but it was not specified how many were banded. Only slight modifications to territories occurred between the 2 years of study. One male moved his territory 150 m the second year. One male returned to find his territory occupied by a younger male. After an hour-long territorial dispute, the territory was divided (R.M. Stewart 1973). In the high Sierra Nevada of California, 9 of 20 (45.0%) males and 8 of 18 (44.4%) females returned the year after they were banded. Eight of the 9 males defended the same territory as in the previous year; 3 of 8 females returned to the same territory but only one had the same mate. This female nested 30 m from her previous nest. She had been 1 of 2 females involved in a polygynous relationship the previous year. The second female did not return and the returning female nested in the exact location where the other female's nest had been (Stewart et al. 1977). In coastal California, the probability of a breeding bird returning was 69% compared with only 7% of

birds that were transients during the breeding season. There was no significant difference in the recapture rates of the sexes. The overall annual survival rate was estimated at 50.3%, but Chase et al. (1997) acknowledged that this may have been an underestimation. There was a strong relationship between the capture rate of juveniles in 1 year and the capture rate of new adults in the following year. The capture rate of summer residents was related to productivity the previous year. In central Colorado, 32-34% of adult males and 28-30% of adult females returned; the overall return rate was 30-31%. In northern Colorado, 44% of adult males and 27% of adult females returned (Ammon and Gilbert 2020).

Limiting Factors

Eggs have been reported in Ontario nests from the second week of June until the first week of July, with most present in the last half of June (Peck and James 1987). Most information on the timing of reproductive activities is for the western subspecies. In coastal California, the time between arrival of the first males and the beginning of pair formation was 15 days. In the interior of California, an average of 8.9 days (range 1-25 days) elapsed between male arrival and pairing. Males arrive there in late March. In Ontario, where birds arrive much later, it is likely that pair bonds are formed shortly after females arrive. In California, nest completion averaged 2.8 days (range 2-6 days). First nests averaged 4.0 days (range 2-6 days) and replacement nests averaged 1.7 days (range 1-2 days). The first egg was laid an average of 1.9 days after the nest was complete (range 1-3 days). The average for first nests was 2.4 days (range 2-3 days), and the average for replacement nests was 1.3 days (range 1-2 days). Eggs are laid at the rate of 1 per day. Incubation begins with the laying of the last egg or during the night following laying of the penultimate egg. The incubation period of the eastern race is 10-11 days, based on a limited number of nests. In California, the incubation period was 11-12 days for 3-egg clutches and 13 days for 4-egg clutches. The average incubation period in Colorado was 11.2 days. All eggs hatch within a 24-hour period in the west. The nestling period in the east is 10-11 days. In Maine, young left the nest at ages 7 and 8 days due to disturbance. In the west, young fledge when they are 8-11 days old (Ammon and Gilbert 2020; Harrison 1951, 1984; Stewart et al. 1977; Tyler in Bent 1953).

In coastal California, 4 of 22 pairs (18.2%) attempted a second brood and 2 were successful. In this area, birds arrive on the breeding grounds in late March or early April, giving them adequate time to raise a second brood. There is no evidence of double broods anywhere else, including in other areas of California. Egg dates in Ontario suggest that no second broods are attempted. In the same area of California where double broods were confirmed, all 15 females that lost nests laid a replacement clutch and 1 female renested 4 times. In the high Sierra Nevada of California, no renesting occurred after clutch loss. No information is available on whether the eastern population renests. Ontario egg dates suggest that renesting may not occur. Clutches of 3-5 eggs were reported in Ontario (average 4.67 eggs, mode 5 eggs). Throughout its range, the Wilson's Warbler lays 2-7 eggs, but mostly 3-6 eggs. The single 7-egg clutch was from Alaska, where most nests contained 6 eggs. In California, the most common clutch size was 5 eggs in the Sierra Nevada and 4 eggs on the coast. Mean clutch sizes include 4.4 eggs for the eastern race, 4.5 eggs in Alaska and the Rocky Mountains, 4.5 eggs in the Sierra Nevada, and 3.9 eggs on the Pacific coast (Alvo in Gauthier and Aubry 1996; Ammon and Gilbert 2020; Bent 1953; Campbell et al. 2001; Harrison 1951, 1984; R.M. Stewart 1973; Stewart et al. 1977; Tyler in Bent 1953).

Both sexes are capable of breeding when they are 1 year old. Yearling males have limited success in establishing territories and breeding. In Colorado, only 2 of 37 territories were held by yearlings and both failed to attract a mate. Over 2 years, 20 floaters were identified in these 37 territories. In the Sierra Nevada, 15% of males were unmated but the age class of these birds was not stipulated (Ammon and Gilbert 2020). The mating system is typically monogamous, but 3 cases of polygyny were confirmed in 1 year in the Sierra Nevada. No polygyny occurred in the same study area in the previous year. Two years later, an additional 2 males were polygynous and one may have been involved in extra-pair copulation with a third female. Polygynous males had larger territories than normal and their females nested approximately 200 m apart on opposite sides of the territory. Polygyny was reproductively advantageous for males but not for females. Two of 7 polygynous males successfully raised 2 broods and 5 raised at least 1 brood. The 7 polygynous males fledged 35 young, an average of 5.0; 13 monogamous males fledged 36 young, an average of 2.8. Females in polygynous relationships raised an average of 2.5 young compared with an average of 2.8 for females in monogamous relationships. In polygynous relationships, males do not feed the young of secondary females until the nestlings of the primary females fledge. Primary females are then left to care for their fledglings without assistance from the male. Over 4 years in the Sierra Nevada, 59% of males were monogamous, 26% were polygynous, and 15% were unmated (Stewart et al. 1977). The pair bond is maintained throughout the breeding season. In California, the pair bond persisted in all 32 pairs, including 13 pairs that lost a nest and attempted renesting. In Colorado, only 1 female returned to her territory and mate of the previous year. None of her eggs were fertilized by that male in the previous year. Males commonly intrude into neighbouring territories and inspect the nest sites. Intrusions are more frequent at replacement than first nests when nesting chronology becomes asynchronous. In Colorado, 53% of broods had evidence of extra-pair paternity, with 20-100% of clutches affected and 32% of young resulting from extra-pair fertilizations. Neighbouring males usually sired extra-pair young, even though floater males were common. The high prevalence of extra-pair fertilization in the reproductive strategy of the Wilson's Warbler may partially explain the tendency for territories to be clumped. No intraspecific egg dumping has been observed, but there was 1 possible case based on DNA analysis (Ammon and Gilbert 2020).

All available information on the Wilson's Warbler breeding season foraging behaviour and diet is for the western subspecies. It typically forages in the shrub layer and rarely on the ground. Most studies demonstrated that it forages at low heights. In the Sierra Nevada, optimum habitat consisted of dense thickets of willow with scattered pines extending 10-13 m above the willows. The pines were a source of abundant prey and females feeding nestlings foraged heavily in the pines. It tended to forage as high as the upper limits of vegetation. Although it favoured pines for foraging in the Sierra Nevada, it avoided conifers in Oregon (Hutto 1981; Morrison 1981; Stewart et al. 1981). Foraging tactics of the Wilson's, Orange-crowned and MacGillivray's warblers were compared in Oregon by Morrison (1981). The Wilson's Warbler was associated with trees, the MacGillivray's Warbler with shrubs, and the Orange-crowned Warbler was intermediate in its foraging height. In this study area, trees consisted of alders about 7 m tall. Where trees were present, the Wilson's Warbler was usually separated from the other 2 species but Orange-crowned Warblers occasionally used trees. Where trees were removed, the Wilson's Warbler increased its use of shrub cover for foraging. It exhibited limited adaptation to foraging in shrubs and declined when trees were

removed. Its abundance was correlated with the abundance of deciduous trees. Where trees were removed, each foraging substrate was used in proportion to its availability. Foraging heights were significantly higher in areas with trees (2.4 m compared with 0.8 m); 17.7% of foraging occurred 0-1 m from the ground in treed areas compared with 68.5% in untreed areas; 56.3% occurred at 1.1-3 m in treed areas compared with 28.4% in untreed area; and 25.9% occurred above 3 m in treed areas compared with 3.2% in untreed areas. In Wyoming and Mexico, Hutto (1981) compared the foraging strategies of the Wilson's, Yellow, and MacGillivray's warblers and the Common Yellowthroat. The Wilson's Warbler predominated in willows; the Yellow Warbler in taller alders, aspens, or cottonwoods; the Common Yellowthroat in cattails and bulrushes; and the MacGillivray's Warbler in wet thickets. The Wilson's Warbler foraged from the ground to more than 4.9 m above it. Six percent of foraging was at a height of 0-0.3 m, 15% at 0.3-0.6 m, 44% at 0.6-1.2 m, 20% at 1.2-2.4 m, 10% at 2.4-4.9 m, and 5% above 4.9 m. It differed significantly from the other species for absolute foraging height and from the MacGillivray's Warbler and yellowthroat for relative foraging height, vegetation density, foraging position, foraging substrate, and feeding methods. The feeding methods differed because the 2 high-foraging species (Wilson's and Yellow warblers) sallied more frequently for aerial insects. The 4 species were least similar in the absolute heights at which they fed and most similar in their feeding methods. Foraging locations may be important in promoting ecological isolation. The Wilson's Warbler foraged higher in August than in June at heights most similar to those of the Yellow Warbler. Late-summer foraging heights were 4% at 0-0.6 m, 10% at 0.6-1.2 m, 31% at 1.2-2.4 m, 46% at 2.4-4.9 m, and 9% above 4.9 m. In June, vegetation density at foraging locations was 0-15% at 28% of sites, 15-50% at 49% of sites, 50-85% at 18% of sites, and 85-100% at 6% of sites. In the Sierra Nevada, aerial foraging occurred at heights of 0.6-16.8 m. Foraging occurred as high as 12.2 m in pines (Stewart et al. 1977). On the California coast, both sexes fed in the understorey and trees, but usually not higher than 1.5 m below the top of the canopy (R.M. Stewart 1973). Foraging is predominantly by gleaning, although the Wilson's Warbler also hovers and sallies. In the Rocky Mountains, 75% of foraging was by gleaning, 15% by hovering, and 10% by sallying. In Wyoming, 56.6% of foraging was by gleaning, 37.4% by sallying, and 5.9% by hovering; 1.8% of foraging was on the ground, 35.2% on bark, 25.6% on foliage, and 37.4% in the air. In the Sierra Nevada, 34.3% of foraging was by gleaning, 41.3% by hovering, 20.0% by partial hovering (moving through the air without flycatching or wing fluttering), and 4.3% by flycatching. On the California coast, 45.1% of foraging was by gleaning, 32.4% by hovering, 21.1% by partial hovering, and 1.4% by flycatching. On San Clemente Island, 63.1% of foraging was by gleaning, 23.3% by hovering, 7.8% by partial hovering, and 5.8% by flycatching. When all 3 California sites were combined, adults hovered or flycatched on 51.2% of food-catching attempts. Hovering and flycatching allows it to capture insects that land on leaves, especially those at the tips of branches that would not support the weight of the bird. Of California prey-catching attempts on solid substrates, 97% were on leaves and 3% were on twigs smaller than 6 mm in diameter (Ammon and Gilbert 2020; Hutto 1981; Stewart et al. 1977).

Nestlings are fed small soft-bodied insects and very small caterpillars (Ammon and Gilbert 2020; Bent 1953; Harrison 1951; R.M. Stewart 1973; Stewart et al. 1977). An analysis of 53 stomachs of one of the western subspecies revealed that the breeding season diet consisted entirely of insects with a few spiders; some fruit was consumed in autumn. The diet consisted of 35% bugs (mostly leafhoppers), 31% hymenopterans (wasps and ants), 11% flies (including many crane flies), 9%

beetles (mostly leaf beetles with a few weevils), less than 5% caterpillars (which were eaten very irregularly), and 1% spiders (Bent 1953). Raley and Anderson (1990) analyzed the contents of esophagi and gizzards in Wyoming and sampled arthropod populations on willows where warblers had been observed foraging. The Wilson's Warbler was selective in the size of prey it consumed. Arthropods 1-3 mm in length were consistently underrepresented in the diet. The size of mayflies consumed was similar to what was available. A total of 53 families of arthropods, excluding spiders, most lepidopterans, and miscellaneous orders such as springtails and book lice, were identified in the diet. Beetles were most preferred, followed by mayflies, stoneflies, flies, and hymenopterans. These were consumed in greater proportion than their availability. Soft-winged bugs were least preferred, followed by larvae (immature beetles, hymenopterans, and caterpillars), spiders, adult lepidopterans, and true bugs. These were consumed in lower proportion than their availability. No clear distinctions could be made about preferences within these groups. Use of beetles, mayflies, and stoneflies was statistically higher than for the 5 groups that were avoided. Use of soft-winged bugs and larvae was statistically lower than for all other groups. Stoneflies larger than 7 mm were underrepresented in the diet although these were more abundant than the size class of stoneflies that it consumed. Large stoneflies may take too long to handle to be profitable. Even though soft-winged bugs were least preferred, leafhoppers comprised 16% of the diet and were therefore important. The larvae group ranked low but comprised 30% of the diet. The larvae and soft-winged bugs are cryptic and leafhoppers respond to disturbance with very quick and erratic jumps. These factors may make these 2 groups of prey less available than their abundance would suggest. Soldier beetles represented a large proportion of the beetles that were consumed. These are noncryptic, have soft elytra, are relatively large (7 mm), are slow fliers, and tend to crawl away from disturbance rather than fly. Consequently, they are easy and profitable prey. All arthropods that ranked high in the diet were noncryptic and patchy in distribution. Hagar et al. (2007) analyzed 87 fecal samples in Oregon and identified 15 groups of taxa. The percent occurrence of taxa within the samples was: 99% flies, 86% soft-winged bugs, 85% spiders, 84% beetles, 63% caterpillars, 46% wasps, 23% leafhoppers, 20% sawfly larvae, 18% adult lepidopterans, 14% arthropod eggs, 5% neuropterans, 5% springtails, 2% mites, 2% book lice, and 1% true bugs. Nine families within 4 orders were also identified: soft-winged bugs: achilid planthoppers, aphids, and froghoppers; neuropterans: green lacewings; beetles: soldier beetles and tumbling flower beetles; and flies: dance flies, fungus gnats, and dark-winged fungus gnats. The average size of prey was 4 mm (range 2-10 mm). The Wilson's Warbler consumed prey that was larger than the most abundant items available. It did not consume the largest available size classes (longer than 12 mm) of adult arthropods, including flies, beetles, and spiders. Larvae, predominantly caterpillars and sawflies, were the largest prey items consumed, ranging from 6 to 26 mm in length. It ate mostly larva longer than 6 mm, which were less frequent than those in the smaller size classes. It consumed a wide variety of prey but ate caterpillars, flies, beetles, and soft-winged bugs more frequently than expected. Caterpillars and sawfly larvae have high calcium concentrations relative to other species and provide an essential resource for egg laying. Regardless of taxa, arthropods 2 mm in length and less were infrequent in the diet even though this size-class was abundant.

Brown-headed Cowbird parasitism does not appear to have been documented for the eastern subspecies of the Wilson's Warbler. In the west in some areas, no parasitism occurs; it is the most

frequent host in other areas. In British Columbia, 1 of 46 nests (2.2%) was parasitized. In the Sierra Nevada, no parasitism occurred in 1 year and 1 nest was parasitized in another year. At 1 California site, the parasitism rate was 0% over 5 years, 0-3% of nests were parasitized in Colorado over 3 years, 2 of 71 Colorado nests (2.8%) were parasitized, and 55% of nests in southern California and 43% of nests at another California site were parasitized. At the 2 latter sites, the Wilson's Warbler was one of the most common hosts. In coastal California, 30 of 90 nests (33.3%) were parasitized. Only 1 (3.3%) successfully fledged a warbler compared with 25% of unparasitized nests. Parasitism significantly affected reproductive success at every stage. The clutch size of parasitized nests was 1.96 eggs compared with 3.48 eggs in unparasitized nests. Hatching success was 36% in parasitized nests and 64% in unparasitized nests, brood size was 0.71 nestlings in parasitized nests and 2.31 in unparasitized nests, and fledging success rate was 4% in parasitized nests and 28% in unparasitized nests. Parasitized nests failed completely except for 1 nest (Ammon and Gilbert 2020; Campbell et al. 2001; Harrison 1984; Michaud et al. 2004; Stewart et al. 1977).

Habitat loss and degradation do not appear to be significant for the Wilson's Warbler in Ontario. Loss of riparian habitat may be contributing to its decline in the west. In Ontario, forest harvesting is not allowed within 200 m of watercourses and water bodies, so its preferred riparian thickets of alder and willow are not affected. Clear-cutting may create wet patches of shrubs that provide suitable habitat until a tree canopy develops (Alvo in Gauthier and Aubry 1996; Ammon and Gilbert 2020; Desrochers et al. 2012).

In Ontario in the Canadian Shield, there was no difference in its abundance in early and mid-successional stages of clear-cuts compared with similar stages after fire. There was no difference in its abundance in mid-successional and mature forests, but it was significantly more abundant in early successional forests than in mature forests (Zimmerling et al. 2017).

In Alberta, the Wilson's Warbler was significantly more abundant near well pads than in adjacent forest interior. There were no significant differences in its abundance near seismic lines and pipelines and adjacent forest interior (Bayne et al. 2016).

Factors that change the density of shrubs may affect the Wilson's Warbler abundance. On Anticosti Island, browsing by white-tailed deer reduced shrub density and shrub-dependent birds once deer densities exceeded 7.5 per km^2. In the west, cattle browsing in woodlands and riparian habitat has adverse effects on the Wilson's Warbler (Ammon and Gilbert 2020; Cardinal et al. 2012). In Ontario, the core breeding range of the Wilson's Warbler is north of the areas of high deer density and it is unlikely that any of its habitat is grazed by cattle. Numbers of this warbler have been demonstrated to decline significantly after herbicides that target deciduous species and promote growth of conifers are sprayed (Ammon and Gilbert 2020). In Alaska, it responded favourably to high infestations of spruce beetles. In areas of high tree mortality, the canopy was opened and shrub growth increased, thereby improving habitat (Matsuoka et al. 2001). The Wilson's Warbler may benefit from insect outbreaks, tree diseases, and blowdown.

In Oregon, Stephens et al. (2015) observed no clear pattern of increases or decreases over a period of 9 years following a forest fire. The Wilson's Warbler was unaffected by the severity of the fire.

Unusually adverse weather conditions during the breeding season can affect reproductive success. In Colorado, 19% of nests containing recently hatched young were deserted during a heavy snowstorm. In 1 year in the Sierra Nevada, a hailstorm destroyed all nests (Ammon and Gilbert 2020; Stewart et al. 1977).

Near Seattle, Marzluff et al. (2007) studied habitat use by the Wilson's Warbler in relation to predator density. It was rare where crows were abundant, but most common where chipmunks and squirrels were most abundant. It was rarely able to avoid habitat patches that supported predators. Its reproductive success was low, probably due to predation.

In Colorado, nest desertion rates were higher in areas used by recreational visitors. The Wilson's Warbler was particularly sensitive to desertion during incubation. In contrast, numerous California nests were within 1 m of recreational trails and none were deserted (Ammon and Gilbert 2020).

Price (2004) concluded that the Wilson's Warbler could disappear as a breeding species from southern Ontario if the average summer temperature increased by 2°C. It is a rare and infrequent breeder in the south, so this may not be a major limiting factor. DesGranges and Morneau (2010) observed that it appeared to be correlated with cooler and wetter summers in southern Quebec and concluded that it was very sensitive to climate change.

Status

Baillie and Harrington (1937) considered the Wilson's Warbler an uncommon summer resident in parts of Thunder Bay, Sudbury, and Cochrane districts, and probably throughout the more northern portions of the province. At that time, the only confirmed breeding records were from Sudbury and Lake Abitibi. The first atlas confirmed that its breeding range extended from the Sudbury area north to Hudson Bay, with isolated records in the southern portion of the Canadian Shield. These more southerly records may have been late migrants. It apparently bred sporadically as far south as the 20°C July isotherm. It was more common in the north than in the south (Helleiner in Cadman et al. 1987). Peck and James (1998a) reported a nest on Manitoulin Island which is the most southerly confirmed breeding record. James (1991) considered the Wilson's Warbler a common summer resident across the province south to Sudbury, with summer sight records south to Algonquin Park and Ottawa. Wilson and McRae (1993) concluded that it was a very common breeding bird in the Moosonee area.

The second atlas demonstrated that there had been no changes in the distribution of the Wilson's Warbler since the first atlas. The few records of breeding evidence south of the Sudbury area were once again considered late migrants. Its probability of observation increased significantly since the first atlas province-wide and in the Boreal Forest Region and Hudson Bay Lowland. It was uncertain if this represented a true increase in numbers and infilling of its range, or greater efforts to survey difficult-to-access habitats. It was most abundant in the Hudson Bay Lowland. It was approximately 3 times more abundant there than in the Boreal Forest Region. The shrub thicket habitat that it prefers is more abundant in the Hudson Bay Lowland (McLaren in Cadman et al. 2007).

Ammon and Gilbert (2020) reported that the Wilson's Warbler increased significantly in Canada at a rate of 6.6% per year 1966-96 according to the Breeding Bird Survey (BBS). The general trend over that time includes increases in the northwestern and northeastern regions and significant

decreases in Pacific coast populations. At the end of that period, there were declines in several eastern regions, continuing declines in western populations, and a decline in the entire North American population. By the end of the 20th century, the entire population was experiencing a decline of approximately 2% per year according to the BBS (Desrochers et al. 2012; Michaud et al. 2004). The BBS is not a reliable indication of trends in breeding populations of the Wilson's Warbler. Most of its range is in areas that are not covered by this survey. There are no BBS routes in the Hudson Bay Lowland where it is most abundant in Ontario. BBS results indicate that it increased at an annual rate of 0.574% in Canada and decreased at an annual rate of 1.31% in Ontario 1970-2021. Trends for 2011-21 were an annual increase of 0.297% in Canada and an annual decrease of 2.88% in Ontario. All results were of medium reliability except that the short-term trend for Ontario was of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

In California, a peak of adult wandering occurred in the latter half of June. First broods are complete by then so adult wandering probably occurs after breeding or attempted breeding when territoriality is waning (R.M. Stewart 1973). In California, adults undertook an altitudinal moult migration after breeding. For every 1,000-m increase in elevation, recaptured birds were 2.47 times more likely to display moult (Wiegardt et al. 2017). It is uncertain if eastern populations exhibit the same wandering tendency. If so, it would occur later in the season, possibly in late July or later.

Young are unable to fly a few hours to a day after fledging. Initially young remain in the underbrush 10-20 m apart. Young may return to the nest at night for several days after fledging in Colorado. Brood division occurs after the young leave the nest. The sexes may care for equal numbers of fledglings or the female may care for more young than the male. Late-season fledglings are attended by the female only. Young can fly strongly by age 13 days and make their first foraging attempts at age 16 days. Broods have been observed being fed 25 days after they leave the nest (Ammon and Gilbert 2020) and began to leave the territory at age 32 days in California (R.M. Stewart 1973). On 4 July near Rivière-du-Loup, Quebec, 11 recently fledged young were captured together in a mist net, suggesting that birds may travel through the understorey in groups (Alvo in Gauthier and Aubry 1996).

In Minnesota, Streby et al. (2011b) captured 30 Wilson's Warblers (7 adults and 23 juveniles) during 4 postbreeding seasons in clear-cuts 2-10 years old. Netting was also conducted during 1 breeding season and a single adult was captured. In clear-cuts 5-12 years old in Quebec, Major and Desrochers (2012) captured 15 Wilson's Warblers in 2 postbreeding seasons. In California, only 3.3% of juveniles were captured in mist nets situated more than 10 m from riparian woodland, the preferred habitat (Chase et al. 1997).

MIGRATION

The Wilson's Warbler migrates nocturnally either singly or in small groups of the same or different species. At daytime stopover sites, it is often seen singly but occasionally in the company of other species. One banded in Ontario at Mitchell's Bay was recovered in Texas, having travelled in a southwestern direction. Another banded at the mouth of the Humber River was recovered in Pennsylvania and had travelled due south (Ammon and Gilbert 2020; Brewer et al. 2018; Kelly et al. 2002a; Paxton et al. 2007, 2013; Ruiz-Sánchez et al. 2015).

Males arrive before females in the spring, and this has been confirmed for the eastern subspecies in Illinois and Ontario. At Prince Edward Point, the mean capture date of males (23.0 May) was 2.1 days earlier than for females (25.1 May), a significant difference (Francis and Cooke 1986; Graber et al. 1983). The interval between arrivals of the sexes of the western subspecies is highly variable, with greatest intervals where there is a long breeding season. Over 5 years in California, males arrived before females by 30, 21, 26, 12, and 6 days. In New Mexico, males arrived an average of 5 days earlier than females. In Arizona, males arrived 9.97 days earlier than females on average and in Alaska males preceded females by 5 and 8 days at 2 different sites (Benson et al. 2006; Otahal 1995; Paxton et al. 2007; Yong et al. 1998). In California, older males appeared to arrive before yearlings (R.M. Stewart 1973). In the west, warblers that bred at southern latitudes the previous year migrated earlier in spring than those that bred further north (Paxton et al. 2007). In New Mexico, the recapture rate in spring was significantly lower for males (5.2%) than for females. The stopover duration of the sexes combined was 2.52 days in spring (Yong et al. 1998). The authors predicted that males should migrate earlier in spring, have a lower capture rate, and have a higher fat deposition rate than females. It is advantageous for males to migrate earlier and faster in spring so they can establish territories in high-quality habitats. It is better for females to arrive later on the breeding grounds because this reduces the risks of adverse weather conditions, food resources are more plentiful, and males have established territories allowing females to assess the relative qualities of territories and males. In California, there were no differences in the stopover durations of the sexes in spring. Males remained on site an average of 4.4 days (range 1-13 days) and females remained on site an average of 3.4 days (range 1-9 days; Otahal 1995). In Arizona, the average spring stopover time was 2.5 days in 1 year and 4.2 days in the second year (Paxton et al. 2008). In Arizona, Hays et al. (2018) captured spring and autumn migrants and used plasma metabolite analyses to determine refueling rates and feather stable isotope analyses to determine origins of individuals. Birds breeding in Alaska to northern British Columbia migrated approximately 6,000 km compared with 2,000 km for those breeding in California. In spring, males arrived an average of 14.3 days before females and shorter-distance migrants also arrived earlier. Later-arriving migrants had higher fat scores and refueling rates, but migration distance and sex were unrelated to body condition, refueling rate, or length of stay. Minimum length of spring stopover was 1-31 days (median 1 day). Many male short-distance migrants stopped over in spring but most females from these areas did not. Many long-distance females stopped over in spring but most long-distance males did not.

In southern and central Ontario, most spring migrants are seen in the latter half of May. Average arrival is mid-May but some may arrive in the first week of May. Most have left by the end of May with a few remaining into early June (Black and Roy 2010; Curry 2006; Fleming 1907; Keast 1980; LaForest 1993; Lancaster et al. 2004; Mills 1981; Tozer 2012; Weir 2008).

In autumn, there is no difference in the timing of migration by the sexes, but juveniles migrate earlier in most locations than adults. In Alaska, juveniles preceded adults by 6, 10, 11, and 13 days at 4 sites. Juveniles arrived 9 days earlier than adults in southwestern Idaho, and young started migration earlier than adults in Virginia and West Virginia. In New Mexico and South Dakota, there were no significant differences in the migration timing of the age classes. Juveniles initiate migration earlier because they do not have to moult, unlike the adults. The differential timing of migration may diminish southward because juveniles migrate slower, remaining longer at stopovers due to their

lower efficiency in foraging and because they may be relegated to inferior habitat. In New Mexico, the recapture rate for adults (7.6%) tended to be lower than for juveniles (9.7%), but not significantly. In autumn, adults had a significantly shorter stopover duration of 2.20 days compared with 2.42 days for juveniles. This suggested that juveniles migrated at a slower rate, and juveniles were in poorer condition than adults with lower fat scores and shorter, more rounded wings, thereby consuming more energy in flight. In Arizona, males tended to arrive later than females but the difference was not significant. Longer-distance migrants and males had higher refueling rates than shorter-distance migrants and females. Stopover durations were shorter in autumn than in spring (range 1-4 days, median 1 day; Benson et al. 2006; Dean et al. 2004; Otahal 1995; Stewart 1986).

Wilson and McRae (1993) observed Wilson's Warblers on 21 and 28 August at Shagamu that were probably autumn migrants. Average arrival in the southern Shield is mid-August, and all pass through by the end of September (Mills 1981; Tozer 2012). In the south, most pass through from late August to early September, with the earliest arrivals in early August. Most leave by the end of September with rare records to early November (Black and Roy 2010; Curry 2006; Fleming 1907; Keast 1980; LaForest 1993; Lancaster et al. 2004; Weir 2008). In the Hamilton area, 1 bird was observed from 26 December to 7 January where it frequented a small stream in a deeply incised valley. There was a severe storm with snow and freezing rain on the last day it was observed (Curry 2006).

During migration, the Wilson's Warbler continues to prefer shrubby areas, although it may occur in lesser numbers in forested areas (particularly those dominated by deciduous trees) and other areas where woody vegetation occurs. Other areas may include suburban habitats, farmsteads and rural residential areas, shrubby roadsides, and urban parks (Ammon and Gilbert 2020; Chapman 1907; Tyler in Bent 1953). In Algonquin Park, it is seen most frequently in dense thickets of willow or alder (MacLulich 1938; Tozer 2012). During spring migration on islands in the Gulf of Maine, it was significantly more abundant on an island dominated by deciduous shrubs and saplings than on a treed island. In autumn, it was significantly more abundant on the same island in 1 of 2 years (Suomala et al. 2010). During autumn migration in Pennsylvania, it was equally abundant in forest edges, shrub-sapling-stage forests, forest-agricultural edges, and suburban forests, but was absent in forest interior and pole-stage forests (Rodewald and Brittingham 2002). In Illinois, it was most abundant in shrub and forest edge habitat, especially in hawthorn meadows, and also occurred in willows. It occurred in lower numbers in bottomland and upland forests (Graber et al. 1983). Tyler (in Bent 1953) stated that the eastern subspecies was more likely to occur in dry habitats in autumn, such as oaks and pines growing on high ground.

The western subspecies appear to be even more reliant upon shrub habitat during migration. In the Yukon, it inhabits deciduous shrubs and trees such as balsam poplar and trembling aspen, and is most common in shrubby wetlands (Sinclair et al. 2003). In British Columbia, it frequents thickets and linear stands of shrubs and low trees at edges of lakes, beaver ponds, stream banks, sloughs, beaches, shoreline spits, airports, sewage lagoons, cleared fields, and hydro rights-of-way. In boreal forests, it occurs mostly in mixed woods and shrubby edges of willow, white birch, and alder in spring. In autumn, it occurs at edges of bogs and fens, in willow hedgerows, and wet areas where willows and other shrubs predominate. In British Columbia, it was significantly more abundant in riparian shrub areas than in forests in autumn. It was more abundant in riparian areas

in spring, but not significantly (Campbell et al. 2001; Wiebe and Martin 1998). During autumn migration in South Dakota, the Wilson's Warbler was more abundant in a 3.5-ha woodlot than in a contiguously forested riparian corridor (Dean et al. 2004).

Three studies in the southwest determined habitat preferences of migrating Wilson's Warblers. In New Mexico, it was more common in willows in spring than autumn but more common in willows than in any other habitat during both migration periods (Kelly et al. 2000). In New Mexico, capture rates differed among habitats in spring when 72% of all birds were captured in willows. In spring, the capture rate of females was highest in willow and saltcedar habitats. Males were more common in the other 4 habitat types: agricultural field–edge, cottonwood with a native understorey, cottonwood with a Russian olive understorey, and cottonwood with a saltcedar understorey. In autumn, there were significant differences in habitat usage by sex and age classes, although there was a more even distribution of birds among habitats. Overall capture rate was highest in agricultural field–edge, followed by cottonwood with a Russian olive understorey, and willows. The capture rate of adults was proportionally higher in willows and cottonwood with saltcedar and native understories than for juveniles. Juveniles were more abundant in agricultural field–edge, cottonwood with a Russian olive understorey, and saltcedar. Capture rates differed significantly among the habitats for the sexes, but these differences were small compared with the variation among age classes within a given habitat. The rate of mass gain varied among habitats, with birds in agricultural field–edge exhibiting the lowest rate of mass gain. Birds in this habitat tended to have longer stopovers (3.16 compared with 2.16 days). In spring, 88% of birds were recaptured in the same habitat compared with 53% in autumn; the difference between sexes was not significant. The seasonal shift in habitat preferences may have been due to changes in resource availability. It was more abundant in willows in spring because this plant supports more arthropods. Habitat switching was more frequent in autumn consistent with juveniles being forced to leave more productive willow habitat where they initially tried to settle (Yong et al. 1998). In Arizona, Paxton et al. (2008) studied movement patterns and habitat usage of spring migrants at a stopover site. The mean rate of movement was 61 m per hour (range 11-173 m) in 1 year and 102 m (range 11-720 m) in the next year. The rate of movement of yearlings was 55% greater than that of adults. The linear movement from sunrise to sunset decreased by 32% each successive day that a bird remained at the site. On average, birds moved 332 m (range 0-6,341 m) from their release point in the morning to their nocturnal roost. With time, movements became more aggregated within localized areas of use. All exploration by birds was restricted to small areas, primarily less than 2 km in diameter within the overall landscape, and they never left riparian habitat. The general location where a bird landed was critical in determining the resources available to it. If food resources are inadequate, the bird may depart rather than extend local exploration over several days. Initially, 84% of observations were in native vegetation when it was flowering, but numbers in native vegetation declined by 7% a day and only 24% of observations were in native vegetation once nonnative vegetation began flowering. As birds gained more information about the distribution of resources, they settled into a high-quality microsite. Flowering phenology strongly influenced the location of warblers such that additional exploration was required later in the season to locate sites dominated by nonnative shrubs.

Recapture data indicate that at least some birds use the same stopover sites in multiple years (Ammon and Gilbert 2020).

During migration, the Wilson's Warbler feeds mostly in shrubs and short deciduous trees, often in willows near water. During autumn migration at Prince Edward Point, foraging occurred 3-6.6 m from the ground. Overall, it has been reported feeding at heights of 0.5-7 m during migration. At Prince Edward Point, 35% of foraging was on outer leaves, 18% on inner branches, 12% on trunks, and 35% on sapling foliage. Foraging was not observed on twigs and inner leaves, outer branches, sapling branches, low shrubs, or on the ground or in the air (Ammon and Gilbert 2020; Keast 1980; Tyler in Bent 1953).

A study of 52 stomachs of the western subspecies revealed that 7% of the diet consisted of fruit pulp that was eaten predominantly during autumn migration in September and October. The Wilson's Warbler may also eat honeydew produced by scale insects. In the Yukon, aphid outbreaks occasionally attract large numbers of autumn migrants (Ammon and Gilbert 2020; Bent 1953; Sinclair et al. 2003).

During autumn migration in New Mexico, the Wilson's Warbler responded positively to food abundance. Its abundance was significantly correlated with abundance of hymenopterans, flies, and beetles captured in traps, but not with abundance of soft-winged bugs. Migrants passing through during peak migration times would be more likely to encounter depleted food resources and have more difficulty in refuelling than those migrating before or after the peak. Depletion of food resources could contribute to early passage of adults relative to juveniles and the use of inferior habitats by juveniles (Kelly et al. 2002b).

In Pennsylvania, an outbreak by the viburnum leaf beetle resulted in almost complete mortality of the southern arrowwood, which was formerly the third most abundant shrub species. After the infestation, the number of spring migrating Wilson's Warblers declined significantly (Smith and Hatch 2017).

During a dry year in Arizona, there were increased daily movements of birds and the minimum stopover time was twice as long as in a year with normal precipitation rates. Drought conditions may reduce arthropod abundance, requiring warblers to travel further daily to obtain sufficient food. It also takes longer to refuel when it is dry (Paxton et al. 2008). An unusually cold spring in Arizona appeared to lower the survival rate of migrants (Ammon and Gilbert 2020).

The Wilson's Warbler collides with tall structures such as television towers and hydro transmission towers during migration. Mortality associated with collisions does not appear to be unusually high. Seventy-eight were killed at the Lennox generating station chimneys 1972-82 (Ammon and Gilbert 2020; Graber et al. 1999; Leighton et al. 2002; Weir 2008).

Band recoveries suggest that domestic cats may cause significant mortality in migration stopover sites (Ammon and Gilbert 2020).

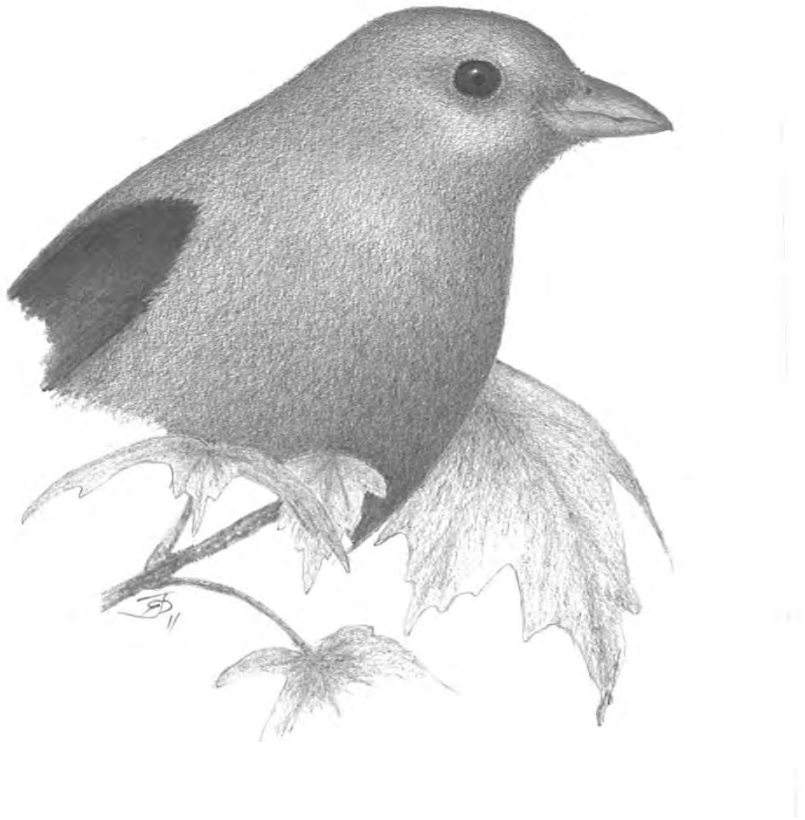
At Delta Marsh, Murphy-Klassen et al. (2005) analyzed the first date of spring arrival 1939- 2001. Arrival date was significantly correlated with temperature. The Wilson's Warbler arrived significantly earlier in the later years, which were associated with increasing temperatures. In New York, Zelt et

al. (2017) compared spring arrival dates, autumn departure dates, and length of the breeding season for 1888-1939 and 1967-2012. There was little climate change during the first period but significant warming occurred in the second period. The Wilson's Warbler arrived significantly earlier, departed significantly later, and had a significantly longer breeding season during the second period.

James (1991) considered the Wilson's Warbler a common migrant, but it is an uncommon migrant in Elgin County, Niagara Region, and Algonquin Park (Black and Roy 2010; Lancaster et al. 2004; Tozer 2012). At Long Point Bird Observatory, captures of the Wilson's Warbler decreased significantly at a rate of 3.2% per year 1961-88. Trends by period included: 1961-70, −5.9%; 1970-79, +9.1%; and 1979-88, −5.3%. It showed a similar but less marked response as the spruce budworm specialists, suggesting that it may be affected by outbreaks to some degree (Hussell et al. 1992).

Scarlet Tanager

Piranga olivacea

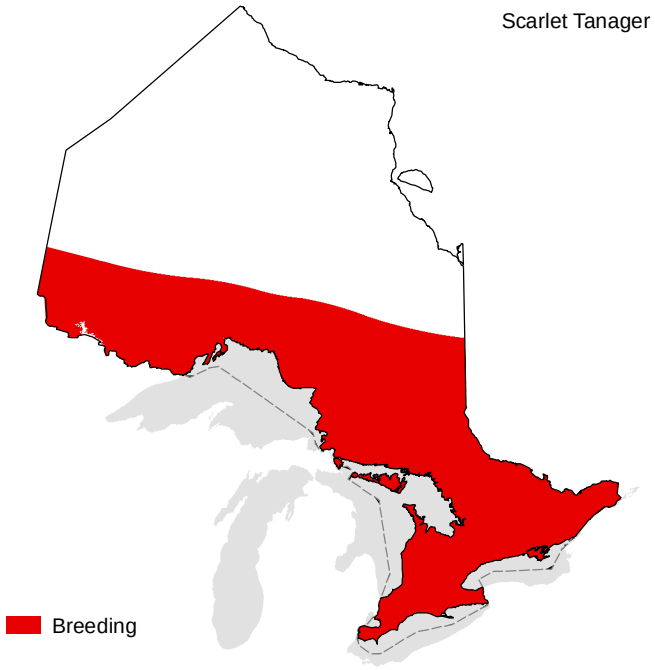


BREEDING SEASON

Habitat Requirements

Ontario Scarlet Tanager nests were near the edge of, or within, deciduous and mixed forests. It preferred deciduous forests. Equal numbers of nests were in closed-canopy woods and near open areas such as fields, roads, and water. Two nests were in a coniferous plantation near deciduous forest, one was in a spruce–sphagnum moss bog, and another was in an open sedge meadow (Peck and James 1987).

The Scarlet Tanager is sparsely distributed in the Boreal Forest Region of Ontario. Erskine (1977) considered it more characteristic of the transitional sugar maple–beech forests of eastern Canada. In the boreal forest, he reported it in pure poplar or white birch stands and poplar stands mixed with balsam fir. North of Lake Nipigon, it nested in tall poplar stands but not in those dominated by black spruce and balsam fir (Sanders 1970). In the Clay Belt, Welsh and Lougheed (1996) found it breeding in only 1 stand dominated by white spruce and balsam fir with minor inclusions of white cedar and



black spruce. The site was moderately rich in nutrients with wet soils. Venier et al. (2009) reported it in low densities in mature (60-223 years) mixed stands near Manitouwadge.

In jack pine stands near Gogama, the Scarlet Tanager was associated only with taller deciduous trees in mixed stands (James and Peck 1995a). In old-growth and mature white pine stands in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, it was never numerous because it was at the northern extent of its range. It was more abundant in old-growth stands, probably because of the higher proportion of deciduous growth (Kirk et al. 2012). In Algonquin Park, it was fairly common in maple stands but uncommon elsewhere (MacLulich 1938). Tozer (2012) concluded that it preferred mature hardwood stands with a small component of hemlock or white pine. It was infrequent in shelterwood cuts in Algonquin Park white pine stands (Kingsley and Nol 1999). Also in the park, Martin (1960) considered the Scarlet Tanager characteristic of deciduous forests but reported it in very low density in a black spruce–white cedar stand. It occurred in northern hardwoods, poplar–white birch stands, and balsam fir–spruce stands mixed with hardwoods. In hardwoods, it occurred at heights of 3-30 m, from the shrub layer to the top of the canopy. It ranged 12 m higher than any other species.

In Durham Region in the off-Shield portion of the Great Lakes–St. Lawrence Forest Region, the Scarlet Tanager occurred in open deciduous forests with standing water, a mature pine plantation with a remnant sugar maple–red oak forest, and mature sugar maple–oak and sugar maple–beech forests (Speirs and Orenstein 1975).

South of the Shield in Ontario, the Scarlet Tanager was positively correlated with the amount of forest 100 m from edge, woodlot size, the amount of forest cover within 2 km, and the amount of regional forest cover. Only the relationship with forest size was significant (Austen et al. 2001). It usually occurred only in larger woodlots in Elgin County (Lancaster et al. 2004).

Throughout its range, the Scarlet Tanager nests mostly in deciduous and mixed forests, particularly those containing hemlock or white pine. In many areas, it highly prefers oak stands over other deciduous species, but it commonly nests in sugar maple and beech forests. In more northern areas, it frequently nests in stands dominated by poplars or white birch, often mixed with spruce, hemlock, or balsam fir. In Virginia and Michigan, it preferred oak and mixed oak-pine stands. Highest densities in Quebec occur in red oak stands. In North Dakota, highest densities occurred in bur oak–green ash stands. It occurs in both upland and lowland stands, but is most prevalent in upland forests (Beals 1960; Bushman and Therres 1988; Faanes and Andrew 1983; Lanoue and Gauthier in

Gauthier and Aubry 1996; Létourneau in Robert et al. 2019; Mossman 1988; Mossman and Hoffman 1989; Mowbray 2020; Shugart and James 1973; Temple et al. 1979; Vega Rivera et al. 2003; Walley 1989b). Less frequently, it nests in other habitats such as extensive plantings of shade trees in suburban areas, parks, and cemeteries; strip-cuts and clear-cuts; pine and oak barrens; orchards; pastures invaded by red cedar; and coniferous plantations (Bielefeldt and Rosenfield 1994; Falardeau et al. 1999; Mossman et al. 1991; Mowbray 2020; Streby et al. 2011b; Tyler in Bent 1958).

Several studies examined habitat of the Scarlet Tanager at the landscape scale. In the eastern United States, 28% of its detections on Breeding Bird Survey (BBS) routes were in fragmented landscapes (Donovan and Flather 2002). Villard et al. (1992, 1995) determined that it acted as a metapopulation in the Ottawa area. They studied 70 woodlots within an area of 125 km^2. The total number of pairs within the study area remained constant over 2 years, but the individual woodlots that it occupied varied. Local extinctions and recolonizations occurred within woodlots, and this occurred in woodlots that were larger than those that consistently supported no tanagers. Its presence in a woodlot was dependent upon patch size, but patch isolation might also be an important factor in determining whether a woodlot is occupied. In Quebec, it occurs mostly in the southern portion of the province in regions where the forest is dominated by sugar maple. In more northern areas, it is associated with the few deciduous and mixed stands. It is mostly absent in the Boreal Forest Region and at elevations above 500 m (Lanoue and Gauthier in Gauthier and Aubry 1996; Létourneau in Robert et al. 2019). In Pennsylvania, it was associated with oak-hickory-maple stands. It occurred in large forest patches in less fragmented landscapes, with 40% forest cover rather than 15% (Keller and Yahner 2007). In North Dakota, it preferred landscapes that were 59-75% forested, with no areas having more than 75% forest cover. In New York, it preferred areas that were 81-100% forested (Cunningham and Johnson 2019).

Although the Scarlet Tanager appears to prefer mature forests, it nests in a wide range of successional stages. Mowbray (2020) concluded that it preferred tall deciduous trees in mature stands. DeGraaf and Chadwick (1987) determined that it occurred predominantly in sawtimber-size northern hardwoods and red maple stands, but it also occurred in other successional stages. Preferred stands had intermediate-sized trees and density and intermediate values of shrub density. In mesic forests in Wisconsin, it occurred predominantly in sawtimber-size stands (Hoffman 1989a). In Maryland, it occurred from early successional to mature stands, but was most abundant in mature stands (Bushman and Therres 1988). In northeastern upland hardwoods, Noon et al. (1979) reported it in 78% of mature undisturbed forests and 43% of disturbed and early successional forests. In northeastern poplar–white birch stands, Back (1979) reported it in sapling-pole-stage stands but not in seedling-stage or mature forests. In northeastern pine stands, it occurred in mature stands and was not documented in seedling- or pole-stage forests (Capen 1979). In Pennsylvania, Haney (1989) reported that it occurred in 100% of old-growth mixed forests, 86.8% of forests statewide, and 90.3% of forests in the Appalachian Plateau. He considered it to have a neutral old-growth affinity. In New Jersey old-field successional habitats, it was absent in 10- and 20-year-old fields and present in a 40-year-old field. Borders of the occupied field were heavily wooded with red maple, pin oak, and red cedar. The centre of the field supported dense shrub growth. This field was surrounded by forest on 3 sides (Suthers 1989); otherwise, the tanager would probably have been absent. In Vermont, Lent and Capen (1995) determined that some territories were exclusively in forest but a few included

areas of small clear-cuts. Overall, it tended to avoid clear-cuts and was associated with increasing successional age, few conifers, and few dead trees. In Minnesota, Streby et al. (2011b) found 2 nests in clear-cuts, with the youngest forest 7 years old.

Several studies examined microhabitat requirements of the Scarlet Tanager. In Virginia, it used hardwood stands more than their availability, tulip tree forests less than their availability, and mixed oak and black locust forests in proportion to their availability. Sites used for breeding had more trees larger than 46 cm diameter at breast height (DBH) and more trees characteristic of mature habitats, such as bitternut hickory, shagbark hickory, pignut hickory, mockernut hickory, red oak, white oak, chestnut oak, black oak, tulip tree, beech, and basswood. Forty-eight tree species occurred within radiotracked locations. Seventy percent of these were hickories, oaks, flowering dogwood, red elm, red maple, and tulip tree. The most abundant species in both breeding and postbreeding areas were hickories, red elm, and flowering dogwood. Pignut hickory was the only species found in breeding areas but not in postbreeding areas (Vega Rivera et al. 2003). In New Jersey, it was more abundant in oak-pine forests than hardwood swamps, but not significantly (Rich et al. 1994). In Maryland, it was negatively correlated with hemlock bottomland forests and was associated with upland hardwoods (Gates and Giffen 1991). In southern Ontario, it was positively correlated with total basal area (BA), forest age and type, and medium- to large-sized white pines. It was negatively correlated with the BA of coniferous species (Kirk et al. 2012). In Wisconsin, the Scarlet Tanager was most common in xeric stands. It appeared to prefer more pioneer woods, but only if they were sufficiently large (Bond 1957). In Vermont, it was associated with hophornbeam, sugar maple, beech, and red oak; moderate amounts of red maple; and limited cover by poplars (Lent and Capen 1988). In Maryland, its density was positively correlated with shrub diversity and negatively correlated with the abundance of pines (Lynch 1987). In New Hampshire and Maine, it was significantly associated with cover type and structure. It was associated predominantly with white pine and swamp hardwoods. The pine stands contained considerable inclusions of deciduous species, particularly in the 2-10-cm size class, so this may have explained its preference for these stands. It also occurred in white birch, northern hardwoods, balsam fir, and hemlock stands. It was absent in poplar and balsam fir–spruce stands. Its abundance was positively correlated with conifers 2-10 cm DBH and foliage volume of deciduous trees larger than 10 cm DBH. It was negatively correlated with canopy closure, deciduous trees larger than 10 cm DBH, foliage volume of trees 2-10 cm DBH, and foliage volume of conifers in all size classes (DeGraaf et al. 1998). In isolated Illinois woodlots, it was negatively correlated with shrubby vegetation (Blake and Karr 1987). In Indiana, it was affected by tree height, being most abundant in trees 16 m tall, less abundant in trees 20-24 m tall, and uncommon in trees 0-12 m tall. It was most abundant where tree densities were 400-600 trees per ha (Grundel and Pavlovic 2007a). Bushman and Therres (1988) reported that it tolerated a wide range of overstorey cover, but preferred a closed canopy. It also preferred a dense understorey and scant ground cover. In Virginia, BA of occupied areas averaged 11 m^2 per ha and the population increased with the BA of trees 19-35 cm DBH. In the mid-Atlantic states, it was positively correlated with slope and percent forest cover within 2 km. It was negatively correlated with the number of trees larger than 3 cm DBH, moisture gradient, and foliage density between 2 and 3 m (Robbins et al. 1989). In Connecticut, it was more abundant when hemlock was less dominant (Buchanan et al. 2016). In Vermont, its mean habitat variables were 30.8% ground cover by green vegetation, 10.0% ground cover by slash, 79.3%

canopy closure, 22.9 m canopy height, 11.7 m canopy depth, 17.3 m^2 per ha BA of deciduous species, 5.0 m^2 per ha BA of coniferous species, 14.1 cm DBH of deciduous species, and 17.3 cm DBH of coniferous species. It was associated with older deciduous stands with a moderately dense understorey. It was in the closed-canopy deciduous association. This guild occurred in beech–yellow birch–sugar maple stands with varying amounts of balsam fir, red spruce, and white pine (Thompson and Capen 1988). In Tennessee, it occurred in deciduous forests with dense canopies. It was significantly correlated with trees larger than 22.8 cm DBH (Anderson and Shugart 1974). In New Jersey, 68% of nests occurred in trees larger than 22.4 cm DBH. In Michigan, its probability of occurrence was greater than 94% in forested areas with a moderate density of large trees and low density of small trees. In Wisconsin, forest size, the openness of the canopy, and density of the shrub layer accounted for 77% of variation in its abundance. Where the Scarlet Tanager is sympatric with the Summer Tanager, the Scarlet Tanager prefers sites with significantly higher canopies, denser canopy cover, a greater variety of tree species, and a higher density of trees larger than 22.4 cm DBH. Where the 2 tanagers occur together, Scarlet Tanager territories have a higher percent canopy cover and more tree species than where the Summer Tanager is absent. In Missouri, 90% of Scarlet Tanager territories were on slopes (68% for Summer Tanagers). Where both species occurred on slopes, the Scarlet Tanager preferred steeper slopes (Mowbray 2020).

The Scarlet Tanager is occasionally classified as a forest-interior species, mostly by authors that did not specifically test where it nested in relation to edge (Askins et al. 1987; Freemark and Collins 1992). Studies that examined where it nests have found no evidence of edge avoidance. In Ontario, it commonly nests at or near forest edges and occasionally even in open habitats (Peck and James 1987). Streby et al. (2011b) reported it nesting in young clear-cuts. In New Hampshire, King et al. (1997) surveyed transects 50 m into clear-cuts, across the border between clear-cuts and forest, and 350 m into forest interior. Areas within 100 m of the clear-cut were classed as edge plots and those further from edge were classed as interior plots. There was no significant difference in the number of territories in edge and interior plots. The distribution of territories differed significantly from the distribution of simulated random territories but was not skewed toward either edge or interior. In Tennessee, Kroodsma (1984) studied the distribution of tanager territories in relation to edge created by a hydro corridor through the forest. There were 29 territories 0-268 m from edge and 6 268-488 m from edge. It did not exhibit any potential edge effect. In Alabama, it increased along a mountain road after it was daylighted (Bushman and Therres 1988). In Manitoba, Walley (1989b) reported a nest at the edge of an aspen forest and another at the edge of a 0.4-ha grassy opening in the forest.

With 1 exception, all studies concluded that the Scarlet Tanager is an area-sensitive species. The exception was in New Hampshire and Maine where DeGraaf et al. (1998) found that it was not correlated with woodlot size. This area is heavily forested, and it is likely that area sensitivity breaks down in landscapes dominated by forest cover. Other studies demonstrated that the amount of forest cover within 2 km can affect its abundance and the minimum size of forest that it will inhabit (Robbins et al. 1989). In the Ottawa area, the mean size of woodlots it occurred in was 18.8 ha (Villard et al. 1992). Because of the interrelationships among forest size, proximity to the nearest forest patch, and amount of forest in the landscape, this figure cannot be used as an estimate of the tanager's forest size requirements across Ontario. In the Canadian Shield and Niagara Escarpment where forest

cover is 80% or greater, it is likely that forests only need to be as large as a territory size to support it. In the extreme southwestern portion of the province where forest cover may be as low as 3% and woodlots are often isolated, it is probable that much larger forests are required to support the tanager than in the Ottawa area. Further research is required to determine the degree of its area sensitivity in different regions of the province. In Waterloo Region, Friesen et al. (1985) did not find it in 3-7-ha woodlots, but it was present in those 8-15 and 20-50 ha in size. Because of the complex relationships among forest size, isolation, and amount of regional forest cover, there are widely varying estimates of the minimum forest size that will support breeding Scarlet Tanagers. In the Appalachians, it has been predicted that it will occur in every size of forests in landscapes that are at least 50% forested. In areas that are 30% forested, patches as small as 10 ha may provide moderately suitable habitat (Vega Rivera et al. 2003). In New York, no tanagers were detected in forests smaller than 10 ha (Roberts and Norment 1999). In New Jersey, it was found only in woodlots larger than 3 ha, and 10-12 ha was considered the minimum to support a viable population (Mowbray 2020). In Wisconsin, Bond (1957) observed it in woodlots as small as 3.2 ha. It was least common in small woodlots and was 34% more common in larger woodlots. Its frequency of occurrence was 20.9% in forests 6.1-14.2 ha, 26.3% in forests 16.2-32.4 ha, and 28.6% in forests larger than 32.4 ha. Lynch (1987) also found that its probability of occurrence increased with forest size: 40% at 10 ha, 70% at 100 ha, 80% at 1,000 ha, and 90% at 3,200 ha. In Maryland, Robbins (1979) estimated that 100 ha were required to support a viable population and that 10 ha was the minimum size of forest it would occupy. In western Maryland, Bushman and Therres (1988) reported that its highest frequency of occurrence occurred in woodlots 38 ha and larger. It was documented in woodlots as small as 1-14 ha and 3-7 ha by other studies. It often breeds successfully in smaller woodlots, probably because the nest tends to be high in the canopy. In the mid-Atlantic states, the area of woodland where its probability of detection was highest was 3,200 ha and larger. Its probability of detection was reduced to 50% of the maximum at 12 ha. The 3 smallest woodlots in which it was documented were 2.1, 3.6, and 4.6 ha (Robbins et al. 1989). In Illinois, Blake and Karr (1987) inventoried isolated woodlots 1.8-600 ha. They found the Scarlet Tanager in forests 16 ha and larger. Askins et al. (1987) considered it area sensitive in Connecticut but did not provide any information on its forest size requirements. In Maryland and Delaware, its probability of detection increased significantly with increasing forest widths: 17% in 50-m wide forests, 20% in 100-m wide, 29% in 200-m wide, 39% in 300-m wide, and 87% in 800-m wide forests (Keller et al. 1993).

Ontario nests were in trees and saplings, with deciduous (12 species, 63.2% of nests) favoured over coniferous (5 species, 36.8% of nests) species. The species most frequently selected were maples (15 nests), hemlock (13 nests), beech (10 nests), birches (4 nests), oaks (4 nests), elms (4 nests), hawthorns (4 nests), pines (4 nests), and spruces (4 nests). The Scarlet Tanager selected mature trees more often than saplings for nesting. Nests were almost always on horizontal limbs out from the trunk, but 3 nests were at the trunk. Distances from the trunk were 0.6-6 m, mostly 1.5-3 m. Nests were usually at crotches or forks of the supporting limb or otherwise secured by upslanting branchlets. One nest was in a tangle of grapevines. Nests were 1.8-20 m from the ground, with most 4.3-9.8 m up. Nests were often concealed by overhanging branches and dense foliage (Peck and James 1987, 1998b). In Muskoka and Parry Sound districts, the Scarlet Tanager has nested in spruce, white pine, hemlock, yellow birch, and maple at heights of 4.9-12.2 m (Mills 1981).

Nests elsewhere are in saplings or trees, with deciduous species preferred over conifers. In Michigan, 50% of nests were in white oak and 35% were in black oak. Oaks are preferred in Maryland but it also nests in maples, hemlock, and tulip trees. Elsewhere, nests have been reported in bur oak, scarlet oak, beech, ash, apple, dogwood, and red cedar. Nests are usually among a cluster of leaves, often above an open area that is used by the male during courtship. Most are on a horizontal branch well out from the trunk with an unobstructed view of the ground and open flyways from adjacent trees. They are typically at a crotch or juncture of more than 2 smaller branches. Nests have been reported 1.5-21 m from the ground. Mean nest heights were 9.0 m in Michigan, 7.1 m in Tennessee, 7.8 m in Maryland, and 10.0 m in Vermont. Michigan nests averaged 2.8 m from the trunk and 1.9 m from the tip of the branch. The tanager selected mature trees as nest sites more frequently than saplings. Average nest-tree diameter in Michigan was 30 cm (Mowbray 2020; Tyler in Bent 1958; Walley 1989b).

The Scarlet Tanager is aggressively territorial, consequently seldom occurring in high densities. Males defend mating, nesting, and foraging areas. The foraging area is the largest but the nesting area is most vigorously defended. Once territories are established, territorial disputes and aggressive interactions decline abruptly. The breakdown of territoriality coincides with dispersal from the area, at least 2 weeks after the young fledge. It also countersings in response to Summer Tanager songs and the 2 species establish non-overlapping territories in areas of sympatry. Territory size varies with forest size, location, and vegetation type. Territory sizes were 0.8-2.4 ha in mixed hardwoods in Missouri and 2.5 ha in mixed oak woodlands in Wisconsin (Mowbray 2020). In New York, male territory sizes did not differ among forest-size classes in 2 years. Territory sizes were 6.7 and 7.6 ha in forests 10-50 ha, 6.13 and 7.19 ha in forests 50-150 ha, and 6.36 and 7.39 ha in forests larger than 1,000 ha (Roberts and Norment 1999). Vega Rivera et al. (2003) radiotracked Scarlet Tanagers in Virginia and determined that there were 2 groups of birds: those that kept the same home range during the breeding and postbreeding seasons and those that established different home ranges during the postfledging period. Some of the latter group moved back and forth between the breeding and postbreeding home ranges but most remained in the postbreeding home range. For the group that remained in the same area, average home range was 5.6 ha with a core area (where 50% of detections occurred) of 0.72 ha. For birds that switched home ranges during the season, the breeding season home range averaged 5.8 ha and the core area averaged 0.93 ha. Mean home range size of males that maintained a single home range was 6.7 ha with a core area of 0.95 ha. Results from 1 female were not included in the mean home range sizes because she moved over a large area and may not have been mated. Her home range size was 46.6 ha and her core area was 3.2 ha. In Pennsylvania, territory size of birds with red elderberry present was similar before (0.64 ha) and after (0.94 ha) the fruits ripened (Stutchbury et al. 2005a). In Quebec, territories were 0.9-1.2 ha in mature hemlock and sugar maple stands and 0.80-3.42 ha in forests of unidentified composition (Lanoue and Gauthier in Gauthier and Aubry 1996).

No information is available on natal philopatry. The only information on adult site fidelity is from Illinois where Robinson (1992) reported that 2 of 4 adults (50.0%) returned to the same territory in the following year.

Limiting Factors

Eggs have been found in Ontario nests from the last week of May to mid-July, with most present in the first half of June (Peck and James 1998b). In Algonquin Park, nests are under construction from late May to mid-June, eggs are present throughout June, nestlings occur from late June to mid-July, and dependent fledglings have been observed from late July to late August (Tozer 2012).

Males establish territories immediately upon arrival at the breeding area. Courtship and mating is completed within a week of the arrival of females and nest building begins immediately. The female selects the nest site, often above an opening that was used by the male during courtship. Most nests are built in 3-4 days (range 2-7 days). Egg laying begins within 2 days of nest completion and 1 egg is laid per day. Incubation is initiated when the last egg is laid. The incubation period is 12-14 days. The nestling period is 9-15 days, with most young leaving at age 9 or 10 days and others on days 11 or 12 (Klatt et al. 2008; Mowbray 2020; Prescott 1964; Tyler in Bent 1958).

A single brood is typically raised. Egg dates for Ontario are indicative of a single brood. Second broods have been reported but the incidence of this is unknown. It is probable that the Scarlet Tanager lays a replacement clutch if the first one fails, but this has not been confirmed. Clutches of 3-4 eggs were reported in Ontario (mode 4 eggs, mean 3.78 eggs). Clutches of 2-6 eggs have been reported elsewhere, with 4-egg clutches most common. Mean clutch sizes include 3.8 eggs in New York and Tennessee, 3.1 eggs in Maryland, 4.1 eggs in Michigan before 15 June (range 3-6 eggs) and 2.6 eggs for later nests with a range of 2-6 eggs (Klatt et al. 2008; Peck and James 1998b; Mowbray 2020; Tyler in Bent 1958).

Both sexes are capable of breeding when they are 1 year old but it is unknown what proportion of birds do. In Virginia, 1 female of unknown age was apparently unmated and 4 yearling males appeared to be unmated. Three of these moved considerable distances but the other remained within a fairly restricted range. In New York, many males in smaller forests were yearlings that were less likely to attract a female. In Pennsylvania, 3 of 9 unpaired males (33.3%) acquired a mate midway through the breeding season, probably due to females switching territories (Fraser and Stutchbury 2004; Mowbray 2020; Roberts and Norment 1999; Vega Rivera et al. 2003).

The Scarlet Tanager is presumed to be monogamous but females will mate with a second male if the first one disappears or dies. Pair bonds are usually retained through the breeding season until the young disperse. There are no records of members of a pair remating in a subsequent year, but limited information is available (Fraser and Stutchbury 2004; Mowbray 2020). Extra-pair copulations appear to be a common mating strategy. In Pennsylvania, 5 of 17 broods (29.4%) contained extra-pair young and 9 of 54 nestlings (16.7%) were the result of extra-pair copulations. Paired males left their territories an average of 0.2 time per hour and spent 4.7% of their time off-territory, presumably seeking extra-pair copulations. Pair members stay close together, possibly in an attempt to reduce the likelihood of cuckoldry. During nest building and egg laying, pairs spent an average of 33.1% of their time within 3 m of each other. This increased to 61% of the time during incubation (Fraser and Stutchbury 2004; Klatt et al. 2008). No evidence of intraspecific nest parasitism has been observed (Mowbray 2020).

Numerous studies described the foraging behaviour of the Scarlet Tanager. It forages on insects, other invertebrates, and fruit. It captures insects on the surface of leaves, flowers, fruit, and bark;

sallies from a perch to catch insects; and occasionally captures prey on the ground. It forages in trees and shrubs for a variety of fruits. It climbs vertically on tree trunks and probes for insects. In spring, it may follow plows to capture earthworms, grubs, ants, and ground beetles. On the ground, it walks through grass and dead leaves and occasionally probes for grubs and worms in lawns. It takes fruit by reaching and plucking or by hovering and plucking individual fruits; it also eats tender buds. It captures adult bees, wasps, and hornets by hawking. Occasionally, it visits bird feeders and it is possible that it eats nectar (Mowbray 2020; Tyler in Bent 1958). Most foraging occurs within forested habitat, but it may feed in open areas during cold, wet, spring weather. During such a period in New Hampshire and Vermont, tanagers left their typical forest habitat and appeared on lawns, in fields, and along roadsides. Hundreds were observed along highways on the gravel shoulders, adjacent mowed grass, and on guardrails. Elsewhere, they were reported hawking insects over a lake and falling into the water, too weak to return to shore; others landed on boats. They readily accepted food when it was offered to them. This foraging behaviour appeared to be a response to the reduced availability of aerial insects in its typical habitat as a result of the weather (Zumeta and Holmes 1978). Stutchbury et al. (2005a) reported it foraging on the fruits of red elderberry in Pennsylvania. It accounted for 45.3% of all bird visits to elderberries. During the fruiting period, males spent significantly more time (12.8%) within 25 m of elderberries than during the pre-fruiting period (4.0%). There was a strong but nonsignificant trend for males to shift their home ranges to include more elderberry plants during the fruiting period. One male travelled 300 m from his territory to an area of ripe elderberries. Most did not make long trips off their territory to find elderberries, but they spent more time near it when it was ripe. Many tanagers did not have elderberries in their territories. On Pelee Island, Nelson (1997) observed a Ruby-throated Hummingbird that darted at a Scarlet Tanager. The tanager lunged forward, grabbed it by the head, beat it to death against a log, and ate it. In Illinois, Gabbe et al. (2002) examined which tree species the tanager preferred to forage in. It greatly preferred cherrybark oak and shellbark hickory, followed by bitternut hickory, silver maple, sycamore, pin oak, shumard oak, and swamp chestnut oak. It greatly avoided foraging in overcup oak and sugar hackberry followed by sour gum, bald cypress, blue beech, Manitoba maple, green ash, pumpkin ash, red maple, and sweetgum. Three strongly preferred trees (shellbark and bitternut hickory and silver maple) were scarce. Some of the species that it avoided were abundant (pumpkin ash, sweetgum, overcup oak, and blue beech). Also in Illinois, Hartung and Brawn (2005) compared its foraging techniques in savannahs and woodlands. There were no significant differences in its tree species preferences or foraging heights. It foraged in black oak and white oak more than expected based on their availability and frequently in hickory. It foraged less frequently in red elm, black cherry, and hackberry. Sixty to 62% of foraging occurred at heights of 6-19 m, 23-31% above 16 m, and 9-15% at 5 m or lower in the 2 habitats. It searched for and captured prey by hanging, hovering, and gleaning, but 48% of total prey-attack manoeuvres were sallying and flycatching. Gleaning represented 20-40% of prey attacks. In Vermont, 85% of foraging occurred on leaves, 7% in the air, and 8% on twigs. Foraging techniques consisted of 50% gleaning, 42% aerial attacks, and 8% hanging (Lent and Capen 1995). In West Virginia, Maurer and Whitmore (1981) did not detect any differences in tanager foraging behaviour in a mature forest and one that was clear-cut 18 years previously. Hovering at leaves was the most frequently used technique. Foraging techniques in the young and mature forests, respectively, were: 74.3% and 67.7% hovering; 25.7% and 32.3% gleaning; 0% and 0% hawking; 17.1% and 12.9% proximal to the trunk; 82.9% and 87.1% distal to the trunk;

74.3% and 83.9% on leaves; 11.4% and 16.1% on branches; and 14.3% and 0% on trunks. There was a significant difference in the preferred trees for foraging: oaks in the young forest and beech in the mature forest. Foraging by species in the young and mature forests, respectively, consisted of 31.4% and 38.7% in maple; 34.3% and 6.5% in oak; 0% and 32.3% in beech; 17.1% and 12.9% in other species; and 14.3% and 9.7% in shrubs. It foraged mostly in the dense canopy layer 6.1-12.2 m above ground. This may have been why the rate of flycatching was lower than in some other studies. Three New Hampshire studies examined the foraging of the Scarlet Tanager. Holmes (1986) compared the foraging strategies of the sexes. Females foraged significantly higher than males (14.8 m compared with 11.7 m). The mean height of song perches (15.5 m) was significantly correlated with the mean foraging height of males. Foraging heights of both sexes were correlated with nest height, but not significantly. Both sexes were predominantly leaf hoverers. Frequency of foraging substrates and manoeuvres for males and females, respectively, were: leaf hovering, 34.9% and 34.6%; leaf gleaning, 28.9% and 28.4%; twig hovering, 0% and 0%; twig gleaning, 2.4% and 0%; branch hovering, 3.1% and 0%; branch gleaning, 8.4% and 4.9%; trunk hovering, 6.0% and 1.2%; trunk gleaning, 2.4% and 0%; hawking in air, 14.5% and 30.9%; and 0.6% and 0% on-ground foraging. The second-most common foraging strategy was gleaning for males and hawking for females. The frequency of foraging on different plant species for males and females, respectively, was: beech, 30.8% and 28.8%; sugar maple, 18.9% and 12.3%; yellow birch, 47.8% and 45.2%; white ash, 0.6% and 2.8%; conifers, 0% and 8.2%; other maples, 1.9% and 2.7%; viburnums, 0% and 0%; and forbs and ferns, 0% and 0%. Female foraging differed significantly from that of males for manoeuvres but not plant species. The amount of foraging in the distal half of trees was significantly less for males (29.3%) than for females (64.6%). Males foraged 70% in the proximal half of trees and took insects more often from bark than females. Females foraged most often in the distal portion of trees where most foliage and foliage-dwelling insects occurred. Male Scarlet Tanagers and Rose-breasted Grosbeaks were more similar to each other in their foraging behaviour than they were to their respective females. Females of these 2 species were more closely aligned with the Red-eyed and Philadelphia vireos in their foraging behaviour than they were to males of their own species. This was due to females of both species foraging higher in the canopy than average and more frequently in white ash than males. Males attacked prey on trunks and branches more often than females. Robinson and Holmes (1982) reported that 55.0% of prey attacks were on leaves and 20.2% were on bark, mostly in the canopy. Most of the available prey was adult and larval moths, adult flies, wasps, beetles, nymphal and adult leafhoppers and treehoppers, and spiders. Most of these occurred on leaf surfaces and not on twigs or small branches. Prey capture techniques included 54.5% hovering, 26.3% gleaning, 0.6% hanging, 0% flush-chasing, 18.3% hawking, and 0.3% other techniques which were mostly probing. The tanager often sat in the open inner branches of large canopy trees and searched outward for insects which were often actively flying wasps and beetles. Although it took some flying insects, it usually waited for insects to land before attacking them, especially large ichneumonid wasps. Holmes and Schultz (1988) studied its use of different species of trees for foraging. On beech, prey attacks were 28% on upper leaf surfaces, 72% on lower leaf surfaces, and 0% on petioles and twigs. On sugar maple, 29% of prey attacks were on upper leaf surfaces, 65% on lower leaf surfaces, 6% on petioles, and 0% on twigs. On yellow birch, 24% of prey attacks were on upper leaf surfaces, 67% on lower leaf surfaces, 0% on petioles, and 9% on twigs. Overall, 26% of prey attacks were on upper leaf surfaces, 68% on lower leaf surfaces, 1% on petioles, and 5% on twigs. On beech, 75% of prey-attack

manoeuvres were by hovering (81% on lower leaf surfaces), and 25% by gleaning (25% on lower leaf surfaces). On sugar maple, 67% of attacks were by hovering (75% on lower leaf surfaces) and 33% by gleaning (50% on lower leaf surfaces). On yellow birch, 78% of attacks were by hovering (75% on lower leaf surfaces) and 22% by gleaning (43% on lower leaf surfaces). On all tree species combined, 39% of attacks were by hovering (80% on lower leaf surfaces) and 61% by gleaning (61% on lower leaf surfaces). Caterpillars that were potentially available as prey occurred at low densities, were highly variable in their distribution among leaves, and differed significantly in abundance among tree species and canopy strata. Caterpillars of owlet, prominent, and geometer moths constituted 95% of lepidopterans on foliage of beech, 84% on sugar maple, and 73% on yellow birch. Most were on leaf blades and on the under-surface of leaves (75% on beech, 62% on sugar maple, and 73% on yellow birch). Prominents were found exclusively on leaves. Owlets and a large proportion of geometers also occurred on petioles and twigs. Twenty-nine percent of the caterpillars were free-living types on beech foliage, 42% on sugar maple, and 58% on yellow birch. Beech supported more caterpillars, mostly leaf miners and leaftiers which are smaller and taken less frequently by birds. Yellow birch had fewer caterpillars, but nearly two thirds were free-living types which are mostly larger and more active larvae. The tanager obtained more than 50% of its prey from foliage and foraged over the full vertical profile of the forest. Ten species of birds were studied and all differed significantly from each other in their use of foliage substrates and tree species. The Scarlet Tanager and 6 other species were considered lower-leaf specialists that predominantly hovered at leaf surfaces to capture prey. The tanager was the only species that attacked in proportion to prey abundance in all 3 tree species.

During the breeding season, the Scarlet Tanager is predominantly insectivorous, but eats a variety of fruits as they ripen later in the season. Nestlings are fed insects and berries. Insects consumed by adults include adult underwing, luna, and cecropia moths; caterpillars of owlet, prominent, geometer, leafroller, and gypsy moths; gall insects; weevils and metallic wood-boring, bark, click, and leaf beetles; crane flies; grasshoppers and locusts; bugs; and wasps. About 12% of the diet consists of fruits including those of juneberries, huckleberries, bayberries, sumacs, blackberries, mulberries, and cultivated cherries (Tyler in Bent 1958). In New Hampshire, emetic diet samples consisted of 7.7% caterpillars, 34.1% hymenopterans, 41.5% beetles, 4.9% flies, and 9.8% other items. Of food items that were observed being preyed upon, 63.1% were caterpillars, 5.2% were adult lepidopterans, 15.8% were beetles, and 15.8% were hymenopterans. The disparity between the results was probably because caterpillars were the most conspicuous prey for observers to see thereby inflating their importance in the diet (Robinson and Holmes 1982). In Michigan, the diet consisted of a variety of adult and larval insects, including hymenopterans (bees, wasps, hornets, ants, and sawflies), moths and butterflies, beetles, flies, cicadas, leafhoppers, spittle bugs, treehoppers, aphids, scale insects, termites, grasshoppers and locusts, dragonflies, dobsonflies, snails, earthworms, and spiders. It ate strawberries and chokeberries in addition to most of the fruits previously mentioned. In West Virginia, it shifted from a diet of predominantly caterpillars early in the summer to higher concentrations of beetles and orthopterans later in summer (Mowbray 2020). Birds foraging along roadsides during adverse spring weather ate mostly ants, beetles, earthworms, and midges indicating that most foraging occurred on the ground (Mowbray 2020; Zumeta and Holmes 1978). Royall (1988) observed a male in a tree crown that swooped down and captured a

large katydid that was flying about 3.7 m above the ground. Near Manitouwadge, Venier et al. (2009) observed no response by the tanager population to changing spruce budworm numbers. In New Hampshire, changes in tanager density among years appeared to be in response to numbers of saddled prominent caterpillars (Holmes and Sturges 1975).

The Scarlet Tanager is a common host of the Brown-headed Cowbird. The tanager accepts parasitic eggs and the cowbird often removes a tanager egg. In Michigan, the average clutch size was 3.7 eggs in unparasitized nests and 2.1 eggs in parasitized nests. In most cases, tanager eggs in parasitized nests are as likely to hatch and produce fledglings as those in unparasitized nests. In Illinois, where parasitism rates and intensity were high, 6 of 7 tanager families had at least 1 cowbird fledgling, only 2 had host fledglings. Parasitism does not appear to cause nest desertion or nesting failure. Parasitism rates vary considerably due to factors such as geography (with higher populations of cowbirds in the Midwest), size of the forest patch, and the degree of fragmentation of the landscape. In Ontario, 7 of 44 nests (15.9%) were parasitized. Parasitism rates reported elsewhere include 1 of 8 nests (12.5%) in Tennessee, 2 of 21 nests (9.5%) in Maryland, 7 of 22 nests (31.8%) in Pennsylvania, 3 of 4 nests (75%) and 16 of 18 nests (88.9%) in Illinois, 10 of 13 nests (76.3%) in Michigan, and 4 of 6 nests (66.7%) in New York (Hahn and Hatfield 1995; Mowbray 2020; Peck and James 1998b; Robinson 1992).

Habitat loss and fragmentation are the most significant limiting factors for the Scarlet Tanager. Fragmentation can lower forest size below the minimum threshold required to support it. Because its presence and abundance are correlated with the amount of forest cover within a landscape, even the loss of unoccupied forests may reduce its probability of occurrence in other forests. Forest fragmentation is considered one of the factors resulting in its decline in Quebec (Lanoue and Gauthier in Gauthier and Aubry 1996; Létourneau in Robert et al. 2019). Rosenberg et al. (1999) used Project Tanager results to determine the effects of forest fragmentation on the Scarlet Tanager. The 4 regions that were analyzed were the Northern Forest (all of Ontario except the Carolinian Zone), the Midwest (which included the Carolinian Zone of Ontario), the Northeast (New England south to North Carolina and Georgia), and the Atlantic Coast from Long Island to North Carolina. The proportions of sites with tanagers were 72% in the Northeast, 50% in the Midwest, 60% in the Atlantic Coast, and 57% in the Northern Forest. It was significantly affected by fragmentation (patch size, percent forest cover within a 10-km^2 block surrounding the site, and distance to the 2 nearest woodlots) in the Northeast, Midwest, and Atlantic Coast populations but not in the Northern Forest. Its probability of detection dropped below 50% at highly fragmented sites in the Midwest and Atlantic Coast. It was strongly negatively affected by edge in the Atlantic Coast and there was a weak effect of elevation in the Midwest. In the Northern Forest, only elevation significantly affected breeding probability, with it more likely to be detected at higher elevations. The cowbird was more likely to be found at fragmented locations and was less common at higher elevations. Avian predators were more common in the Northeast and in areas with more edge in the Atlantic Coast. Mammalian predators were more common at highly fragmented sites in the Northeast, Midwest, and Northern Forest. The response of the Scarlet Tanager to habitat fragmentation varied significantly geographically. The response to fragmentation by the cowbird and predators was opposite to that of the tanager. Results demonstrated that the Scarlet Tanager was negatively affected by fragmentation, with the greatest negative effects in the Midwest and Atlantic Coast

where forests are highly fragmented. It appears to be less sensitive to fragmentation in areas where the forest is largely intact, such as the Northern Forest. In Pennsylvania, Rodewald and Yahner (2001) examined the collective nesting success of the Eastern Wood-Pewee, Red-eyed Vireo, Wood Thrush, Ovenbird, and Scarlet Tanager at the landscape (314 ha), local (25 ha),and nest-patch (0.04 ha) scales. Daily nest survival was lower in landscapes disturbed by agriculture than those disturbed by silviculture for all species combined and canopy nesters (including the tanager) but not for ground or understorey nesters. Nest-patch microhabitat and distance to edge were not associated with nest success for any guild. Squirrels, American Crows, and cowbirds were more abundant in landscapes disturbed by agriculture. Chipmunks were equally abundant in landscapes disturbed by agriculture and forestry. Lower nest survival in lands disturbed by agriculture was best explained by greater abundance of some avian and mammalian predators, particularly squirrels. In New York, Roberts and Norment (1999) studied the effects of patch size and local-scale isolation on the reproductive success of the Scarlet Tanager. Pairing success, fledging success, and density varied significantly with forest area and were higher in larger patch sizes. Pairing success was greater than 75% in all occupied sites and was 100% in forests larger than 1,000 ha, a significant difference. Fledging success increased significantly with forest size. In 2 years, fledging success was 28% and 0% in woodlots 10-50 ha, 38% and 58% in woodlots 50-150 ha, and 80% and 75% in woodlands larger than 1,000 ha. Males breeding in forest patches with increased canopy cover and lower oak density had higher pairing success than those in patches with reduced canopy cover and higher oak density. This appears to be the only study that found that it did not prefer oaks. Those breeding in large forest patches with more surrounding forest cover had higher fledging success than those in small patches and less surrounding forest. The researchers could not determine if the fragmentation effects were due to patch size, isolation related to the amount of forest cover within 1 km, or interactions between these variables. Results also suggested that canopy cover, BA, and tree species richness affected nest success. Total BA and tree species richness were significantly higher in forests larger than 1,000 km than in smaller patches. The highly fragmented landscape of Illinois is considered a sink where more than 80% of nests are parasitized and the predation rate is 69-78% (Robinson 1992). In West Virginia, Farwell et al. (2019) studied the effects of shale gas infrastructure (access roads, pipelines, and well pads) on the Scarlet Tanager. It was more abundant distant from all types of facilities, but not significantly.

The effects of forest management on the Scarlet Tanager are variable. Most studies concluded that it tolerates a wide range of forest prescriptions and that harvesting has minimal effects. In the Boreal Forest Region of Ontario and Canada, there was no change in its abundance when 30%, 50%, or 70% of the tree cover was removed (Vanderwel et al. 2007, 2009). In Algonquin Park, Tozer et al. (2010) detected no effects from single-tree and group-selection harvesting. Jobes et al. (2004) found that it was significantly more abundant in sites that were selectively thinned 1-5 years previously than in sites that were unharvested or harvested 15-20 years previously. Near Sault Ste. Marie, it was equally abundant before and after selective harvesting; the BA did not change significantly (Holmes and Pitt 2007). South of the Canadian Shield in Ontario, Holmes et al. (2004) found no difference in its abundance in unharvested stands, those that were selectively thinned, and those where heavy diameter-limit cuts occurred. In Indiana, Robinson and Robinson (1994) observed no effects on the Scarlet Tanager due to selective logging that created openings 0.02-0.4 ha in area. In New York,

Webb et al. (1977) detected no changes in its relative abundance in forests where 0%, 25%, 50%, 75%, and 100% of the merchantable trees were removed. In Maryland, Bushman and Therres (1988) concluded that a wide range of forest management practices were acceptable. In Pennsylvania, it was more common in stands where snags were retained in improvement cuts than where snags were removed (Stribling et al. 1990). Also in Pennsylvania, it decreased by 32% when 1-ha blocks of aspen and mixed forest were clear-cut; the decline was nonsignificant (Yahner 2003). In New York, 2 of the woodlots studied by Roberts and Norment (1989) underwent a selective harvest that resulted in the removal of the largest trees. This resulted in an increase of male territory sizes and reduced pairing success in the harvested areas. In Michigan, sites that were selectively harvested supported Scarlet Tanagers prior to cutting but not afterwards in the same season or in the next year (Mowbray 2020). In Minnesota, harvesting reduced BA to 7-10 m^2 per ha and this had an adverse effect on the tanager (Hanowski et al. 2003).

The Scarlet Tanager may avoid housing. In Waterloo Region, the number of houses near a site significantly affected the number of breeding neotropical migrants with a significant decline in diversity and abundance as the level of development increased. Results were presented for the guild as a whole and not for individual species, but the Scarlet Tanager followed this pattern (Friesen et al. 1995). In North Carolina, Lumpkin and Pearson (2013) determined that it decreased significantly with the number of buildings within 200 m.

The Scarlet Tanager appears to be particularly vulnerable to extended periods of cold wet weather when it first arrives in spring. During a period of mean daily temperatures of 8-10°C and 1-12 mm of rain daily, numerous tanagers were found grounded along highways. The area affected included from southern Maine to eastern Vermont, including most of the northern half of New Hampshire. Of 485 birds observed along a small subsample of highways, the Scarlet Tanager represented 46.4% of live birds, 83.5% of dead birds, and 51.9% of all birds. The live tanagers were very sluggish, allowing close approach, and had difficulty flying, preferring to hop away. Breeding density at a study area in New Hampshire was half that of the previous year and nesting success appeared to be poor. Densities in the 2 subsequent years were half that of the 5 years prior to the cold spring and the lowest in 8 years of study. BBS results determined that it declined by 30% in New Hampshire and 50% in Maine in the year of the cold spring compared with previous seasons. It may be more affected than other species because of its greater dependence on large-sized insect prey. These are relatively rare in the environment and may be particularly depressed in abundance during cool wet weather. The tanager is also larger with greater metabolic needs (Zumeta and Holmes 1978). Mowbray (2020) reported that 27 were found dead after a thunder and hail storm in Louisiana. It may also be killed by vehicles while foraging along roadsides in adverse weather conditions.

In Pennsylvania and New Jersey over a 15-year period, hemlock declined from representing 56% of the total BA to 46% due to the hemlock woolly adelgid; the amount of deciduous understorey increased. The tanager increased in response to hemlock decline and exhibited the greatest increase in occupancy of all species (Toenies et al. 2018).

In a New York woodlot, Litwin and Smith (1992) attributed a 50% decline in the Scarlet Tanager to changes in forest succession. This occurred despite the forest becoming more consolidated and less isolated. Over the 30-year period, the species composition of the forest changed with almost

complete extirpation of elm, severe declines in beech, and increases in basswood, silver maple, sugar maple, red ash, and white ash. The canopy became more closed with a resulting decline in the shrub layer and hophornbeam, a midcanopy species. The decline was attributed to loss of vertical and horizontal heterogeneity and an overall decline in productivity associated with forest maturation.

In Georgia, Klaus et al. (2010) observed no effect of wildfires or controlled burns on the Scarlet Tanager. Even high-intensity fires that resulted in significantly less canopy cover had no effect.

Price (2004) predicted that the range of the Scarlet Tanager might contract in southern Ontario if the average summer temperature increased by 2°C. In New York, Kirchman and Van Keuren (2017) examined whether its range shifted in response to climate change over a 40-year period. It was associated with lower elevations of 500-650 m. There was no change in its range over time, but the range of many other species shifted upwards.

Status

McIlwraith (1894) stated that the Scarlet Tanager was restricted to the southern portion of the province and that it was not abundant anywhere. In Elgin County, it was considered common in 1891, moderately common in 1954, and uncommon in 2000 (Lancaster et al. 2004). Baillie and Harrington (1937) considered it fairly numerous in the southern half of the province. It bred north to at least Sault Ste. Marie and Algonquin Park and probably west to Lake of the Woods. The first atlas confirmed that it nested from the Lake of the Woods area east to Lake Abitibi southward through the remainder of the province. Its northern limit was delimited by the northern extent of the Great Lakes–St. Lawrence Forest Region with minor intrusions into the southern portion of the Boreal Forest Region. Gaps in its distribution were associated with the deforested area around Sudbury and areas of intensive agriculture in the southwest. Highest densities occurred in the southern Shield portion of the Great Lakes–St. Lawrence Forest Region from Kingston to Algonquin Park (Cadman in Cadman et al. 1987). James (1991) considered the Scarlet Tanager uncommon in the south and rare in the north to Sioux Lookout and Kapuskasing with sight records north to Moosonee.

The second atlas indicated that there had been no change in the Scarlet Tanager's range or probability of observation since the first atlas. It was most abundant in the southern portion of the Canadian Shield along the St. Lawrence River north to Ottawa and North Bay. High densities also occurred on the Bruce Peninsula and the heavily forested Norfolk Plain near Long Point. Density was low further to the north and in the intensively farmed areas of southwestern Ontario (McLaren in Cadman et al. 2007).

BBS data indicate that the Scarlet Tanager population has been stable since 1966, although changes in abundance occur within and between regions. Trends in abundance may be influenced by changes in habitat structure, variations in arthropod abundance, forest fragmentation, and source-sink dynamics. Long-term population trends may be misleading because BBS surveys often record unmated males in small woodlots and pairs in woodlots where they are unlikely to produce any young (Mowbray 2020). BBS results indicate annual decreases of 2.08% in Canada and 0.449% in Ontario 1970-2021. Trends for 2011-21 were annual increases of 0.741 in Canada and 0.522% in Ontario. All results were highly reliable except that the short-term trend for Ontario was of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Most young walk from the nest when they fledge but some may fly as far as 15 m from the nest. The young are capable of short fluttery flight at age 10 days. Adults attend to the fledglings for 10-14 days after leaving the nest (Mowbray 2000). This author suggested that young remain in or near the natal territory until they fledge but studies conducted during the postfledging period indicate that many move to early successional habitat once they are independent. Tyler (in Bent 1958) reported that fledglings from 1 nest stayed in the area with the female for 26 days until 1 August. Another brood moved from the nest on the same date, travelled about 60 m down a valley and remained with the female until 15 August when all of them disappeared. In Virginia, 1 pair split the brood with each adult caring for 1 fledgling (Vega Rivera et al. 2003).

The 8-9-week postfledging period is important because the prebasic moult and premigratory fattening must be accomplished. The Scarlet Tanager has a gradual moult and does not lose its flight capability. Vega Rivera et al. (2003) radiotracked adults through the breeding and postfledging periods in Virginia. Eight males and a female did not change their home ranges during these periods. Even though they did not change areas, they shifted their core areas. Nine males and 2 females established postfledging home ranges more than 300 m from the breeding home range. Two males moved back and forth between their breeding and postfledging home ranges. One returned to the breeding home range 3 times and remained there until autumn migration. The other moved back and forth 4 times and remained in the postfledging home range until migration. The fact that some birds returned to the breeding home range suggests that it is important to maintain a presence, perhaps to retain control in subsequent breeding seasons. One female and 3 males established postfledging home ranges more than 3 km from the breeding home range. One of the males returned to his breeding home range in mid-September and disappeared 10 days later. During the postbreeding period, 3 males visited the same forest fragments 0.6-1.1 km from their breeding home range and 2 males moved to the same site 3.3 and 3.9 km from their breeding home ranges. Individuals moved as far as 11 km from the nesting territory, suggesting that they may have been scouting over an area of approximately 38,000 ha or even larger because some birds were not re-encountered. Eleven birds apparently left the area before the moult prior to 1 August. Early departure did not appear to represent the initiation of migration because 75% of birds remained after 1 August and did not depart until mid-September. Those that left did so in July prior to the moult, a condition unfavourable for migration. Television tower kills in Florida do not show evidence of migration until September. It may leave breeding home ranges prior to migration to find high-quality habitats with an abundant food source and low predator pressure. Rappole and Ballard (1987) captured a moulting female on 21 August in Georgia 100 km south of the nearest breeding population.

During the postfledging period, the Scarlet Tanager may continue to inhabit forests or move to early successional habitats such as clear-cuts. In Virginia, Vega Rivera et al. (2003) determined that its habitat did not change significantly between the breeding and postfledging periods at a macro level, remaining in forested habitat. There were some slight changes in vegetation composition between the 2 seasons. During the postfledging period, it used mixed oak and hardwood stands more than their availability, tulip tree forests less than their availability, and black locust in proportion to its availability. Results were similar in both periods except that mixed oak stands were used more

than their availability in the postfledging period and equal to their availability in the breeding season. Postfledging sites had more trees and higher BA (because of a higher density of trees 4-46 cm DBH), more snags, and more trees characteristic of early successional areas (red elm, hackberry, tree-of-heaven, black locust, sassafras, Manitoba maple, persimmon, and apple) than breeding sites. The 3 most abundant tree species in both breeding and postfledging sites were hickories, red elm, and flowering dogwood. Tree-of-heaven, sassafras, and red maple occurred only in postfledging sites.

Both adult and juvenile Scarlet Tanagers have been captured in clear-cuts during the postfledging period, often in high numbers, in Ohio, Pennsylvania, Minnesota, West Virginia, Virginia, and Missouri. It commonly uses early successional habitat throughout its range during the postfledging period. In Ohio, it seldom inhabited clear-cuts 10 years and older with a closed canopy and limited fruit. In Pennsylvania, it was significantly more abundant in clear-cuts than adjacent mature forests. There were no significant differences in coverage by shrubs, forbs, and grasses in the 2 habitats but the shrub species composition varied. Raspberries and cherries dominated the clear-cuts. Forests were dominated by beech and red maple seedlings and lacked raspberries. In Ohio, it preferred small (4.0-9.3 ha) to large (13.3-18.1 ha) clear-cuts. It was 4.5 times more abundant in small cuts. It may have preferred smaller cuts because they permitted increased access to both habitats. Tanagers were observed returning to the mature forests after foraging on fruit in the clear-cuts. Also in Ohio clear-cuts, it was positively correlated with canopy cover by vegetation taller than 4.5 m and negatively correlated with the density of shrubs 0.5-1.5 m tall (Marshall et al. 2003; Porneluzi et al. 2014; Stoleson 2013; Streby et al. 2011b; Vitz and Rodewald 2006, 2007).

In Virginia, Vega Rivera et al. (2003) determined the home range sizes of Scarlet Tanagers during the postfledging period. For those that remained in the breeding season home range, there was no difference in the size of their home ranges during the breeding (5.6 ha) and postfledging (5.4 ha) periods, or in their core areas (0.72 and 0.62 ha), respectively. For birds that established a distant postfledging home range, these were significantly larger (34.5 ha) than breeding (5.8 ha) home ranges. Core areas were also larger during the postfledging period (5.8 ha compared with 0.93 ha). For 2 birds that moved back and forth between their breeding and postfledging home ranges, sizes were significantly larger during the postfledging period. Their home ranges were 2.6 and 2.7 ha in the breeding season compared with 9.3 and 23.6 ha in the postfledging period. Core areas were 0.67 and 0.46 ha in the breeding season and 4.9 and 11.7 ha in the postfledging period.

In Ohio clear-cuts, numbers of the Scarlet Tanager peaked in mid-July then quickly decreased. Its capture rate was positively correlated with fruit abundance, predominantly raspberries. Its capture rate was 2.5 times greater in nets with more than 600 fruits within the net belt than in nets with less than 100 fruits. Eighty-one percent of captured birds had fruit stains on their bills. As the fruit declined within the clear-cuts, so did the tanager (Vitz and Rodewald 2007). Vitz and Rodewald (2012) used feather isotopes to determine the diet of the Scarlet Tanager during the postfledging period. They found no evidence that it adopted a strongly frugivorous diet at this time. Although it has been confirmed eating fruit, results indicated that the diet consisted mostly of arthropods.

MIGRATION

The Scarlet Tanager is a long-distance neotropical migrant that winters in northwest South America. It may migrate singly or in small loose flocks with other neotropical migrants such as vireos, thrushes, and warblers. Most migration occurs at night (Mowbray 2020; Tyler in Bent 1958). In Ohio along the southern shore of Lake Erie, it made spring morning flights about an hour after sunrise. These were oriented west to northwest along the coastline, with no birds crossing Lake Erie. The purpose of these flights was possibly to compensate for the drifting effects of winds experienced during the night, with winds almost exclusively from the west. The principal direction of nocturnal flight was north or northeast (Tuck et al. 2018).

Timing of spring migration appears to be related to foliage development, as this influences food availability, territory establishment, mating, and courtship on the breeding grounds (Mowbray 2020). Consequently, climate change has the potential to alter the timing of migration. From 1967 to 2011 in New York, the trend was toward earlier arrival and later departures but this was not significant (Zelt et al. 2017). In Massachusetts, there was no change in the mean arrival date 1851-1973 and 1988-2007 (Ellwood et al. 2010). Males arrive in spring a few days to a week before females (Mowbray 2020; Weir 2008). At Long Point, the mean capture date for males was significantly earlier than for females. Mean capture dates were 11.2 May for adult males, 15.8 May for yearling males, 22.1 May for males of unknown age, and 20.0 May for adult females (Stewart et al. 2002). In southern Ontario, most arrive in early to mid-May with the earliest migrants appearing in mid- to late April (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). In the southern Shield, migration begins around the second week of May and continues until the end of the month (Mills 1981; Tozer 2012).

There appears to be no temporal segregation of the sex and age classes during autumn migration. Departures from the breeding grounds may begin in mid- to late August, but most birds do not leave until mid- to late September (Mowbray 2020). In the southern Shield, tanagers start migrating south in August with most gone by mid-September but a few remain into early October (Mills 1981; Tozer 2012). In the south, migrants arrive in mid-August and depart in late September, with some remaining until mid-October or rarely early November (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

During migration, the Scarlet Tanager is associated mostly with forested areas with tall trees, but it also occurs in more open habitats such as savannahs and woodlands, parks, and gardens (Mowbray 2020). During spring migration in Indiana, it was most abundant in trees 20-23 m tall (Grundel and Pavlovic 2007a). In Pennsylvania, it was associated with larger forests in spring but occurred in all sizes of forests in autumn (Keller and Yahner 2007). During spring migration in Wisconsin and Minnesota, it occurred in upland forests dominated by oaks or oaks mixed with sugar maple, beech, and red elm. It was absent in floodplain forests dominated by Manitoba maple, green ash, and white elm (Kirsch et al. 2013). During spring migration in Ohio, it was more common in mature upland than mature riparian forests, but not significantly (Rodewald and Matthews 2005). During spring migration in Pennsylvania, it was significantly more abundant in forested than shrubby habitat (Smith and Hatch 2008). In Pennsylvania, Smith and Hatch (2017) studied the effects of southern arrowwood loss on spring migrating tanagers. This shrub was defoliated and killed by

the viburnum leaf beetle, resulting in a significant decline of this shrub. Tanager captures declined by 45%, but this was not significant. There were insufficient data to determine if its body mass declined. Rodewald and Brittingham (2002, 2004) compared tanager usage of different habitats during autumn migration in Pennsylvania. Highest abundance occurred in forest-agricultural edges. Usage of forest interior, suburban forests, pole-stage forests, and shrub–sapling-stage forests was similar and significantly lower than for forest edges.

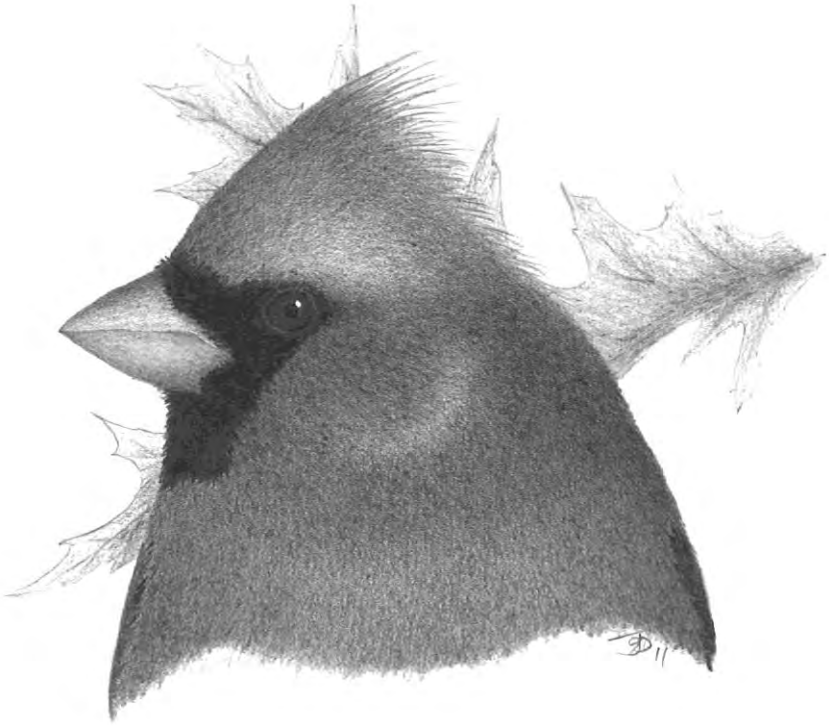
The Scarlet Tanager may eat a higher proportion of fruit during autumn migration (Mowbray 2020). In Ontario, it has eaten the fruits of wild raisin, mountain-ash, and honeysuckles (Mills 1981; Tozer 2012).

During migration, the Scarlet Tanager is frequently killed at buildings, communication towers, and other tall structures. In the United States, it is 18.5 times more likely to strike a high-rise than the average for birds. It was not among the top 20 species most likely to be killed for all building types combined, 1-3-storey residences, or low-rises. Thirteen were killed at the Lennox generating station chimneys near Kingston 1972-82 (Loss et al. 2014; Mowbray 2020; Weir 2008).

James (1991) considered the Scarlet Tanager an uncommon migrant in Ontario. Captures at Long Point Bird Observatory decreased nonsignificantly at a rate of 1.4% per year 1961-88. Annual trends by periods were: +15.3% 1961-70; –10.2% 1970-79; and –11.5% 1979-88 (Hussell et al. 1992).

Northern Cardinal

Cardinalis cardinalis

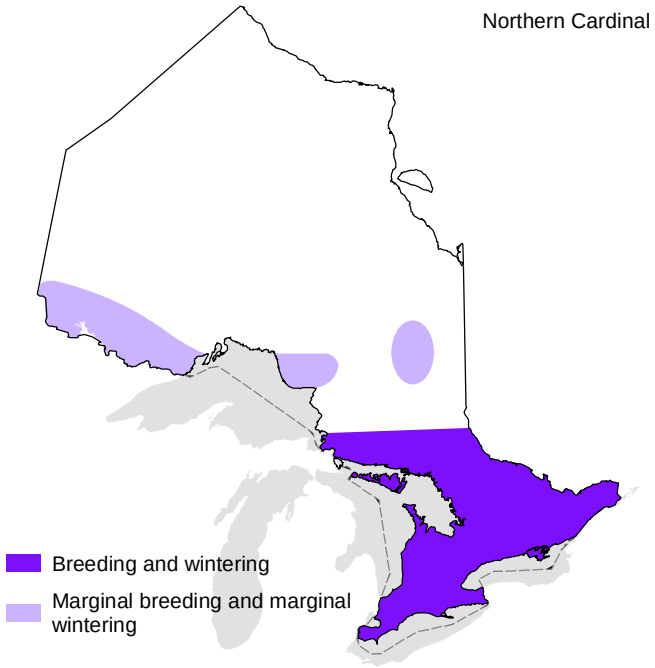


BREEDING SEASON

Habitat Requirements

Ontario Northern Cardinal nests were in urban gardens, parks, golf courses, and nurseries (38.9% of nests); in open deciduous, mixed, and coniferous woodlands, at either their edges or in clearings (35.9% of nests); in rural fields and pastures overgrown with hawthorns or other shrubs or saplings, in parks, in fencerows, and in orchards (24.9% of nests); and in a sand-dune area (0.3% of nests). An unspecified number of nests were in or near marshes and wooded swamps (Peck and James 1987).

South of the Canadian Shield in the Great Lakes–St. Lawrence Forest Region, Weir (2008) reported that the cardinal was most abundant in villages, towns, and cities, but also occurred in more natural habitats north to the edge of the Shield. In Durham Region, Speirs and Orenstein (1975) found it in only 1 of 11 forested plots that they surveyed: an open-canopy deciduous forest with a rank growth of ferns and raspberries. Dow (1969a, 1969b, 1994) studied the cardinal near Elmira when it was still uncommon and becoming established in the area. Its only vegetational requirement was an adequate amount of woody cover that was suitable for nesting. It was



associated only with woodlots and was not detected in hedgerows. The woodlots were mostly dominated by sugar maple–beech but it also used lowland white cedar stands with alders, willows, and many dead elms. It also favoured woods and swamp edges containing considerable white birch and poplar. Home ranges were 62.4% wooded. Average characteristics of home ranges were 18% forbs, 55% graminoids 0.25-0.8 m tall, 1% graminoids 0.8-2 m tall, 10% woody plant cover less than 0.25 m tall, 18% deciduous leaf coverage, 6% coniferous foliage cover, 20% dead wood, 4% rocks, 5% water, and 12% marsh. Only 2 of 10 home ranges contained vegetation taller than 18.3 m. It selected song perches for their conspicuousness rather than their height and often selected dead elms as perches. It had difficulty perching on the flexible tops of white cedars and did not stay in them long. Population density was significantly correlated with distance to the nearest river or bottomland.

In the Carolinian Forest Region, the cardinal was common on the University of Western campus and adjacent riparian woods along the Thames River (Lemon 1969; Scott and Lemon 1996). Dodds and Otis (2009) reported it in fairly high density in wooded areas dominated by ash at Point Pelee.

In southern Ontario south of the Shield, abundance of the cardinal was significantly negatively correlated with forest cover more than 100 m from edge, the amount of forest cover within 2 km, and the amount of regional forest cover. It was negatively correlated with woodlot size, but not significantly (Austen et al. 2001). In a sparse and pioneering population at Elmira, 54% of males were in woodlots larger than 10 ha, 1% were in woodlots smaller than 2 ha, 7% in woodlots 1-20 ha, and 5% in extensive forests (Dow 1969a). It may select moderately sized woodlots first, with more extensive use of smaller woodlots and hedgerows once the population grows.

The Northern Cardinal nests in a wide variety of habitats that support woody vegetation. Highest densities occur in urban areas where there is a proliferation of shrubs, especially nonnative species such as honeysuckles and buckthorns. It occurs in areas dominated by shrubs and saplings, but is common in ornamental plantings in lawns and forest edges and gaps. It nests in hedgerows, deciduous scrub, small woodlots, urban parks and open spaces, shrubby borders of agricultural fields, riparian forests, regenerating clear-cuts and burns, marsh edges, grasslands supporting shrubs, successional fields, orchards, pine and oak barrens, conifer plantations, reclaimed mines, and savannahs. It tends to avoid open habitats without woody cover and extensive forests, although it will nest at their edges and in gaps and much less frequently in forest interior. Outside urban areas, it prefers sites with dense shrubs or tangles of vines over shrubs or saplings. Some authors reported

it as being ubiquitous, being present in all habitat types they studied (Austin 1968; Bielefeldt and Rosenfield 1994; Bond 1957; Bowen et al. 2007; Conner et al. 1983; Conover et al. 2009; Dow 1969a; Fitch 1958; Ford et al. 2001; Gentry et al. 2006; Graber and Graber 1963; Halkin et al. 2021; Hurst and Bourland 1996; Kerr 1968; Leston 2006; Margeneau et al. 2019; Michaud in Robert et al. 2019; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991; Paquin in Gauthier and Aubry 1996; Schneider and Miller 2004; Suthers 1988; Walk et al. 2011).

Some studies examined cardinal habitat at the landscape level. In the eastern United States, 58% of detections of the cardinal on Breeding Bird Survey (BBS) routes were in fragmented landscapes (Donovan and Flather 2002). In Quebec, highest densities occurred in the deciduous forest regions of the southwest in regions dominated by sugar maple–bitternut hickory and sugar maple–basswood. It rarely occurred at elevations above 200 m (Michaud in Robert et al. 2019). In Illinois, densest populations occurred in urban habitats, possibly due to the presence of feeders (Walk et al. 2011). In Ohio it was significantly more abundant in urban than rural forests, being 1.67 times more abundant in urban areas in the summer and 5 times more abundant in the winter. It may be more abundant in urban areas because of the warmer winter temperatures, presence of feeders, and abundant nest sites in ornamental trees and shrubs (Leston 2006). In Alabama, it was less likely to abandon areas surrounded by development sites with high shrub density and ground cover (McClure et al. 2013a). In South Dakota, it was significantly more abundant in contiguous riparian forests than in small isolated woodlots (Gentry et al. 2006). In South Carolina, it was significantly more abundant in oak-hickory woodlots surrounded by field and scrub habitats than those surrounded by closed-canopy forests (Kilgo et al. 1997). In New York, it preferred landscapes that were 42-71% forested (Cunningham and Johnson 2019).

Numerous studies determined microhabitat preferences of the cardinal. In Michigan, those nesting near Cooper's Hawks' nests sang from similar heights (2.46 m near hawk nests and 2.83 m where hawks were absent). Perches were significantly less exposed at hawk nests (Duncan and Bednekoff 2006). In Tennessee, 20% of cardinals occurred in narrowly wooded stream edges that represented only 3.6% of the available habitat and 41.2% occurred in hedgerows that were 12.5% of available habitat, indicating that these were preferred sites. Home ranges contained 37% forbs 0.8-2.0 m tall, 55% woody plants less than 0.25 m tall, 54% coverage by deciduous leaves, 2% conifer coverage, 8% dead wood, 1% rock, 1% standing water, and less than 1% marsh (Dow 1969a). In Texas, it was positively correlated with the number of shrub species and stems, foliage density 1 and 3 m above ground, and the percent coverage by pines 5-16 cm diameter at breast height (DBH). It was negatively correlated with vegetation height, percent canopy closure, foliage density 12-15 m above ground, the number of tree stems 17-32 cm DBH, and percent coverage of pines 17-32 cm DBH. It was common in clear-cuts and often occurred in mature forests where there were openings in the canopy with a subcanopy of shrubs. It preferred some tall live or dead trees for singing perches (Conner et al. 1983). In South Carolina, the cardinal occurred significantly more often in forest gaps 0.13, 0.26, and 0.50 ha in size than in the adjacent forest in all seasons. During the breeding and postbreeding seasons, it was significantly more abundant in gaps than edge habitat between gaps and forests. In autumn, it was equally abundant in gaps and edges and almost absent in forest. Gap interiors were densely vegetated and supported early fruiting shrubs such as sumac and blackberry. Poison ivy and hawthorn were common at gap edges. It did not shift its habitat use in response to

seasonal fruit availability (Bowen et al. 2007). Moorman et al. (2012) determined that usage of forest gaps was not driven by changes in arthropod abundance. Cardinals were attracted to forest gaps by the vegetation structure rather than the abundance of fruit or arthropods. In Mississippi, it was more abundant in agricultural fields with borders retained around them, and more abundant in 10-m-wide borders than those 30 m or wider. It appeared to benefit mostly from borders near wooded edges and used the borders for foraging (Conover et al. 2009). In Chicago, its abundance was positively correlated with the amount of coverage by honeysuckle and declined with tree density and distance to edge. Management that completely removed invasive shrubs could be detrimental (Schneider and Miller 2014). In the mid-Atlantic states, it was positively correlated with foliage density 2-3 m from the ground and canopy height. It was negatively correlated with the amount of forest cover within 2 km (Robbins et al. 1989). In North Carolina, it was negatively correlated with canopy cover (Lumpkin and Pearson 2013). In Maryland, it was positively correlated with herbaceous cover and negatively correlated with shrub density (Lynch 1987). In Tennessee, the cardinal inhabited areas with dense subcanopy vegetation with open canopies on flat slopes. These were mostly recently abandoned farmlands. It selected areas with a high biomass of trees 8.5-22.8 cm DBH (Anderson and Shugart 1974). In Iowa riparian stands, it was positively correlated with horizontal and vertical patchiness of habitat, grasses and forbs, and snags 3-9 m tall (Stauffer and Best 1980). In Wisconsin, it occurred in more pioneer woods and was most common in xeric stands. It was very rare in more climax stands (Bond 1957). On reclaimed mines in West Virginia, it was most abundant in shrublands with retained trees followed by remnant forest patches, grasslands, and intact forests (Margeneau et al. 2019). On strip mines in Illinois, it was most abundant in late shrub communities where the oldest trees were 37 years old, followed by upland maple-oak forests and early shrub communities where the oldest trees were 10 years old (Karr 1968). In Texas, cardinal nests were in open habitats with few trees and high coverage by grasses. Mean nest-site characteristics were 6.32 m of canopy directly above (range 2.07-22.64 m), 5.02 m to the nearest rock 20 m or longer or log 7.5 cm or more in diameter, 1.81 m to nearest understorey tree 7.5 cm or greater in DBH (range 0-14.1 m), 4.64 trees 7.5 cm or greater in DBH within 10 m (range 0-60), 13.61 understorey trees 7.5 cm or greater in DBH and 2 or more m in height within 30 m (range 0-51), 14.37 cm litter depth within 1 m (range 0-55 cm), 28.62% grass cover within 2 m (range 0-94%), 2.26% bare ground within 2 m (range 0-38%), 3.89% woody debris within 2 m (range 0-34%), 3.66% coverage by rocks within 2 m (range 0-50%), 16.78% herbaceous cover within 2 m (range 0-98%), and 1.00 m to the nearest canopy opening greater than 3 m in diameter (range 0-5.78m; Sperry et al. 2012). In Texas, better-quality territories had fewer trees and more understorey vegetation. The mean characteristics of 27 territories were 0.60 m^2 per m^3 foliage density 0-3 m from the ground, 0.27 m^2 per m^3 foliage density at ground level, 0.13 m^2 per m^3 foliage density 1 m from the ground, 0.12 m^2 per m^3 foliage density 2 m from the ground, 0.08 m^2 per m^3 foliage density 3 m from the ground, 0.04 m^2 per m^3 foliage density 7-13 m and 13-20 m from the ground, 0.20 m^2 per m^3 foliage density above 20 m from the ground, 26.85% canopy closure, 13.41 m vegetation height, 3.12 tree species, 7.47 trees smaller than 6 cm DBH, 8.21 m^2 per ha basal area, 8.37 shrub species, 29.96 shrub stems, 42.91% ground cover, and 3.78 grams of arthropod biomass. Mean characteristics within 8 m of 30 nest sites were 0.28 m^2 per m^3 foliage density at ground level, 0.23 m^2 per m^3 foliage density 1 m above ground, 0.32 m^2 per m^3 foliage density 2 m above ground, 0.15 m^2 per m^3 foliage density 3 m above ground, 0.02 m^2 per m^3 foliage density 7-13 and 13-20 m above ground, 0.29 m^2 per m^3 foliage density more than 20 m

above ground, 11.98 m vegetation height at the nest, 7.43 m^2 per ha basal area, 2.88 m nest-plant height, 45.09% horizontal concealment of the nest, and 64.57% vertical concealment of the nest (Conner et al. 1986).

Most researchers concur that the Northern Cardinal is an edge species, although it may nest in gaps in forest interior (Bowen et al. 2014). In Tennessee, it was most abundant within 30 m of edge, declining significantly to 22% of the edge density 120 m from edge. Nonetheless, it occurred in low density as far as 458 m from edge (Kroodsma 1984). In Missouri, it preferred to nest within 20 m of edge and avoided areas more distant from edge. Only 1 nest was further than 40 m from edge (Woodward et al. 2001). In New Jersey, Suthers (1988) reported that it preferred to feed in shrubs on edges.

The cardinal is not usually considered an area-sensitive species. It commonly nests in very small patches and urban areas with scattered woody cover. In some areas, populations are so dense that large patches are frequented as often as small patches. In certain areas, larger wooded areas may be preferred. In Connecticut, its abundance was significantly negatively correlated with forest size (Askins et al. 1987). In Virginia, it was more abundant in woodlots 4-24 ha in size than in blocks of contiguous forest larger than 50 ha (McShea and Rappole 1997). In red maple swamps in Rhode Island, it was most abundant in stands less than 1 ha in area, but not significantly (Golet et al. 2001). In riparian forests of differing widths in Maryland and Delaware, it was one of the most abundant species. There was no difference in its probability of detection in forests 50 m wide and those 800 m wide (Keller et al. 1993). In Illinois, its abundance was significantly correlated with patch size of isolated woodlots, but only in 1 of 2 years (Blake and Karr 1987). In South Dakota, it was significantly more abundant in large riparian forested corridors than in small isolated woodlots (Gentry et al. 2006). It is possible that some small isolated woodlots are deficient in key habitat features such as invertebrates or shrubs and saplings.

Ontario nests were in living deciduous trees, shrubs, and vines (63.3% of nests), and in living coniferous trees and shrubs (35.2% of nests). The most frequently used species were hawthorns (57 nests), cedars (55), spruces (41), grapevines (27), and honeysuckles (12). Only 1.5% of nests were in dead or dying trees or shrubs. In residential areas, the cardinal often used hedges and small ornamental trees and shrubs as nest sites and several were very close to buildings. In other habitats, it often nested in shrubby tangles and vine-covered trees and shrubs. Unusual nest sites included 2 in upturned tree roots (1 over water), 1 on top of a fence in a shrub, 1 in a roll of fence in raspberries, 1 in a climbing rose on a lattice, 1 in vines on a cottage wall beneath the eaves, and 1 in a tree in a greenhouse. Most nests were in crotches, with some on horizontal branches. They were either against the main trunk or more frequently 0.6-1.5 m from it. Most nests were located from the centre to near the top of the shrub or tree. Nests were 0.5-4.9 m from the ground with most 1.2-2.1 m up (Peck and James 1987). Peck and James (1998b) reported an exceptionally high nest 22 m from the ground in a white pine. All 8 nests that Dow (1969b) found near Elmira were in white cedars, which represented only 17.5% of trees within the home ranges. Conifers provided the best cover early in the season. Nests averaged 1.64 m from the ground (range 1.2-2.7 m).

The cardinal typically nests in shrubs and tree saplings, often in thick tangles of vines. The few that are in larger trees are often among dense foliage of vines but they may be concealed in trees

without vines. It uses a wide variety of tree and shrub species for nesting. In Michigan, 334 nests were found in 53 species of shrubs and trees: 21% in hawthorns, 19% in dogwoods, 9% in honeysuckles, and 8% in wild grape. Coniferous species it nested in included red cedar, white cedar, white spruce, pines, and hemlock. Of 121 Ohio nests, 65% were in honeysuckles or multiflora rose and 7% were in red cedar. Of 140 Indiana nests, 34% were in white elm, 21% in hawthorn, 15% in sugar maple, and 13% in red cedar. The remainder were in wild grape, dogwood, black locust, honeysuckle, Manitoba maple, elderberry, and rose. In Wisconsin, it nested mostly in honeysuckle shrubs and under the leafy canopy of wild grape growing over shrubs or lower tree branches. In Tennessee, it nested in young conifers of many species, privet hedges, rose and honeysuckle vines, various shrubs, blackberry thickets, and saplings of hackberry, elm, hawthorn, and locust. Individuals exhibit no preference for species and may nest in 2-3 different species within a single breeding season. In Iowa, 50% of nests were in shrubs, 20% were in deciduous saplings, 20% were in deciduous trees, 10% were in coniferous trees, and 0% were in forbs or grasses. It has nested on the side of a house, on a feeding shelf outside a second-storey window, among upturned tree roots, inside a chicken coop, in a bale of wire in an open-ended shed, and in a woven-wire sparrow trap on a beam in an outbuilding. The nest is usually in a fork of twigs or small branches or among mats of vine stems. It is wedged into position and not attached to the substrate. Nests are usually very well concealed in a tangle of vegetation. Most nests were 1-2.5 m from the ground, but a few very high nests have been reported. In Tennessee, nests were 0.5-8.5 m from the ground, averaging 1.28 m up before 15 May and 2.0 m later in the season. This did not include an unusually high nest found in a beech tree, but the height of the nest was not specified. Another Tennessee study reported nests 0.76-3.66 m from the ground, with most 1.2-1.5 m up. In Ohio, 2,962 nests ranged from 0.5 to 20 m above ground (mean height 2.87 m). Only 5% of nests were more than 7 m up. Mean nest height in Texas was 1.58 m. Ohio nests were 0.5-18 m from the ground and the mean height in Oklahoma was 1.8 m with a range of 0.38-4.6 m (Austin 1968; Brackbill 1950a; Conner et al. 1986; Halkin et al. 2021; Kearns and Rodewald 2017; Laskey 1944; Stauffer and Best 1980; Stoklosa et al. 2014). The cardinal rarely uses old nests. One used the lower part of a nest that remained from the previous season as the foundation for a new nest (Halkin et al. 2021; Hawksley and McCormack 1951; Laskey 1944).

Males chase all male intruders and some females out of the territory, and females chase out intruding females. Both sexes frequently intrude on other territories, so chases are common. Territorial defence begins in early spring (January to March) and ceases in late summer or autumn. Guarding and defence of the nest against predators are weak and usually ineffective (Breitwisch et al. 1999; Dow 1969b; Halkin et al. 2021; Laskey 1944; Lemon 1968; Nealen and Breitwisch 1997). In dense populations, the home range and territory coincide. In a pioneering population at Elmira, most cardinals did not have neighbours and had very large home ranges (Dow 1969a). Territory boundaries tend to be similar year to year even if they are occupied by different individuals (Halkin et al. 2021). In Texas, territory size was correlated with vegetation height and negatively correlated with foliage density 0-3 m from the ground and at the ground, and the number of shrubs. Territories were larger in areas with mature trees and smaller where only shrubby vegetation was present. A threshold amount of understorey foliage was required in territories (Conner et al. 1986). At Elmira, home ranges averaged 18.81 ha (range 10.97-23.34 ha). In denser populations at Melbourne and

Simcoe, home ranges averaged 4 ha. In dense populations in Tennessee, home ranges and territories coincided and averaged 1.18 ha (range 0.51-2.32 ha). In Ontario, a 4-ha woodlot was never found to support more than 1 pair. In Tennessee, as many as 6 pairs inhabited 1.2-ha woodlots (Dow 1969a). The Ontario study was completed more than 50 years ago when the cardinal was much less common. Territories and home ranges may continue to be large on the periphery of its range, but are probably more typical of other locations where it is more abundant in the province. In Ohio, territories were 0.3-2 ha with larger territories occurring in rural landscapes. A Missouri territory that encompassed 2 residential yards was 0.28 ha. Two Illinois territories were 0.13 and 0.18 ha. Territory sizes may have been underestimated because few observations were made. In Texas, territories were 0.2-0.9 ha and home ranges were 0.8-1.5 ha. Territory sizes of 1.4-1.6 ha have been reported in Arizona; mean territory size in Texas was 0.64 ha; 193 territories in Indiana, Ohio, Tennessee, and Arizona were 0.21-2.60 ha (means 0.93-1.50 ha); Kansas territories averaged 1.3 ha (Brewer 1955; Conner et al. 1986; Dow 1969a; Fitch 1958; Halkin et al. 2021; Hawksley and McCormack 1951; Humbird and Neudorf 2008; Paquin in Gauthier and Aubry 1996; Shustack and Rodewald 2011).

Most yearlings nest close to their natal area, but a few disperse further and these birds appear to be largely responsible for range extensions. In southern Ontario, 26 yearling males first nested an average of 1.55 km (range 0.2-5.3 km) from their natal territories. Yearling females nested 2.61 km (range 0.35-5.3 km) from their natal territory. Males from last broods dispersed further than those from earlier broods. Males from last broods that fledged before late July dispersed further than those from last broods that fledged after late July (Halkin et al. 2021). In Tennessee, 2 yearling males nested 0.8 and 1.6 km from their natal territories, and 1 yearling female first nested 4.0 km from her natal territory (Laskey 1944).

Adult site fidelity is very high, with most birds remaining in the same territory their entire life, or moving only short distances. At London, 65% of breeding birds returned in the following year (Scott 1967). In Ohio, 143 of 241 males (59.3%) and 105 of 184 females (57.1%) returned in a subsequent year (Shustack and Rodewald 2011). Of 1,621 birds in Tennessee, none were found more than 6.4 km from the banding site. Birds were highly sedentary, travelling only a few kilometres in their lifetime (Laskey 1944). Beddell (1963) analyzed banding recoveries and found that most birds were recovered within 8 km of the banding site, although some long-distance movements occurred. Adults of both sexes usually occupy territories with the same or very similar boundaries year to year, but may shift between non-overlapping territories in successive years. In Ontario, yearling birds were more likely to shift territories than adults, possibly because they may be forced to nest in suboptimal habitat in their first year. Of 13 yearling males, 8 (61.5%) remained in the same territory, 4 (30.8%) moved to an adjacent territory, and 1 (7.7%) moved 1.6 km. Of 7 yearling females, 4 (57.1%) remained in the same territory, 1 (14.3%) moved to an adjacent territory, and 2 (28.6%) moved further than 400 m (Halkin et al. 2021). In Kansas, the apparent survival rate was 40% for males and 36% for females; the overall rate of return and survival was 38% (Verheijen et al. 2017).

Dow and Scott (1971) analyzed banding returns for 1,486 cardinals recovered prior to 1962. Only 153 (10.3%) were recovered outside the 10-minute block where they were banded. The mean distance moved by all birds was 77.1 km. The longest distance was 893.2 km almost due east from northern Illinois to central Pennsylvania. One adult flew 523.0 km from New Jersey to New

Hampshire in 71 days. Nine other cardinals dispersed more than 320 km and 14 more moved further than 160 km. Two moved east from southern Michigan to southwestern Ontario, and 12 moved within southwestern Ontario. There was no apparent pattern to the direction of dispersal. More distant dispersal occurred in the first year of life but dispersal by older birds continued throughout their lives. Females decreased dispersal distances with age and were more sedentary than males. The number of cardinals dispersing represented less than 0.004% of birds, but many additional individuals must make shorter movements. Adults tended to disperse greater distances than juveniles. There was no evidence that birds on the periphery of the range dispersed further than those in the centre of the range.

Limiting Factors

Eggs have been reported in Ontario nests from the second week of April until mid-August, with most present from mid-May through the first week of June (Peck and James 1987). At London, the laying period lasted approximately 120 days from mid-April until mid-August (Scott et al. 1987).

Courtship occurs soon after the initiation of song very early in spring, typically in February in Ontario. In Ohio, nesting activity began earlier in urban than rural areas. Older males establish territories before yearlings. Nest-site visiting and displays with nesting material may occur 5-16 days before the initiation of construction of the first nest. Nests are built in 2-9 days. During adverse weather, it may take 3-4 weeks to complete a nest. Egg laying begins 1-8 days after nest completion with the interval shortening as the season progresses; 1 egg is laid per day. The egg-laying period extends into August throughout the cardinal's range and into September in more southern areas. One clutch was still being incubated in mid-October in West Virginia. Incubation begins with the laying of the last egg. At London, the mean incubation period was 12.2 days. Incubation periods of 11-13 days have been documented in Ontario and elsewhere. Brooding of the nestlings by the female is almost continuous for the first 3 days. The nestling period is 7-13 days but most commonly 9-10 days if the nest is undisturbed (Austin 1968; Halkin et al. 2021; Hawksley and McCormack 1951; Koenig and Stahl 2007; Laskey 1944; Peck and James 1987; Potter 1989; Scott and Lemon 1996; Shustack and Rodewald 2011).

In Ontario, the cardinal often successfully rears 2 broods. At London, all second broods fledged from clutches that were initiated when the rate of cowbird parasitism had begun to decline in early July. A median of 28 days elapsed between fledging and laying of the first egg of the next clutch. There is an early report of a pair successfully rearing 4 broods in a season at Toronto (Austin 1968; Peck and James 1998b; Scott and Lemon 1996). Double broods are common throughout the cardinal's range, but 3 or even 4 broods may be attempted. Three successful broods have been reported in Quebec and Tennessee, with Tennessee birds attempting a fourth brood unsuccessfully in 2 consecutive years. In Ohio, birds that initiated nests in early April made 4 nesting attempts. Those initiating nesting in late May made only a single attempt. In Kentucky, the mean number of nests initiated by 17 pairs was 2.94. When a single young fledges, the second nest is initiated about 12 days later. If 2 or more young fledge, the second nest is delayed to an average of 19.2 days after fledging (Halkin et al 2021; Laskey 1944; Pacquin in Gauthier and Aubry 1996; Ritchison et al. 1994; Shustack and Rodewald 2011). The cardinal is a frequent renester if early nests fail. It may attempt as many as 8 clutches within a season. In Ohio, 29.7% of females renested after an unsuccessful

attempt, similar to the 30.1% that attempted another brood after a successful nest (Halkin et al. 2021; Shustack and Rodewald 2011; Stoklosa et al. 2014). At London, 84 females that renested after failure laid their first egg in the replacement nest an average of 5.53 days after the loss (range 3-16 days). Renesting intervals were longest and most variable in April and May and shorter later on. Prior to 17 May when the interval length was most variable, the time between nests was dictated by temperature. Only 27.3% of intervals were within 6 days during below-average temperatures; 85.7% of warm-weather intervals were within 6 days. The stage at which failure occurred had no effect on the renesting interval. It cannot physically renest within a period shorter than 4 days because it takes that long for the egg to develop. When shorter intervals occur, the first egg of the second clutch would probably have been the last egg of the previous clutch (Scott et al. 1987). In Ontario, clutches of 2-5 eggs have been documented (mode and mean, 3 eggs). Single clutches of 6 and 8 eggs were reported (Peck and James 1998b), but it is likely these were laid by more than 1 female. Elsewhere, clutches of 1-5 eggs have been reported. The mean clutch size in Kansas was 3.31 eggs. Single-egg clutches may be a result of partial predation. Three-egg clutches are the most abundant in most populations (Austin 1968; Halkin et al. 2021; Laskey 1944; Rice 1969; Scott and Lemon 1996).

Both sexes are capable of breeding in their first year (Halkin et al. 2021). Yearling males have difficulty establishing a territory because adults defend the same area year to year. At London, 3 yearling males eventually acquired territories after they became vacant. Three others acquired territories of inferior quality with little vegetation. They did not return the next year. Three yearling males did not attract a mate, although females occasionally visited their territories. Unmated females also occurred. These trespass into territories in an attempt to mate with the male, even if he is already mated (Lemon 1968).

The mating system is monogamous (Halkin et al. 2021). Male bigamy is rare with only 3 cases confirmed. Two occurred in London where unmated females persistently trespassed into males' territories, resulting in mating and bigamy by the male. Neither case was successful because the male tended to them less. The females eventually disappeared, although one did build a nest (Lemon 1968). Another case of bigamy occurred in Ohio. The male occupied one of the largest territories in the study area. The mate of the neighbouring female disappeared and the bigamous male further expanded his territory to include hers. The nests of the 2 females were 60 m apart and out of sight of each other. The male fed the primary female but not the secondary female. He fed the nestlings at both nests at approximately the same rate. The incidence of bigamy at 2 locations was less than 5% and more likely less than 1% (Bretwisch et al. 1999). Monogamous pairs may remain mated for several years (Laskey 1944) and some pairs remain on their territories year round. In Ohio, 2 of 10 pairs (20.0%) divorced between seasons and 2 of 21 pairs (9.5%) divorced within seasons. Upon divorce or death, mates are replaced by unmated individuals or neighbours that have also lost their mates. New pairs form during the breeding season or even in autumn (Halkin et al. 2021; Ritchison et al. 1994).

Extra-pair copulations may be a common mating strategy, although the incidence of extra-pair fertilizations in cardinal populations appears to be lower than for most passerine species. Both sexes occasionally leave their territories during the breeding season, with females moving as far as 75 m and males as far as 100 m (Halkin et al. 2021). Males guard females in an effort to reduce the

incidence of extra-pair copulations. Pairs spend more time together during the female's fertile period, with males in close contact with fertile females 72.8% of the time during initial nesting attempts. Attentiveness may decline with subsequent nestings. In Kentucky, 5 of 37 nestlings (13.5%) were extra-pair young; they were present in 3 of 19 broods (15.8%). Males benefit from extra-pair copulations by increasing their reproductive success at the expense of other males. Males contribute significantly to the care of nestlings and their assistance may be essential. They may gain more from parental efforts than by pursuing extra-pair fertilizations, which may explain the low incidence of this mating strategy. Female cardinals have more opportunities to assess the quality of males than females of migratory species, so extra-pair fertilizations may be less likely to be beneficial to them (Ritchison et al. 1994). Nonetheless, females have been observed soliciting extra-pair copulations on neighbouring territories (Halkin et al. 2021). In Texas, all females made extra-territorial forays to either forage or seek extra-pair copulations. Supplemental food was supplied on some territories. If females left territories to forage, those with supplemental food should leave less frequently than those without supplemental food. Females with supplemental food spent significantly more time off their territory than those without supplemental food. Results supported the hypothesis that the extra food allowed females to spend more time off their territories, possibly in search of extra-pair copulations (Humbird and Neudorf 2008).

Intraspecific nest parasitism is a rare breeding strategy. In Oklahoma, 3 of 93 nestlings (3.2%) were not related to the female tending the nest, indicating that egg dumping had occurred (Halkin et al. 2021). Peck and James (1998b) reported 2 nests with clutches of 6 and 8 eggs. The abnormally high clutch sizes may have been a result of intraspecific nest parasitism.

The bill of the cardinal is highly adapted for extracting seeds by crushing or cutting shells. At Elmira, foraging sites underwent strong seasonal changes. Early in the breeding season, most foraging occurred on the ground in freshly cultivated fields, old grassy meadows, or in leaf litter in forests. As the season progressed, foraging sites shifted with the availability of food. It consumed tree buds just before leafout. When the canopy was fully developed, it foraged among the leaves for insects. Individuals tended to exploit whatever was available in their territory. It foraged in coniferous foliage 1.9% of the time, less than its availability (Dow 1969b). It actively moves along branches to search the foliage for insects and takes fruit from trees, shrubs, and vines. It pecks grapes with its bill, removing the pulp and seeds and discarding the skin. It has been observed catching termites in flight. One captured large goldfish in an outdoor pool (Halkin et al. 2021). In Florida, it fed on the nectar of 2 plants. It picked off the blossoms, consumed the nectar in them, and discarded them, dropping them to the ground (Russell 1951; Wible 1974). It occasionally drinks from sapsucker wells in maple trees (Austin 1968).

The red colour of the cardinal results from ingestion of carotenoid pigments obtained from the diet and may signal the quality of individuals. Fruits and insects are high in carotenoids; seeds have low carotenoid concentrations. The relationship between plumage brightness and condition is most pronounced in rural birds. In urban areas, carotenoid-rich foods from anthropogenic sources and invasive shrubs are more available to birds over a wide range of conditions. Males with brighter plumage have higher reproductive success and territories with greater vegetation density (Halkin et al. 2021; T.M. Jones et al. 2010). Plumage brightness of the adults affected the rate at which they fed

their nestlings. Male feeding rates were unaffected by the brightness of their breast plumage but the underwing brightness of females was positively correlated with the number of feedings per nestling per hour. Females mated to bright males fed their nestlings less than those mated to duller males. Females mated to bright males may increase their reproductive success by decreasing their provisioning effort while preparing physiologically for the next nesting. The underwing colour of a female appears to be an indicator of quality that may be maintained by sexual selection (Linville et al. 1998).

The male plays an important role in reproductive success. He feeds the female during incubation both on and off the nest. This allows her to be more attentive and potentially reduces the incubation period and increases nest success. Males feed the nestlings at a higher rate than females. Only males maintain their feeding rate per nestling as brood size increases and increase their feeding effort as the nestlings age. When males disappeared or were removed, there was no significant difference in the number of nests that failed. Females increased their feeding rates to compensate for the males′ absence. Males also care for the first brood if females initiate another nest. The rate of feeding by adults is unrelated to their age or experience (Filliater and Breitwisch 1997; Halkin et al. 2021; Laskey 1944; Linville et al. 1998; Ritchison et al. 1994).

Nestlings are highly insectivorous, with 94.75% of their diet consisting of animal food; 5.25% of the diet is vegetable matter. Two nestlings had eaten cicadas, caterpillars, grasshoppers, and spiders. Four others had consumed 17.25% cicadas, 20% grasshoppers, 21.25% caterpillars, and 23.25% beetles. Young have been fed dragonflies, mulberry seeds, horse flies, snails, and grass seeds (McAtee 1908). Young at 1 nest were fed goldfish (Halkin et al. 2021).

Adult cardinals feed on a mix of animal and vegetable foods, with animal foods predominating in the early portion of the breeding season. Late in the breeding season and during the postfledging period, fruits become important in the diet. The winter diet is comprised of 88% vegetable matter. This proportion is probably higher in more northern areas that are snow-covered for most of the winter. In the northeast, the main vegetable foods include fruits and seeds of wild grape, smartweeds, dogwoods, sedges, mulberries, sumacs, vervains, tulip tree, corn, and oats. In the southeast, it also consumes foxtails, blackberries, and panic grasses. It eats seeds of croton, hackberries, bush-clovers, and blazing-stars (Halkin et al. 2021). In spring in Ontario, it has been documented feeding on sugar maple sap icicles (Simpson 2025). Stutchbury et al. (2005a) studied its frugivory on red elderberry in Pennsylvania. The cardinal was one of the most abundant species, occurring on 71% of surveys but was rarely observed foraging on elderberries. It foraged on elderberries at 5.9% of sites and made only 1.9% of all bird visits to elderberries. Other authors have reported it feeding on cicadas and fruits of mulberries, hollies, and red cedar (Dow 1969b; Holt 1916; Petrides 1942; Royall 1995). Beal et al. (1916) reported that the diet of the cardinal in the southeastern United States consisted of 29% animal and 71% vegetable matter. The dominant animal foods were caterpillars, beetles, grasshoppers, and true bugs. The beetles were predominantly weevils but it also ate click and leaf beetles. The vegetable food was mostly weed seeds but also wild fruit and grain. When eating fruit, it typically eats only the seeds and rejects the pulp. Wild grape is a favourite, but it also eats seeds of dogwoods, blackberries, hackberries, greenbriers, cherries, blueberries, elderberries, pokeweed, and juneberries, and fruits of prickly-pear cactus, sumacs, holly, hawthorns,

and mulberries. Weed seeds comprised more than 33% of the diet with smartweeds most important. It also ate seeds of foxtails, crabgrass, dodder, dock, sow thistles, plantains, tumbleweed, lamb's-quarters, chickweeds, beggarticks, partridge pea, and buttonweed. McAtee (1908) analyzed the contents of 408 stomachs from 20 states, the District of Columbia, and Ontario, but a high proportion of samples were from Texas. The diet consisted of 28.99% animal and 71.1% vegetable matter. Animal food reached its maximum of 78.4% of the diet in May; the minimum was 4.9% in January. The plant material consisted of 36.38% weed and other seeds, 24.17% wild fruit (of which usually only the seeds were eaten), 8.73% grain, and 1.73% miscellaneous material. Of the weed seeds, smartweeds were most important at 5.57% followed by foxtails at 3.21%. Other seeds it commonly consumed included those of barnyard grass, crabgrass, goose grass, sedges, blue and white vervain, and ragweeds. It ate fewer seeds of dodders, vetches, docks, sow thistles, sunflowers, violets, geraniums, stargrass, corn, gromwell, spiderwort, lamb's-quarters, chickweeds, beggarticks, and clovers. Grapes were the most important wild fruit, representing 17% of the diet from November to April. Dogwood fruits, mostly those of rough-leaved and flowering dogwood, were next in importance, representing 3.97% of the annual diet. Other fruits comprised 8.3% of the diet, mostly blackberries and raspberries, but also mulberries and hackberries. Less-frequently consumed fruits included those of greenbriers, solomon's-seal, chokecherry, sweet cherry, apple seeds, blueberries, spicebush, pokeweed, prickly-pear cactus, poison ivy, elderberries, roses, juneberries, hollies, red cedar, and hawthorns. Corn was the most important grain, comprising 7.1% of the diet. Most was eaten in winter and was waste grain. Wheat, oats, sorghum, and rice comprised the other 1.62% of grains in the diet. Miscellaneous vegetation included acorns, hickory nuts, maple samaras, tulip tree seeds, galls, and buds. The animal food included millipedes, centipedes, insects, spiders, clams, and snails. It has been reported eating a mouse. Insects were most important, comprising 26.25% of the 18.99% animal food. Beetles represented 10.48% of the diet with weevils most important at 3.26%. Other beetles that it consumed were scarab, june, metallic wood-boring, click, long-horned, leaf, darkling, and blister beetles. Grasshoppers constituted 6.43% of the diet, but it also ate crickets and katydid eggs. Butterflies and moths represented 5.1% of the annual diet but 26.71% of the May diet. These were mostly caterpillars but it ate some adults. Bugs comprised 3.72% of the diet, including cicadas, leafhoppers, jumping plant-lice, treehoppers, scale insects, stink bugs, assassin bugs, and chinch bugs. Hymenopterans represented about 1% of the diet, mostly wasps, but ants and sawflies were also eaten. It rarely ate flies and mayflies. Snails were commonly consumed, 1 slug was eaten, and 1 bird had eaten several small clams that it must have obtained from water.

Two studies compared the feeding ecology and seed preferences of the cardinal with other species. In an aviary experiment, Browning et al. (1981) provided seeds of round-headed bush-clover, blazing-star, and 2 types of sunflowers to the cardinal. The cardinal selected sunflower seeds and ate few bush-clover and blazing-star seeds. It gained 1% of its weight daily when feeding on sunflower seeds and lost 12-13% of its weight when feeding on the other 2 species. Bush-clover was of the lowest nutritional quality and least preferred; sunflowers were the highest quality. In North Carolina, Pulliam and Enders (1971) compared the feeding ecology of the cardinal, Field Sparrow, Dark-eyed Junco, White-throated Sparrow, and Song Sparrow. Vegetable matter comprised 100% of the cardinal's January diet, dropping to a low of 40% in July and increasing to 90% from October to March. This pattern was similar for all species. The mean size of seeds it consumed was 3.1 mm.

Almost all foods larger than 3.5 mm were soft fruits; smaller seeds were hard grains, achenes, and nutlets. The main habitats it used were dominated by crabgrass, broomsedge, or shrubs. Cardinal habitat use overlapped 51% with the Field Sparrow, 73% with the junco, 65% with the Song Sparrow, and 72% with the White-throated Sparrow. Seed-site use overlapped 100% with the Field Sparrow, 98% with the junco, 99% with the Song Sparrow, and 100% with the White-throated Sparrow. Twenty-three percent of cardinal feeding observations were of birds perched on plants, 9% on bare ground, and 68% standing on the ground feeding from a standing plant. The cardinal spent the most time (34%) in forests of the species and ate the most fruit (32%) thereby reducing competition. The authors concluded that these species were limited by the food supply, with the presence of any species reducing the total number of individuals of any other species that a site could support.

The cardinal is one of the Brown-headed Cowbird's more common hosts. Despite this, parasitism has a low effect on the reproductive success of the cardinal, and reproductive success of cowbirds in cardinal nests is very low. The cardinal is an acceptor of cowbird eggs (Rothstein 1975). Its primary defence is nest abandonment. Using data from the Ontario Nest Records Scheme (ONRS), Graham (1988) determined that 52% of parasitized nests were abandoned compared with 4% of unparasitized nests, a significant difference. Egg acceptance rates were 25% before the peak of clutch initiation and 52% later. Cowbird eggs are occasionally buried in cardinal nests, but this is probably due to parasitism occurring before the nest is complete. McLaren et al. (2006) also used ONRS data to conclude that there had been no change in frequency or intensity of cardinal nest parasitism in response to population changes of the cowbird. At London, cardinals rarely deserted parasitized nests unless there was obvious interference by the cowbird. Cowbirds began parasitizing nests there in late April, about a week after cardinals initiated nesting, with peak parasitism rates reaching 100% at the end of that month. There was a decline in the rate of parasitism in May and June that was likely due to cowbirds selecting alternative hosts. The incidence of parasitism declined rapidly in July, dropping to 0% by August. This was a result of the reduction in reproductive activity of the cowbird. Seventy-five percent of parasitized nests lost an egg compared with 12.5% of unparasitized nests. This was attributed to cowbird removal of eggs. Reduction of clutch size appeared to be the only negative impact of parasitism on the cardinal. Hatching and fledging success rates for cardinals were similar in parasitized and unparasitized nests. In contrast, very few cowbirds survived in cardinal nests and many that did fledge died a few days after leaving the nest (Scott 1963, 1977; Scott and Lemon 1996). Eckerle and Breitwisch (1997) reported similar results in Ohio, with the timing of parasitism similar and the only cost to cardinals being egg removal by cowbirds. They concluded that the lack of rejection behaviour by the cardinal may be due to the low costs of parasitism. Stoklosa et al. (2014) studied parasitism on the cardinal in Ohio in relation to distance to forest edge. Early in the nesting season, the risk of parasitism was lower in nests further from edge but the opposite was true later in the season. Cowbirds may spend more time searching for prey in forests later in the season as arthropod abundance increases and move further into forests to seek alternative host species. Peck and James (1998b) reported that 72 of 358 nests (20.1%) were parasitized in Ontario. At London, 72 of 85 nests (89.7%) were parasitized 1960-69 (Scott 1977). From 1955 to 1968, about 230 of more than 700 nests (about 33%) were parasitized (Scott and Lemon 1996). Parasitism rates in other areas include 6 of 231 nests (2.6%) in Georgia (Kilgo and Moorman 2003), 139 of 347 nests (40.1%) and 55 of 115 nests (47.8%) in Ohio (Eckerle and Breitwisch 1997;

Stoklosa et al. 2014), 10 of 15 nests (66.7%) in Kansas (Rivers et al. 2010), 1 of 7 nests (14.3%) in New York (Hahn and Hatfield 1995), and 13 of 39 nests (33.3%) in Illinois (Chapa-Vargas and Robinson 2013).

Habitat loss is not a limiting factor for the cardinal. Forest fragmentation and urbanization have created considerable habitat for it. Modern subdivisions are considerably less likely to provide suitable habitat due to the high density of houses and small yards with limited planting of shrubs.

Several studies examined whether urban areas and forest edges, 2 preferred habitats, are ecological traps, enticing cardinals to nest where reproductive success is likely to be low. In Ohio, Leston (2006) reported no significant differences in productivity and return rates of adults in urban and rural forests. The cardinal strongly selected for exotic shrubs as nest sites and urban forests with lower canopy heights where these shrubs were common. Even though nests in exotic shrubs were more than 2 times likely to fail as those in native trees and shrubs, overall productivity in urban forests was similar to that of rural forests. It was concluded that there was no evidence that urban forests acted as ecological traps. In Missouri, Woodward et al. (2001) observed no difference in nest success in relation to distance from edge and concluded that edge did not act as an ecological trap. In Illinois, Chapa-Vargas and Robinson (2013) determined that nest success decreased slightly but nonsignificantly as the amount of agricultural habitat within 500 m of the nest increased. They concluded that the landscape was saturated with predators and that nesting success did not increase with increasing proportions of natural habitat. In Indiana, Ford et al. (2001) compared parasitism and nest survival rates in a 1.1-km forested floodplain corridor and an 87%-forested landscape. There was no difference in the parasitism rates in the 2 habitats. Cardinals in the forested landscape produced 2 times as many fledglings per nesting attempt than those in the riparian corridor. In Ohio, Shustack and Rodewald (2011) found no differences in productivity of birds nesting in rural and urban areas and there was no particular advantage or disadvantage to nesting earlier in the season. In Missouri, Peak et al. (2004) studied cardinal nest success in narrow (55-95 m) and wide (400-530 m) riparian forests. The habitat, edge, timing of nesting, and nest site had limited effects on nest success. Even wide corridors were insufficient to increase nest success in agricultural landscapes saturated with predators.

In Texas, Conner et al. (1986) examined characteristics of successful and unsuccessful territories. Territories with successful nests had higher foliage density 2 m above ground throughout the territory than those with unsuccessful nests. Fledging success and the number of young in nests were positively associated with arthropod biomass, which in turn was correlated with foliage density 0-3 m from the ground, percent ground cover, and shrub species diversity. Arthropod biomass was negatively correlated with the number of trees, basal area, and tree height. There was no correlation between nest height and nest success.

Several studies examined cardinal nesting in relation to predator populations. In Ohio, first nests of cardinals were located in areas of high activity of avian predators and cowbirds, significantly higher than in random locations. Second nests were not associated with high levels of activities of these species. Nest survival decreased when both avian and mammalian predator activity was high but increased over the season when only mammalian predator activity was high. There was little evidence that cardinals used predator activity as information to select nest sites. Other cues such as

nesting habitat, food resources, and social information may be more important in nest placement and habitat selection (Kearns and Rodewald 2017). Also in Ohio, Malpass et al. (2017) determined the effects of bird feeders on nest predation of the cardinal. Neighbourhoods with at least 15 feeders had 2.7 times more American Crows and 3.2 times more cowbirds than those with 3 or fewer feeders. Nest survival of the cardinal was not related either to the number of feeders or predators. In Texas, cardinal nest survival was negatively correlated with rat snake activity, which was low in the early and late nesting season and peaked mid-season. Snakes were found in areas with more habitat structure than cardinals. Nest-site attributes had little influence on nest survival, which was related predominantly to snake activity (Sperry et al. 2012).

McAtee (1908) reported that the cardinal was highly sensitive to disturbance and would abandon unfinished nests and even full clutches if disturbed. It is quite possible that it is now more habituated to human activity. Smith-Castro and Rodewald (2010) studied its response to human disturbance along recreational trails in Ohio. When approached directly, 67% of females flushed from nests compared with 11% when a human passed by on a trail. Birds with nests closer to the ground had a greater tendency to flush. Birds did not appear to habituate to humans, with those closer to trails having an increased tendency to flush. There was no association between nest survival and the tendency of a female to flush. Human disturbance related to trail use had only short-term effects with no effects on nest survival. Battle et al. (2016) conducted a similar study in urban and rural areas in Virginia. The average flight initiation distance was 8.5 m in urban habitats and 13 m in rural habitats. Although the difference was not significant, birds in urban habitats may have been more habituated to human activity. Baldassarre et al. (2024) reported almost identical results in New York. The average flight initiation distance was 8 m in urban habitats and 17.5 m in rural habitats. In Virginia, McShea and Rappole (1997) determined that birds more than 50 m away from the observer sang more frequently than closer birds. In the late 19th and early 20th century, the cardinal was a common household pet. In some areas, great numbers were captured and sold into captivity. Many were also killed for the millinery trade (McAtee 1908).

Forest harvesting tends to have either no or positive effects on the cardinal. In small clear-cuts in Pennsylvania aspen and oak stands, there were no significant differences in its abundance before and after cutting (Yahner 2003). In southern Ontario deciduous woodlots, there were no significant differences in its abundance in uncut stands, those that were selectively thinned, and those where heavy diameter-limit cuts were made (Holmes et al. 2004).

Drought may end the nesting season prematurely by reducing the availability of insect prey (Halkin et al. 2021).

In Tennessee, the cardinal responded favourably to fire in pine-oak forests. It occurred more frequently only after high severity burns that resulted in more than 60% mortality of the canopy and loss of most of the understorey (Rose and Simons 2016).

In Delaware, density of the cardinal was similar in areas with low, moderate, and high white-tailed deer populations. Shrub-nesting species combined were consistently found with greater species richness and abundance at low deer densities (Tymkiv et al. 2012).

In West Virginia, Farwell et al. (2019) investigated the effects of shale gas infrastructure (access roads, pipelines, and well pads) in a large contiguous forest. There was no significant difference in the cardinal's abundance near or distant from any of these facilities.

Near Missouri lead mines, the probability of a female fledging a young decreased from 60% to 48% in areas with elevated lead concentrations in soil. Most nest failures were due to predation, suggesting that lead affected birds' behaviour and activity at the nest or affected nest-site quality (Thompson et al. 2024).

In North Carolina, the abundance of the cardinal increased with increasing temperatures (Lumpkin and Pearson 2013). Price (2004) predicted that its range in southern Ontario might expand if the average summer temperature increased by 2°C.

Status

The Northern Cardinal is a recent addition to the avifauna of Ontario. Its range expansion into the province was part of a larger range extension that was probably prompted by increased habitat availability as a result of forest fragmentation and urbanization coupled with provision of bird feeders and amelioration of winter temperatures. Fairly uniform peripheral expansion of its range occurred prior to 1943, with a smaller amount of dispersal by birds in the centre of its range and a high amount in the northwest. From 1943-52, there was a decrease in its dispersal in the west and an increase in the east 1953-62. The decrease in dispersal in the west was roughly equivalent to the increase in the east. Juveniles exhibit a marked increase in dispersal after their first year. Dispersal and pioneering occurs in the early years of life, but not all in the first year. In Elmira, 64% of territorial males were yearlings compared with 11% in Tennessee, indicating a high proportion of pioneering by yearlings in Ontario at a time when Elmira was near the northern extent of its range. In comparison, 28% of territorial males at London were yearlings in an area where populations had been established longer. Dispersal occurs both before and after the breeding season from December to April and August to December, by juveniles and adults respectively. Dispersing cardinals tend to follow river systems and settle close to them. Others pioneer in cities near feeders in winter and remain to breed. It appears as though there has been a loosely cyclical pattern of expansion and retraction whereby birds move up waterways to establish local populations only to be extirpated by severe winter weather (Austin 1968; Dow 1994; Dow and Scott 1971; Halkin et al. 2021).

The first record of the cardinal in Ontario occurred at Chatham in 1849. Breeding was first confirmed at Point Pelee in 1901 with subsequent early breeding records at Chatham in 1909, London in 1915, Brantford in 1919, Toronto in 1922, Orillia and Port Hope in 1938, Owen Sound in 1942, Meaford in 1943, and Tweed in 1953 (Baillie 1967; Dow 1994). McIlwraith (1894) considered it a casual visitor along the southwest border. There were a few reports from Port Rowan and Dunnville where it purportedly nested in conifers. In Elgin County, it was accidental in 1891, a common resident in 1954, and a common and widespread resident in 2000 (Lancaster et al. 2004). The first Hamilton record was in 1894 and the first for Guelph was in 1898. It is now an abundant and ubiquitous permanent resident in these areas (Curry 2006). Fleming (1907) considered it accidental in Ontario and concluded that it probably occurred only in winter. Baillie and Harrington (1937) concluded that the cardinal was fairly common in southern Ontario north to at least Simcoe County

and east to Ottawa, with accidental occurrences in Algoma and Parry Sound districts. Its known breeding range was confined to the area south and west of Toronto. In Niagara Region in 1936, it was slowly extending its range from the west but was still rare in the eastern portion of the region. There were no records from the Niagara Falls area but it was fairly common along the Lake Erie shoreline in the western portion of the region (Sheppard et al. 1936). There appears to have been a large increase in its range in Ontario in 1938 so that by 1965-67 the northern extent of its breeding range was a line from Goderich to Port Hope. Its distribution was influenced by lake-effect snowfall with heavy snowfall producing the main limiting factor by diminishing food availability (Dow 1994). It was first seen in Northumberland County in the late 1930s and at Presqu'ile in 1957, where it is now a permanent resident (LaForest 1993). The first record for the Kingston area was in 1951 but it was not confirmed as a breeder until 1968. It is now a fairly common to common permanent resident there (Weir 2008). The first record for Muskoka and Parry Sound districts was in 1954 where it is still uncommon (Mills 1981). The first atlas revealed that the cardinal nested in most squares south of the Canadian Shield, with more records in eastern Ontario and the Ottawa area than previously reported. There were scattered records on Manitoulin Island, where breeding was confirmed, in the southern Shield, and in northern Algoma District. Evidence of possible breeding was obtained near Thunder Bay and Marathon (McNicholl in Cadman et al. 1987). James (1991) considered the cardinal a common permanent resident south of the Shield; rare north to Manitoulin Island and North Bay; and an occasional straggler north to Rainy River, Thunder Bay, and Kirkland Lake.

The second atlas indicated that there had been no significant change in the cardinal's range since the first atlas. The population appeared to continue to grow, particularly south of the Shield in the Great Lakes–St. Lawrence Forest Region. Its probability of observation increased significantly there, particularly in southeastern Ontario and along the southern edge of the Shield. It also occurred in more squares in the southern Shield and on Manitoulin Island. There were additional records from the north near Atikokan, Cochrane, and Kenora, which represented significant northward movement. It was most abundant along the north shore of Lake Erie and southwestern Lake Ontario northeast to Toronto. An area of higher density also occurred in the urban portion of Ottawa (McLaren in Cadman et al. 2007).

In Ontario, BBS data indicated that the cardinal increased at an annual rate of 3.2% 1983-2013, the 24th highest rate of all Ontario birds (Cadman et al. 2016). It appears to have increased in much of its range in addition to expanding its range. BBS results indicate that it increased at annual rates of 3.66% in Canada and 3.09% in Ontario 1970-2021. The trends 2011-21 were annual increases of 4.72% in Canada and 3.74% in Ontario. Results were highly reliable for the long-term Canadian and short-term Ontario trends; the other results were of medium reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Young are unable to fly when they leave the nest, or can fly weakly, and are capable of strong flight when they are 19 days old. At 1 nest, young travelled 18 m from the nest across a yard to a privet shrub where they remained overnight. Birds in urban yards tend to remain close to the nest for several days. For the first 11 days after fledging, young rarely move from the branches where they are perched. From 12-20 days after fledging, they move more, occasionally leaving the natal territory

but still receiving most of their food from the parents. In southern Ontario, young were fed an average of 32 days after fledging with an average of 39.2 days in Ohio. Complete independence may not be attained until the young have been out of the nest for 56-59 days. Prior to the female initiating another brood, the earlier brood is split between the adults. Once the female starts the next nest, the male cares for all the fledglings. The male feeds them until the next brood hatches, and the first brood leaves the natal territory about this time. The last brood of the season is attended to by both adults and tends to remain on the natal territory longer than earlier broods and is fed for longer (Austin 1968; Halkin et al. 2021; Laskey 1944; Van Tyne 1951).

Ausprey and Rodewald (2013) studied the movement patterns and habitat use of cardinal fledglings in Ohio. The mean 95% home range of 20 fledglings was 2.33 ha (range 0.92-6.75 ha); the mean 50% kernel home range was 0.48 ha (range 0.21-4.6 ha); and the minimum 95% convex polygon was 0.93 ha (range 0.18-2.74 ha). Young dispersed from the natal territory an average of 47 days after fledging (range 35-55 days). The distance from the nest on the breakpoint day was 23.1-51.3 m. The natal-range size was correlated with fledglings' distance to forest edge, with birds near edges having smaller ranges. Distance from the nest to the range was negatively correlated with the extent of urbanization in the surrounding landscape and percent cover by honeysuckle at the nest. Thirteen of 20 fledglings (65.0%) dispersed from the natal territory. Birds that dispersed locally did so within their natal forest but others made extended movements to other forest fragments or into the surrounding landscape matrix. Birds leaving the natal forest dispersed significantly further (median 594 m, range 349-985 m) than locally dispersing birds (median 171 m, range 93-569 m). Of birds that dispersed, 11 went to a single dispersal area, 1 moved to 2 sites, and 1 moved to 3 sites. Six birds that dispersed made exploratory movements into their future home range before dispersing. Birds in forests with higher densities of conspecifics dispersed later than those in forests with low density. The extent of movement was inversely related to preferred habitat attributes, with less movement from sites with extensive honeysuckle cover or those in heavily urbanized landscapes. Proximity of forest edge, which often supports dense vegetation, contributed to the size of the eventual home range. Cover of honeysuckle increases with urbanization, so fledglings at urban sites likely had more protective cover from this shrub and moved less. Movements appeared to be related to habitat but the timing of movement was associated with density which may have been a social cue indicating habitat quality. In this study, most birds dispersed near their natal ranges or did not disperse within the life of the transmitters. It is probable that stationary fledglings dispersed later. Other studies determined that juveniles generally move no more than 100 m and many remain within a few kilometres of the natal area.

Fledgling position in the canopy was influenced by the presence of honeysuckles. The average height of fledglings' perches was 4.1 m. Fledglings in honeysuckle were significantly lower (2.1 m) than those in other substrates. Fledgling age and position were not significantly related. Microhabitats used by fledglings differed significantly from random. Selected areas had 1.7 times more honeysuckle cover and 1.3 times more saplings than random areas. Areas used by fledglings had significantly more surrounding vegetation than nest sites. Fledglings selected areas with 2.2 times more shrub coverage than occurred at nests (Ausprey and Rodewald 2011).

In Ohio, Ausprey and Rodewald (2011) studied fledgling survivorship along a rural to urban gradient and how the presence of Amur honeysuckle influenced survival. Cardinal density was 1.7 times higher in urban forests than rural forests during the breeding season and 4.0 times higher in the postfledging period. Mortality of fledglings was greatest in the 3 days following fledging. Their survival rate increased as the number of saplings 3-8 cm DBH increased and the number of small (8-23 cm DBH) and medium-sized (23-28 cm DBH) trees decreased. The survivorship on days 1-3 increased from 73% to 95% as the number of saplings increased from 0-46. Survival increased as the landscape became more urban, and was 59% higher in the most urban areas than the most rural areas. Survival tended to be higher in urban areas in the first 3 days when mortality was highest. Fledglings were more likely to survive as the structural complexity of forests increased, and urban forests were denser due to the presence of honeysuckle. Survivorship was not related to the extent of urbanization but rather to the structural complexity of the vegetation, whether or not it was honeysuckle. Although urban areas tend to have higher predator densities, presence of outdoor pet food, refuse, bird feeders, and other food sources may weaken the link between predator populations and bird depredation rates. In this area, urban forests appeared to act as source populations for the cardinal.

Limited information is available on the diet of fledglings but they probably eat mostly insects. They have been fed cicadas, grasshoppers, snails, weevils and other beetles, caterpillars, and blackberry seeds. Young at a feeder ate bird seeds, elderberries, suet, bread, and cheese. Adults at the same feeder ate all these items plus canary seed, corn, nut meats, and sunflowers. Fruit becomes important in the adult diet during the postbreeding moult. In Ohio, the adult diet consisted of 58% fruit, 18% unidentified, 16% insects, and 8% seeds (Halkin et al. 2021; McAtee 1908; Nice 1927; Van Tyne 1951).

Flocks of cardinals begin to assemble after the autumn moult. These start as family groups and enlarge as birds from adjoining territories join. Flocks may remain intact until early spring when individuals begin to establish territories. Other birds remain in their territories year round and briefly join these flocks as they pass through the territory (Halkin et al. 2021; Laskey 1944).

MIGRATION

The Northern Cardinal is usually considered a permanent resident that exhibits no evidence of migration. Many birds remain on their breeding territories in the winter and essentially for their lifetime once they reach breeding age. Reports of migration are often dismissed as representing juvenile dispersal (Halkin et al. 2021).

There is some evidence that at least a proportion of the population undertakes migratory movements. Brewer et al. (2018) reported that northern populations are partly migratory. Dow (1994) reported that there appeared to be a well-defined movement through Long Point in late April and early May at a time when most birds were breeding. This suggested that dispersal was more than casual random movement away from natal areas. Austin (1968) reported that there was a decided trend of movement north and northeast in late summer and autumn that might account for many northern winter records and for its northward spread. In Illinois, Graber and Graber (1963) reported that there appeared to be a southward shift of the population in midwinter. In 1957, populations in the northern and central portions of the state were lower in January than in June and

the southern population was 2.1 times higher in January than in June. Fitch (1958) also noted seasonal fluctuations in populations in Kansas. It suddenly became more abundant in late autumn of each year. Even larger numbers sometimes occurred in late winter when the weather was severe and the ground was covered by snow.

WINTER

Some cardinals of both sexes remain on their breeding territories all winter. Others join loose flocks that form in September and disband in February once mating activity resumes. Flocks often consist mostly of juveniles but some adults occur, usually with the sexes equally represented. There is a possibility that adults in flocks may be migrants. The number of birds in flocks remains fairly constant but flock membership frequently changes. Flocks tend to move over the landscape, with individuals dropping out as a similar number join. Individuals may move 500-900 m and change flocks and rarely remain with the same flock if it travels further than 1.6 km. Birds that remain on their territories join flocks temporarily as they move through. Flocks are often associated with American Tree Sparrows, Dark-eyed Juncos, Song Sparrows, and American Goldfinches (Dunn and Tessaglia-Hymes 1999; Halkin et al. 2021; Laskey 1944; Lemon 1969; Shustack and Rodewald 2011).

The cardinal typically occurs where the average minimum January temperature is above –15°C. River valleys strongly influence its distribution, with highest densities along major river systems (Root 1988). Smith (2003) analyzed Winter Bird-Population Study data for southern Ontario and determined that the cardinal was most abundant in urban natural areas. Densities per km^2 were 28 in commercial and residential areas dominated by buildings and pavement, 24.3 in urban public spaces smaller than 10 ha, 16.4 in urban public spaces larger than 10 ha, 7 in urban natural areas with water, 1.9 in rural forests, 1 in rural farmlands, and 0 in cropland.

In Illinois, the cardinal was more likely to visit open field habitats in winter than in spring (Graber and Graber 1963). In Arkansas, Kentucky, and Mississippi, Evans et al. (2015) studied its response to buffers of grasses and forbs around fields of corn or soybean stubble. It was more abundant in fields with than without buffers and in fields with buffers less than 23 m in width than wider buffers, but these relationships were not significant. Doherty and Grubb (2000) examined its use of isolated woodlots 0.05-6.01 ha in Ohio during winter. It was less likely to be present as woodlots became more isolated but its density decreased with increased connectiveness. Its density increased with increased coverage by swamps but highest densities occurred in beech–sugar maple woodlots. In Texas, the winter population increased with shrub density and soil moisture. It was most abundant in riverine forests, with a density of 692 per km^2. Densities in other habitats included 148 in oak woodlands, 114 in brushland with 2 layers, 106 in dense brushland, 67 in open brushland, 47 in grass-forb prairie, and 2 in scrubby grassland (Halkin et al. 2020).

The cardinal may have a large home range in winter. In Tennessee, birds frequently moved to a site 1.2 km away to feed on hackberry and sunflower seeds (Laskey 1944). In Kansas, winter home ranges averaged 4.9 ha for 49 males and 9.3 ha for 31 females. This excluded movements of about 800 m by 1 male and 2 females (Fitch 1958). In Kentucky, winter ranges averaged 19.9 ha for males, 23.1 ha for females, and 21.2 ha overall. Daily home ranges averaged 1.17 ha (range 0.32-3.38 ha). Home ranges overlapped with conspecifics by as much as 3.36 ha. Over the course of a winter, an

individual may move back and forth between feeding stations as far as 2.1 km apart and as far as 4.5 km in 1 direction (Halkin et al. 2021; Paquin in Gauthier and Aubry 1996).

In winter, the cardinal prefers to feed on the ground or in short vegetation under woody cover (Dunn and Tessaglia-Hymes 1999). The winter diet consists mainly of seeds. In Ontario, it has eaten seeds of giant ragweed and riverbank grape (Dance 1986, Dance et al. 2012). It rarely feeds on tree seeds, including those of tulip tree. In Florida, it fed on attached pine cones in the mid- to upper canopy. It rarely visits pine forests and typically feeds on the ground. It walked or hopped along branches or made short flights within trees to visit cones. This was the first documentation of it eating pine seeds (McNair 1997). Searles (1989) reported a male and female cardinal feeding on a Black-capped Chickadee carcass.

The cardinal is a common visitor to bird feeders and is common at feeders all winter. Feeders in rural areas are visited less frequently than those in urban areas, but flock sizes tend to be larger in rural areas (Dunn and Tessaglia-Hymes 1999). Stanbeck and Powell (2010) studied its feeder preference based on distance from cover, presence and absence of Cooper's Hawks, and type of seeds provided. They installed feeders 1.5 and 15 m from dense vegetation cover, provided sunflower seeds in some feeders and mixed seeds in others, and played Cooper's Hawk calls. Prior to playing the calls, the cardinal visited feeders with sunflowers significantly more than those with mixed seeds, and significantly more visits were made to feeders closer to cover. Exposure to Cooper's Hawk calls resulted in a dramatic and significant shift in feeder use. On playback days, instead of preferring the higher-quality seed in the exposed feeder, it had a significant preference for the lower-quality seed in the safer location. On days when no hawk calls were played, 67% of visits were to the exposed feeder when it contained sunflowers compared with 36% of visits on playback days. Horn et al. (2014) provided tube, hopper, and platform feeders to participants in Canada and the United States. The cardinal preferred platform feeders over the other 2 types. In North Carolina, Millican et al. (2012) provided feeders with safflower or sunflower seeds. Both sexes visited the sunflower feeders significantly more often than the safflower feeders and both preferred sunflowers when no conspecifics were present at a feeder. Females avoided all conspecifics when visiting feeders regardless of which feeder was occupied. They visited the safflower feeder significantly more frequently than the sunflower feeder when it was occupied. Females were particularly adverse to visiting feeders that were occupied by males. Males avoided feeders occupied by other males, visiting safflower feeders significantly more often when the sunflower feeder was occupied by another male. Males preferentially visited feeders occupied by females even when they contained the less preferred food. The landing of a new bird usually resulted in the departure of the first bird. Other authors noted that males are often aggressive toward females in winter. Females do not exhibit aggression to males at any time of the year (Laskey 1944; Lemon 1968).

Horn et al. (2014) and Johansen et al. (2014) provided 10 types of seeds to participants in Canada and the United States, who made 54,017 observations of feeding cardinals. The cardinal preferred black oil sunflowers over all other seeds. In 93% of observations, it selected seeds with a hull, 46% of the time it selected seeds with greater fibre content, and 27% of the time, it selected seeds with more protein content. The cardinal is one of few species that readily eats safflower seeds at feeders, and sunflowers are a staple. Preferred seeds were those of striped and black oil sunflowers, hulled

sunflowers, mixed seeds, and safflowers. Black oil sunflowers were preferred over all other seeds. It also eats millet, canary seed, whole and cracked corn, wheat, peanuts in any form, pet food, peanut butter mixes, bird puddings, fresh fruit, baked goods, canola, and water (Dunn and Tessaglia-Hymes 1999). Austin (1968) reported it eating raisins, pieces of apple, and bread at feeders.

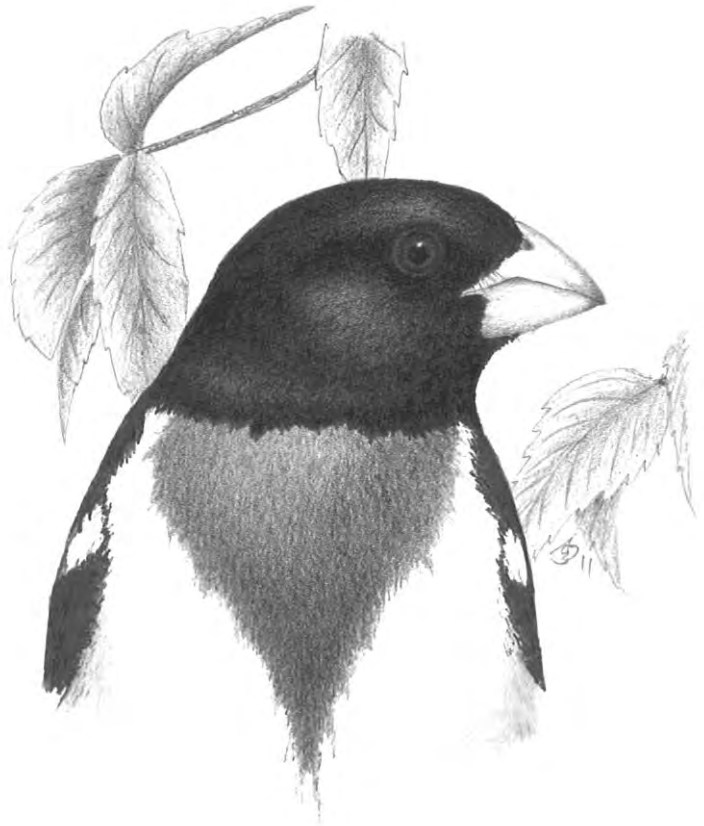
Severe winter weather is probably the most important factor limiting the northern range expansion of the cardinal. After a severe winter storm in Illinois, its density declined significantly in bottomland and upland forests. A slight population decline occurred in urban residential areas. The effects of the storm may have been lessened by the presence of feeders and ornamental plantings. Some cardinal carcasses were found and it was believed that most of the population decline was due to mortality (Graber and Graber 1979).

Loss et al. (2014) determined that the cardinal was 27.5 times more likely to strike a 1-3 storey residence than average. It was among the top 20 species striking residences but not among those most likely to strike low-rises or high-rises. Although building strikes by the cardinal may occur at any time of the year, they are most prevalent when visiting winter bird feeders.

The winter population of the cardinal has increased in Ontario and elsewhere. This is due to a combination of habitat modifications by humans that are beneficial to the cardinal, and to winter bird feeding (Halkin et al. 2021). Cardinals may range into northern Ontario well north of the breeding range, particularly in November. This may be the mechanism of northward expansion of the breeding range, facilitated by warmer temperatures and bird feeders (Ratcliffe et al. 2021). Freedman and Riley (1980) analyzed Christmas Bird Count (CBC) data for southern Ontario 1929-77. Numbers increased greatly over this time. Bedell (1963) summarized CBC data for Ontario for 1938-60. Numbers reported ranged from 3 to 127 seen per 100 party-hours. The lowest count was in 1938 and the highest was in 1948. The cardinal was first recorded on the Hamilton CBC in 1930 and has been observed every year since. Numbers continue to climb consistently (Curry 2006). CBC data indicate that it increased in Ontario at annual rates of 3.25% 1970-2021 and 1.70% 2009-21 (National Audubon Society 2022).

Rose-breasted Grosbeak

Pheucticus ludovicianus



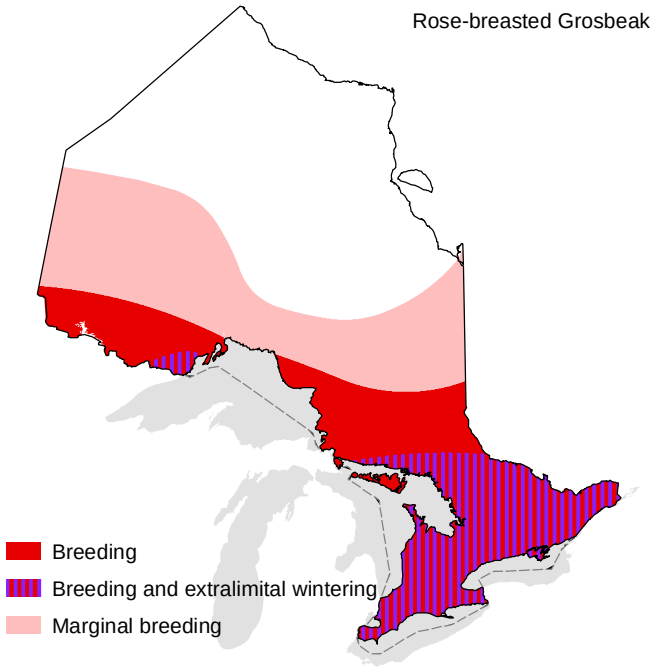
BREEDING SEASON

Habitat Requirements

In Ontario, 69.2% of Rose-breasted Grosbeak nests were in woodlands, including 31.5% in deciduous, 24.3% in mixed, 0.9% in coniferous, and 12.5% in unspecified stands. Of the remaining nests, 25.2% were in shrubby areas and overgrown fields and pastures; 2.5% were in shrubby road and railway rights-of-way; 2.5% were in gardens, parks, and cottage areas; 0.3% were in sand dune areas; and 0.3% were on rock outcrops. Woodlands that it used most frequently open second growth rather than mature dense stands. Many nests were at shrubby edges and clearings or near paths and shorelines, suggesting that it preferred to nest near open areas. It exhibited no preference for moisture regime, nesting in dry habitats as well as moist woods, swamps, willow swales, and bogs (Peck and James 1987).

In the Clay Belt of the Boreal Forest Region, Welsh and Lougheed (1996) found the Rose-breasted Grosbeak in a trembling aspen stand that was wet and nutrient-rich. Near Hearst, Welsh

and Fillman (1980) reported it in 9-, 13-, and 17-year-old clear-cuts in upland mixed forests. All were characterized by dense coverage by mountain maple and beaked hazel 2-5 m tall. North of Lake Nipigon, Sanders (1970) reported it in overmature trembling aspen stands. Near Manitouwadge, Venier et al. (2009) reported it in boreal mixedwood forests. It was most abundant in stands 24-36 years old, followed by those 1-21 years old and 60-223 years old.



In Quetico Park in the Canadian Shield portion of the Great Lakes–St. Lawrence Forest Region, the Rose-breasted Grosbeak was most abundant in stands 112-370 years old, uncommon in stands 1-23 years old, and absent in stands 67-72 years old (Apfelbaum and Haney 1985). In jack pine stands near Gogama, it was associated only with the deciduous elements of mixed forests. It was present in more open parts of mixed forests that were more than 20 years old (James and Peck 1995a). It was absent in pure jack pine stands near Parry Sound. It occurred at low densities in open jack pine stands mixed with trembling aspen, white birch, sugar maple, white pine, and white spruce (James 1979a). It occurred predominantly in second-growth deciduous forests in Parry Sound and Muskoka districts (Mills 1981). In Algonquin Park, it was fairly common in deciduous woods, particularly at edges of openings (MacLulich 1938). Martin (1960) reported it in the park in hardwoods and poplar–white birch stands mixed with balsam fir, spruce, and hardwoods. Kingsley and Nol (1999) studied it in shelterwood cuts in white pine stands in Algonquin Park. It was associated with dense deciduous cover in the canopy and subcanopy. It was equally abundant in stands with no recent history of cutting and those 2-16 years old. Kirk et al. (2012) examined its presence in old-growth and mature white pine stands in the Shield portion of the Great Lakes–St. Lawrence Forest Region. It occurred in low numbers in both age classes of forest but tended to be more abundant in mature than old-growth stands. In Muskoka District and Haliburton County, singing posts were associated with deciduous woods with a dense understorey. Nest sites had low canopy volume and very high shrub cover, typical of stands of immature trees. Its preference for high tree density and extensive shrub cover resulted in it inhabiting areas where large trees had been removed and the understorey had been allowed to develop. Cottage lots that have been cleared and allowed to succeed naturally to the immature tree stage create suitable breeding habitat (Clark et al. 1983).

In the off-Shield portion of the Great Lakes–St. Lawrence Forest Region, Burke and Nol (2000) studied the Rose-breasted Grosbeak in 40 woodlots ranging in size from 11.75 to 2,353 ha. They also surveyed it in 2 continuous forests in the Shield. All woodlots were older than 40 years in agricultural or suburban settings, and were deciduous closed-canopy forests dominated by sugar maple and

beech with hophornbeam, white ash, and white pine. Woodlands were classified as small with an average size of 93 ha (range 11.75-365 ha) with a core area of habitat greater than 100 m from forest edge of 7.8 ha, large with an average size of 849 ha (range 81-2,353 ha) with a core area of 121 ha, and continuous forest (the 2 Shield sites). Daily nest mortality rates were highest in small woodlots and declined with forest size, with nests in large woodlots less vulnerable to predation than expected. Woodlot size was the most important factor affecting reproductive success with the amount of forest cover within a 10-km radius in fragmented landscapes having no significant effect. There was no difference in success rates in large and continuous forests. Nests within 100 m of forest edge were depredated at a significantly higher rate than those further from edge. In small woodlots, the number of fledglings produced per nest was one half to two thirds that produced in large and continuous forests. Friesen et al. (1999a) studied the Rose-breasted Grosbeak in 41 woodlots in the Region of Waterloo that were dominated by sugar maple, beech, and white ash. Twenty-six were classified as small (3-14 ha) and 15 were large (26-140 ha). All but 1 forest were smaller than 50 ha. Their edge categories were 0-5 m from edge, 5-25 m, 25-50 m, 50-100 m, and more than 100 m. They found no significant difference in nest success related to forest size or distance from edge. The lack of size effect may have reflected the small range of available woodlot sizes. Nest success tended to be higher along the forest edge than 100 m or more from edge, but the study woodlots may have consisted entirely of edge. A high percentage of nests within 5 m of edge succeeded, suggesting that this area may not be as hazardous for nesting birds as often thought. Results of these 2 studies demonstrate that woodlot size and edge effects on nest survival may differ even within the same general area. Nest success may be related to other factors such as the types of predators present, habitat quality, and food abundance. In Durham Region, the Rose-breasted Grosbeak nested in open deciduous woods with an abundance of shrubs and saplings, a black spruce bog surrounded by a red maple–poplar swamp, in sugar maple–oak and beech–sugar maple woodlots, and in an old beech stand. Speirs and Orenstein (1975) considered it typical of mid-forest succession where it was most abundant, but it also occurred in other stages of succession.

L.A. Smith et al. (2007) studied nest-site selection by the Rose-breasted Grosbeak in the Carolinian Forest Region. The 23 woodlots they surveyed were upland deciduous forests 15-270 ha in area. Three types of forest management treatments were surveyed: those with no recent history of harvesting and those harvested by standard selective thinning and heavy diameter-limit cuts. Nest-site microhabitat was characterized by an open canopy and subcanopy, with deciduous saplings selected for nesting more often than tall trees. There was no significant difference in the coverage by seedlings (15%) and regenerative cover 0.5-1.3 m tall (32%) at nest sites and random areas. There was a tendency for the coverage of regenerative cover to be higher at nest sites. It selected nest sites with significantly more sapling cover (41%) in heavy cuts than in standard cuts (21%) and reference sites (24%). Canopy closure was significantly lower in all treatments at the nest (37%) than at random sites. Nest sites had a significantly lower basal area (BA) than random sites (18 compared with 23 m^2 per ha). Nests were significantly lower in heavy cuts (4.38 m) than in standard cuts (11.0 m) and reference sites (8.46 m). Nests were more concealed in heavy (74%) and standard (73%) cuts than reference sites (65%). Nest sites differed across treatments. In selective cuts and reference stands, nests were often in areas with less canopy cover, more sapling cover, and lower BA, and there was a tendency for more regenerative cover than at random sites. Heavy cuts had

denser regeneration and sapling layers and more open canopies. In these woodlots, it nested lower and had more concealed nests. It consistently selected nest sites with reduced BA, a tendency for more regenerative cover, more sapling cover, and less canopy cover than random sites, and this preference became stronger in heavy cuts. In the Hamilton area, McIlwraith (1894) reported that the Rose-breasted Grosbeak preferred to nest along wooded banks of streams. Dodds and Otis (2009) found it in 2 stands containing a high proportion of ash trees in Point Pelee. In 1 plot, ash represented 18% of the canopy cover with trees with an average diameter at breast height (DBH) of 26.5 cm. In the other plot, ash averaged 41.1 cm DBH and represented 38% of the canopy cover.

Two Ontario studies examined Rose-breasted Grosbeak habitat at the landscape level. Nol et al. (2005) studied the effects of large woodlots that were potential source areas on the probability of smaller woodlots supporting it. They considered large woodlots with more than 90 ha of core area more than 100 m from edge as putative source habitats and small woodlots as putative sinks. Large forests averaged 283 ha of core area compared with 7.5 ha for small woodlots. The odds of a small woodlot being occupied was not affected by regional forest cover, although the range of forest cover was low, or by the number of nearby large forests. The odds of a woodlot being occupied increased significantly as the distance to the nearest large woodland decreased. Occupancy was approximately 30% in small woodlots 2.5 km from a large woodland, 24% at 5 km, 20% at 10 km, 15% at 15 km, and 10% at 20 km. This study underscored the importance of maintaining large forests in the landscape. Retention of small woodlots is also important. These act as a reservoir for excess individuals if catastrophic events result in vacancies in source woodlands. Even sink woodlots produce some fledglings that contribute to the population. Austen et al. (2001) determined that its abundance was positively correlated with the amount of forest cover further than 100 m from edge and negatively correlated with woodlot size, forest cover within 2 km, and regional forest cover. All these relationships were nonsignificant.

Other studies examined the habitat of the Rose-breasted Grosbeak at the landscape level. Cunningham and Johnson (2019) determined that it occurred in areas having 65-75% tree cover in North Dakota, with no areas having greater than 75% tree cover. In New York, it occurred in areas with 61-80% tree cover. In Quebec, it nests in regions dominated by deciduous and mixed forests, being most common in the sugar maple–dominated landscape and, to a lesser extent, in the balsam fir–yellow birch landscape. It is uncommon in the balsam fir–white birch landscape. In extensively forested landscapes, it was associated with natural openings such as clearings and edges of watercourses and water bodies, beaver ponds, and old burns (Pelletier and Dauphin in Gauthier and Aubry 1996; Toussaint in Robert et al. 2019). In Saskatchewan, it was randomly distributed among fragmented and forested landscapes, but was more common in large forest fragments or areas with high forest cover within 5 km. Its abundance was significantly correlated with forest size and amount of local forest cover (Hobson and Bayne 2000). In Pennsylvania, Rodewald and Yahner (2001) combined data for all species and determined that daily nest survival was higher in forests disturbed only by silviculture than those disturbed by agriculture. Agricultural landscapes probably supported a greater abundance of avian and mammalian predators.

Although almost all information on the habitat of the Rose-breasted Grosbeak is related to forests, it also nests in dense shrubby old fields and regenerating clear-cuts and burns that are

essentially devoid of trees. In Quebec, it nests in strip-cuts with dense deciduous regeneration but not in conifer-dominated regrowth. It also nests on shrubby hydro corridors. In New Jersey, it was absent in 10- and 20-year-old fields but present in a 40-year-old field. The borders of this field were treed but the centre was dominated by dense shrubs and saplings. It was considered a shrub species that preferred edges. An occupied clear-cut in Minnesota had average characteristics of 2.1 m shrub height, low shrub patchiness, 398 cm per m^2 BA of shrubs, moderate shrub density, 3.4 m^2 per ha tree BA, 73 trees per ha with DBH greater than 7.6 cm, 3.6 m^2 per ha dead tree BA, and 70 trees per ha with a DBH greater than 7.6 cm (Falardeau et al. 1999; Hoffman 1989a; Keller et al. 2003; Niemi and Hanowski 1984a, 1984b; Yahner et al. 2002).

The Rose-breasted Grosbeak prefers deciduous woods but also occurs in mixed-wood stands, with it declining as the proportion of conifers increases. It inhabits both upland and lowland forests and shrubby ecotones at edges of woods at streams, ponds, marshes, roads, or pastures. It commonly uses second-growth woodlands but may occur in all ages of forests. It also breeds in well-vegetated suburban areas, parks, gardens, and orchards. In the southern portion of its range, it breeds mostly in mountain deciduous forests. In the north, it occurs in stands of poplars or white birch mixed with conifers. It also occurs in oak savannahs and some conifer forests dominated by pines, tamarack, white cedar, or spruces. Many occupied forests support shrubs that produce berries later in the season, such as highbush cranberry, blueberries, chokecherry, honeysuckles, mountain-ash, cloudberry, and raspberry. In extensive forests, it is often associated with openings such as beaver ponds, muskegs, swamps, stream sides, dry hillsides, and utility corridors (Austin 1968; Campbell et al. 2001; Capen 1979; Dawson 1979; Mossman et al. 1991; Wyatt and Francis 2020).

Some information is available on the microhabitat requirements of the Rose-breasted Grosbeak. Essentially all researchers concur that shrubs or saplings are an important component of its habitat. In New Hampshire, it declined in abundance when the forest changed from one characterized by a dense closed canopy with an open subcanopy and a dense low shrub layer to one with a more open and patchy canopy, a denser and taller shrub and subcanopy layer, and a more sparse low shrub layer (Holmes and Sherry 2001). In Vermont, Thompson et al. (1988) concluded that it was associated with deciduous forests with a dense understorey. Average habitat characteristics included 35.4% ground cover by green vegetation, 8.0% ground cover by slash, 83.0% canopy closure, 21.5 m canopy height, 11.4 m canopy depth, 17.8 m^2 per ha BA of deciduous species, 3.3 m^2 per ha BA of coniferous species, 11.3 cm DBH for deciduous trees, and 11.9 cm DBH for coniferous trees. In Iowa, it was positively correlated with sapling richness and vertical patchiness and stratification of vegetation (Stauffer and Best 1980). In Wisconsin upland forests, it preferred an open canopy with moderate growths of saplings and shrubs (Mossman and Hoffman 1989).

Other studies examined the preference of the Rose-breasted Grosbeak for stand types and age of forests. In the Boreal Forest Region, Erskine (1977) considered it typical of aspen or white birch stands. It also occurred in stands dominated by balsam fir, usually mixed with aspen or birch. In northeastern northern hardwoods, it was equally abundant in mature undisturbed habitats and disturbed and early successional habitats (Noon et al. 1979). In northeastern poplar–white birch stands, it occurred in all ages of stands from the seedling stage in young burns to mature forests (Back 1979). In Alberta boreal forests dominated by poplars, it was significantly more abundant in

forests 23-26 years old than in mature and old-growth stands. It was positively correlated with the density of aspens (Schieck et al. 1995). In northeastern mixed-wood forests, Temple et al. (1979) considered it a late seral species, but not one of mature forests. It was associated with increasing abundance of sugar maple and yellow birch. In Saskatchewan, it was more common than expected in trembling aspen stands and used mixed and white spruce stands according to their availability (Hobson and Bayne 2000). In the Prairie Provinces, it occurred in mixed and deciduous forests and was absent in black spruce and species-poor jack pine stands. It was associated with fairly dry stands that were moderately rich in nutrients (Kirk et al. 1996). In Pennsylvania, it occurred in 36.4% of old-growth mixed forests, 63.9% of forests statewide, and 83.5% of forests in the Appalachian Plateau. Haney (1999) considered it to have a negative old-growth affinity. In the same state, it was the sixth most abundant species in clear-cuts 3-6 years old (Dessecker and Yahner 1987). In Vermont, it was associated with beech and sugar maple with high numbers of aspen and white birch. It was negatively correlated with red maple. It was correlated with increasing successional age, increasing amounts of conifers, and a moderate number of dead trees (Lent and Capen 1995). In Wisconsin, it was associated mostly with xeric stands where it was abundant. It was an insignificant component of the avifauna in more mesic stands, if it was present at all. In many of the more mesic stands where it occurred, the terrain was steep and it occurred at the higher points. It was more likely to occur in early and mid-successional than late successional stands, being most abundant in the pioneer 60% of the seral gradient. It was most common in pioneer stands where sturdy oak saplings and thick oak branches and twigs were available for the bulky nests (Bond 1957). In New Hampshire and Maine, it was most abundant in poplar and white birch followed by, in decreasing order of abundance, northern hardwoods, white pine stands, spruce–balsam fir stands, swamp hardwoods, balsam fir stands, and hemlock stands. It was positively correlated with canopy closure, percent ground cover, and deciduous trees 2-10 cm DBH. It was negatively correlated with coniferous trees 2-10 cm DBH (DeGraaf et al. 1998). In North Dakota, it was most common in late seral stages of deciduous forests. It preferred semiopen mesophytic stands and was more than 3 times as abundant in lowland forests than upland bur oak stands (Faanes and Andrew 1983).

Most authors concur that the Rose-breasted Grosbeak is not area sensitive (Bond 1957; Golet et al. 2001; Stauffer and Best 1980; Wyatt and Francis 2020). There is no evidence that it is area sensitive in Ontario. In Missouri, Hayden et al. (1985) considered it area sensitive, but at a level of significance of 0.25 rather than 0.05. They observed it in woodlots as small as 2.2 ha and it reached 100% occurrence in forests 42.2-53.6 ha. They reported that it occurred in woodlots as small as 1.2 ha in New Jersey. In North Dakota, Grant and Berkey (1999) considered it area sensitive because its probability of occurrence increased with forest size. Nonetheless, the probability of occurrence was 20% in 1-ha woodlots and 50% probability of occurrence was achieved in woodlots 8-20 ha. In the mid-Atlantic states, Robbins et al. (1989) concluded that its abundance was positively correlated with forest area. Its probability of occurrence reached its maximum in woodlands larger than 3,000 ha but the probability of occurrence was not reduced to 50% until woodlots were 1.0 ha in size. The minimum size of woodlots that it was detected in at least twice was 11.3, 24.1, and 123.0 ha. They sampled woodlots as small as 0.2 ha. In this area, the Rose-breasted Grosbeak is at the extreme southeastern corner of its range and often confined to mountainous areas, so results are not typical of the core of its range.

Ontario nests were elevated in a wide variety of living trees, shrubs, and vines. Small or sapling trees were preferred over large trees. Deciduous trees, shrubs, and vines (30 species, 87.1% of nests) were greatly favoured over coniferous trees (6 species, 12.9% of nests). The most commonly used species were hawthorns (77 nests), maples (74 nests), cherries (21 nests), beech (21 nests), birches (16 nests), and spruces (13 nests). Nests were usually in the upper half of the nest species and more often near than distant from the trunk. Nests were 0.2-6 m from the trunk, with most 1.2-2.4 m from it. Most (64.8%) nests were in upright crotches rather than on horizontal branches at forks (35.2%). Nests were 0.8-16.8 m from the ground, with most 1.8-3.7 m up (Peck and James (1987). Near Rutherglen, 2 nests were in white birches 12.2 and 15.2 m from the ground. Most nests were 1.2-6.1 m from the ground. Other nest-tree species included white spruce, balsam fir, red maple, and white pine. One nest north of Toronto was 1.5 m up in a hemlock on the edge of an overgrown pasture (Austin 1968). Nests in Muskoka and Parry Sound districts were 11-15.2 m from the ground in a variety of deciduous species plus hemlock and spruce (Mills 1981). In Waterloo Region and Wellington County, 76% of nests were in deciduous saplings, shrubs, and vines. They were typically in forest openings with a more open canopy and subcanopy than random sites (Wyatt and Francis 2020). The average height of 50 nests at London was 6 m. These included one that was 2 m up in a dogwood, another 2.5 m up in a blue beech on the upper surface of a branch overhanging a pond, and a third 2.5 m up on a horizontal branch of a Manitoba maple (Scott 1998). Friesen et al. (1999c) reported that 3 nests found the previous year in Waterloo survived the winter. One was repaired and reused.

Of 47 Iowa nests, 21% were in shrubs, 6% were in deciduous saplings, and 72% were in deciduous trees (Stauffer and Best 1980). In British Columbia, 13 of 15 nests (86.7%) were in deciduous trees, mostly in trembling aspen and willows; the others were in deciduous shrubs. The Rose-breasted Grosbeak selected small or sapling trees more often than large trees. Nests were in forks or crotches of upright stems, closer to the top than the bottom of the tree, and usually closer to the trunk than away from it. Nests were 1.2-9.1 m from the ground, with most 2.2-4 m up (Campbell et al. 2001). Nests have been reported in apple trees, small elms, Osage orange hedges, hawthorns, pear, Manitoba maple, chokecherry, hophornbeam, and alders (Austin 1968; Rothstein 1973b).

The Rose-breasted Grosbeak defends its territory mostly by singing. Male-male interactions are most common, followed by male-female and female-female interactions. Agonistic behaviour is much less frequent after egg-laying starts. Breeding pairs are intolerant of conspecifics. Territories seldom overlap and trespassing rarely occurs (Ivor 1944; Wyatt and Francis 2020). Limited information is available on territory size. New York territories averaged 0.77 ha (range 0.34-1.3 ha; Wyatt and Francis 2020). Pelletier and Dauphin (in Gauthier and Aubry 1996) reported territory sizes of 0.8-1.2 ha in Quebec.

No information is available on natal philopatry except that 0 of 81 juveniles returned in New York (Yunick 1996b). Limited information is available on adult site fidelity. In Massachusetts, 9 of 27 adult males (33.3%) and 2 of 20 females (10.0%) returned in a subsequent year. One bird returned in 5 years (Smith 1966). In New Jersey, 7 of 94 yearling birds (7.4%) returned (Suthers 1988). Two of 6 adults (33.3%) returned the next year in New Hampshire (Whittle 1938). In New York, Yunick (1996b)

banded at 2 stations: 1 in spring only and the other year-round. At the spring-only sampling area, 24 of 81 adult males (29.6%), 7 of 26 yearling males (26.9%), a total of 31 of 107 males (29.0%), 14 of 104 adult females (13.5%), and 45 of 211 adults (21.3%) returned. At the year-round sampling area, 25 of 130 adult males (19.2%), 5 of 47 yearling males (10.6%), 30 of 177 males (16.9%), 17 of 120 adult females (14.2%), and 47 of 297 adults (15.8%) returned. Males were more likely to return than females at the spring-only site but there was no difference at the year-round site. The lower return at the spring-only site may have been due to territorial males excluding others from the vicinity of the nests. Results suggested that adult males may have been more site faithful than yearling males, but some birds may have been migrants.

Limiting Factors

Eggs have been found in Ontario nests from the second week of May until the third week of July, with most present in the first half of June (Peck and James 1987). In Algonquin Park, nests are under construction from mid-May to late June, eggs are present late May to early July, nestlings are present early June to late July, and dependent fledglings have been seen mid-June to mid-August (Tozer 2012).

Some birds may be paired when they arrive on the breeding grounds, but pairing usually occurs shortly after arrival. Territorial males are initially aggressive toward females on their territories, but after 1-2 days, the male follows the female or vice versa. The earliest males to arrive stay to breed while migrants continue to move through for several weeks afterwards. In southwestern Ontario, mean nest initiation dates were 18-19 May. Nests take 2-5 days to build and the female may begin laying eggs a day before the nest is complete. One egg is laid per day. Incubation appears to start before the clutch is complete, possibly with the laying of the second egg. The incubation period for Ontario nests was 11-14 days, consistent with reports from elsewhere. The nestling period varies from 9 to 17 days, but is mostly 10-12 days (Austin 1968; Ivor 1944; Peck and James 1998b; Smith et al. 2006; Scott 1998; Wyatt and Francis 2020).

The Rose-breasted Grosbeak rarely attempts to raise 2 broods. Ontario egg dates indicate that single broods are typical, although there are reports of second broods. Two semicaptive pairs at Erindale successfully reared 2 broods and a pair in Michigan attempted 2 broods. These appear to be the only confirmed double broods for the species, although double-brooding has been suspected in other cases, including in Ontario. In all confirmed cases, the second nest was initiated shortly before the young in the first nest fledged. Second nests were 12-35 m from the first nests (Ivor 1944; Peck and James 1998b; Rothstein 1973b). Smith et al. (2006) monitored 213 nests in southwestern Ontario and observed no cases of double-brooding. They observed only 1 renesting attempt after nest failure. The replacement nest was 30 m from the original nest, but was subsequently abandoned. This may be the only confirmed case of renesting (Wyatt and Francis 2020). Clutches of 2-5 eggs have been reported in Ontario, with 3- and 4-egg clutches most common; average clutch size was 3.44 eggs (Peck and James 1987). In southwestern Ontario, there were no differences in clutch sizes in uncut forests and those thinned selectively or heavily at 2.56, 2.71, and 3.02 eggs, respectively (Smith et al. 2006). Across its range, the clutch size is typically 3-5 eggs, with 4-egg clutches most frequent (Austin 1968; Wyatt and Francis 2020).

Both sexes are capable of breeding when they are 1 year old. Yearling males arrive later than older males and may not be successful in obtaining a territory or attracting a mate. Unmated birds remain solitary throughout the breeding season. Once a bird breeds, it is presumed to do so each year thereafter. The Rose-breasted Grosbeak is apparently monogamous, with no cases of polygyny reported (Wyatt and Francis 2020).

The Rose-breasted Grosbeak usually forages at all canopy levels at the periphery of foliage and branches where the leaf cover is densest. Foraging in the understorey is more common later in summer when understorey fruits are available. It occasionally gleans from the ground. When feeding on flowers, it cuts and discards the petals and eats the base containing the ovaries and seeds (Wyatt and Francis 2020). In Vermont, 95% of foraging occurred in foliage and 5% in the air. Sixty-four percent of foraging was by gleaning, 31% by aerial manoeuvres, and 5% by hanging (Lent and Capen 1995). It has been observed eating elm seeds, often hanging head-downward in the manner of a chickadee. It may also open the long seed pods of catalpa to obtain the seeds (Austin 1968). Hartung and Brown (2005) studied the foraging behaviour of the Rose-breasted Grosbeak in open-canopied savannahs and closed-canopy woodlands in Illinois. There were no differences in its foraging methods in the 2 habitats, and it selected tree species according to their availability. Foraging occurred in black and white oaks, hickory, black cherry, black locust, hackberry, and several miscellaneous species. It preferred to forage in the lower canopy levels (0-5 and 6-10 m from ground) rather than at heights of 11-15 m and higher. The 2 lower layers were used more than expected, but not significantly. In closed-canopy woodlands, it exhibited a strong preference for the subcanopy and appeared to avoid the upper canopy level. Foraging manoeuvres in savannahs were 56% gleaning, 36% hovering, 5% sallying, and 3% flycatching. In woodlands, they were 46% gleaning, 38% hovering, 5% sallying, and 4% flycatching. Robinson and Holmes (1982) described its foraging behaviour in New Hampshire. Of attacks on arthropods, 75.9% were on leaves and 16.4% were on bark. Foraging techniques included 55.8% gleaning, 36.7% hovering, 3.5% flush-chasing, 2.4% hawking, and 1.5% hanging. They considered it a variable-distance searcher that ate medium- to large-sized insects such as caterpillars. It searched near and far substrates, hopping along branches while carefully peering under leaves. It occasionally gleaned insects from upper leaf surfaces. As it approached the distal end of a branch, it stopped and searched foliage as far as 1-2 m away. It was highly variable in its foraging behaviour, occasionally searching the leaf litter on the ground, hunting along tree trunks, or moving among the foliage. Other species that were most similar in their searching behaviour differed in their microhabitat use. In New Hampshire, Holmes and Schultz (1988) examined its foraging in relation to food availability. It foraged more on upper and lower leaf surfaces than expected and less than expected on petioles and twigs. The differences were significant on yellow birch but not on sugar maple or beech. On all species combined, 61% of foraging was by gleaning (61% on lower-leaf surfaces) and 39% by hovering (80% on lower-leaf surfaces). Free-living types of caterpillars, which are most available as prey, constituted 29% of caterpillars on beech foliage, 42% on sugar maple, and 58% on yellow birch. Beech supported more caterpillars, but most were leafminers and leaftiers which are small and seldom taken by birds. Yellow birch had fewer caterpillars, but most were free-living types that were larger and more active. The Rose-breasted Grosbeak foraged preferentially in yellow birch. It infrequently foraged on twigs and petioles, but did so more in yellow birch than other tree species. It changed foraging tactics in

different tree species, hovering less often in beech. Ten bird species foraged predominantly on caterpillars in this area and all but the Black-throated Blue Warbler foraged throughout the height of the vegetation. All 10 species differed significantly from each other in their use of the foliage substrates. In New Hampshire, Holmes (1986) compared the foraging behaviours of male and female Rose-breasted Grosbeaks. Females foraged significantly higher (average 12.9 m) than males (10.8 m). There was a positive but nonsignificant relationship between female foraging height and nest height. Male foraging height was significantly correlated with song-perch height. Both sexes foraged over almost the entire vertical profile of the forest, and both mostly gleaned on leaf surfaces. There were significant differences in their use of tree species for foraging. Males foraged with equal frequency on beech, sugar maple, and yellow birch. Females foraged more often on yellow birch and appeared to avoid beech. Male foraging tactics were most similar to those of male Scarlet Tanagers. This was due to females of the 2 species foraging higher in the canopy and more frequently in white ash than males. Males of the 2 species attacked prey on trunks and branches more often than females. Birds foraged more near the centre of their activity areas: song perches for males and nests for females.

In southwestern Ontario, adults fed nestlings soft-bodied insects heavily coated with saliva. They were fed more and larger insects as they aged and were fed insects almost exclusively except for a small amount of tree leaves (Ivor 1944). The stomachs of 4 nestlings contained 78% animal and 22% vegetable matter. The animal food included 20% caterpillars (including those of sphinx moths), 25% beetles (weevils and metallic wood-boring, click, and leaf beetles), and wasps. Adults were observed feeding nestlings Colorado potato beetles and caterpillars that were mostly leafrollers (McAtee 1908). Austin (1968) reported that young were fed elderberries, insect larvae, various seeds, butterflies and moths, flies, crickets and grasshoppers, beetles, and spiders.

Insects are important in the adults' diet during the breeding season, but the Rose-breasted Grosbeak is almost entirely frugivorous during late summer and autumn migration (Wyatt and Francis 2020). Favourite foods of semicaptive birds in southwestern Ontario included mealworms, raw peanuts, and sunflower seeds (Ivor 1944). In New Hampshire, 16 emetic samples revealed a diet consisting of 15.6% caterpillars, 1.3% adult lepidopterans, 11.7% hymenopterans, 62.3% beetles, 6.5% flies, and 2.6% spiders. The diet determined by field observations consisted of 82.9% caterpillars, 7.3% beetles, and 7.3% hymenopterans (Robinson and Holmes 1982). Austin (1968) reported that it ate blossoms of hickory and beech trees, white ash buds, and European mountain-ash fruit. Stutchbury et al. (2005a) reported that it was the second-most common visitor to red elderberry after the Scarlet Tanager. Beal (1897a) reported that the Rose-breasted Grosbeak was one of few birds that attacks the Colorado potato beetle. Its vegetable food consisted of buds and blossoms of forest trees and seeds, but it also consumed peas from gardens. McAtee (1908) analyzed the contents of 176 stomachs. The diet consisted of 52% animal matter and 48% vegetable matter, with consumption of animal prey peaking at 74.25% in June at the height of the breeding season. The animal food consisted almost entirely of insects: 36% beetles, 6.43% hymenopterans, 3.82% caterpillars, 2.38% scale insects, and 3.33% miscellaneous invertebrates. The beetles included weevils, fireflies, and ground, lady, metallic wood-boring, click, long-horned, scarab, dung, and leaf beetles. Leaf beetles were the most commonly consumed beetles, especially the Colorado potato beetle. The hymenopterans included parasitic wasps, sawfly larvae, ants, and bees. In addition to

scale insects, other bugs it ate included stink bugs, treehoppers, and aphids. Grasshoppers constituted only 0.2% of the diet. It rarely ate spiders and their egg sacs, flies, and snails. The vegetable food consisted of 19.3% wild fruit, 15.74% weed seeds, 5.09% grain, 1.37% garden peas, and 6.5% other material including small quantities of cultivated fruit, buds, and tree flowers. Common and red elderberries were the most frequently consumed fruits with blackberries and raspberries second in preference. Other fruits it commonly ate included those of mulberries, juneberries, pin and black cherries, chokecherries, rough-leaved and flowering dogwoods, wintergreen, hawthorns, strawberries, pokeweed, juniper, and sour gum. It eats more weed seeds in August and September than in other months. Seeds of smartweeds are most selected with amaranths next in importance. It also eats seeds of foxtails and other grasses, nightshades, sedges, common and giant ragweed, vervain, docks, milkweeds, sunflowers, jewelweeds, bloodroot, and sycamore. Some ate plant galls for the vegetable matter. The grain consumed included corn, wheat, and oats, which was mostly waste grain but some grain may be taken from the plants and fed to nestlings. It has eaten buds of beech, cherry, pear, wild plum, silver and red maple, Manitoba maple, and elm. It cuts off buds close to the twig, eats the soft pip, and drops the shell. It probably eats tree flowers more than buds and has eaten flowers of hickory, elm, walnut, and oak. Near Manitouwadge, its abundance did not change in response to a spruce budworm outbreak (Venier et al. 2009).

Friedman (1929) considered the Rose-breasted Grosbeak a fairly common host of the Brown-headed Cowbird and Austin (1968) repeated this assertion. More recent information indicates that it is an infrequent host, probably because both sexes incubate and the nest is seldom left unattended (Friesen et al. 1999a; Wyatt and Francis 2020). This grosbeak is an acceptor of cowbird eggs (Rothstein 1975), but parasitism has minimal effects on it. In southwestern Ontario, there was no significant difference in the number of young fledged from parasitized and unparasitized nests. Only 2 of 138 nests (1.5%) failed due to parasitism. The grosbeak is also a poor host, fledging few cowbirds. In this study, only 3 of 16 parasitized nests (18.75%) produced a cowbird fledgling, contributing only 4 cowbirds to the population (Smith et al. 2006). Peck and James (1998b) reported that 28 of 367 Ontario nests (7.6%) were parasitized. Habitat conditions may affect the rate of parasitism. In eastern Ontario, Burke and Nol (2000) reported that 0% of nests were parasitized in small and continuous forests compared with 7.4% in large forests. In Waterloo Region, Friesen et al. (1999a) reported an overall parasitism rate of 10%: 18% in small woodlots and 5% in large woodlots. In southwestern Ontario, parasitized nests were significantly lower (2.9 m compared with 4.3 m) and had significantly more vegetation 0.5-1.3 m tall (57.9% compared with 34.9%) than unparasitized nests. All parasitized nests were in woodlots that had been heavily cut; none occurred in uncut or selectively harvested woodlots. Sixteen of 138 nests (11.6%) were parasitized (L.A. Smith et al. 2006, 2007). Parasitism rates reported from elsewhere include 3 of 42 nests (7.1%) in Quebec (Pelletier and Dauphin in Gauthier and Aubry 1996), 0 of 18 nests in British Columbia (Campbell et al. 2001), 1 of 15 nests (6.7%) in New York (Hahn and Hatfield 1995), 0 of 13 nests in Minnesota (Hanski et al. 1996), 1 of 5 nests (20.0%) in Wisconsin (Brittingham and Temple 1996), 0 of 2 nests in Indiana (Robinson 1992), 0 of 3 nests in Illinois, and 0 of 18 nests in Iowa (Wyatt and Francis 2020).

The greatest limiting factor for the Rose-breasted Grosbeak may be its low reproductive output. This is due to its rarely renesting or raising second broods. Reproductive success is further diminished in landscapes fragmented by agriculture or development where predators are more

abundant. In southern Ontario, only populations in large contiguous forest appear to be self-sustaining (Wyatt and Francis 2020). In southeastern Ontario, Burke and Nol (2000) determined that productivity levels in large forests (average 849 ha) and continuous forests were above maintenance levels and acting as sources. Those in small forests (average 93 ha) were sinks but close to maintenance levels. This was determined under the assumptions that most birds renested after nest failure and that most raised 2 broods. Subsequent research indicates that these assumptions are rarely met. If the Rose-breasted Grosbeak is not double-brooded in their study area, large forests would function as sinks and continuous forests would be close to maintenance levels, with 1.3 nests required for maintenance. Populations remained constant over a 4-year period, suggesting a source-sink metapopulation. Fragmentation in that area probably has not proceeded to the extent that the woodlots investigated are too isolated on a landscape scale to prevent colonization from source populations. This grosbeak is not area sensitive and does not preferentially select territories in large woodlots. Consequently, a large proportion of the population may breed in sink habitats that are incapable of sustaining the population. In their study area, only 1% of forests were larger than 200 ha and 82% had no core area, so the majority of the habitats were sinks. Loss of large forested tracts would probably result in dramatic population declines. Sink habitats are still important because they produce some young and may function as sources in some years. In Waterloo Region, populations were sinks with 0.98 fledgling produced per female and 1.2 required for a viable population (Friesen et al. 1999a). In southwestern Ontario, only 75 of 193 nests (38.9%) produced fledglings. Losses of 19-24% of the population were estimated due to low productivity (L.A. Smith et al. 2007). Similar productivity was reported by Hanski et al. (1996) in Minnesota, where 38% of nests were successful. Canopy cover was the only variable that affected nest success, which was unrelated to distance from forest edge, nest height, or nest concealment.

In Waterloo Region, Friesen et al. (1995) studied the effects of residential housing on the Rose-breasted Grosbeak. They surveyed small (3-4 ha), medium-sized (8-15 ha), and large (20-50 ha) woodlots with 0, 1-3, 8-15, and more than 25 houses within 100 m. Its frequency of occurrence increased with increasing forest size, but was still as high as 57% in small woodlots. Its frequency of occurrence tended to decline with increasing numbers of houses, but not significantly.

Numerous studies examined the effects of forest management on the Rose-breasted Grosbeak. With a few exceptions, most of these considered only how its abundance was affected but some Ontario studies examined its effects on nesting success. Results are highly variable, depending on the forest management technique. Forest management has been variously described as having no effect, being detrimental, or highly beneficial. In Algonquin Park, it exhibited no response to typical and intensive group-selection cuts (Tozer et al. 2010). Jobes et al. (2004) reported no differences in its abundance in the park in uncut stands and those logged 5 or 15-20 years previously. In partial cuts in the Boreal Forest Region of Ontario, Vanderwel et al. (2007) reported that it declined by 25% when 50% of trees were removed, by 50% when 60% of trees were removed, and by 75% when 80% of trees were removed. In the same area, it was less abundant in early regenerating clear-cuts than early regenerating burns, more abundant in mid-successional clear-cuts than burns, more abundant in early regenerating cuts than mature forests, and less abundant in mid-successional cuts than mature forests. All relationships were nonsignificant (Zimmerling et al. 2017). In southern Ontario, there was no difference in its abundance in stands that were selectively thinned and those that were

heavily thinned by diameter-limit cuts (Holmes et al. 2004). In southwestern Ontario, the Rose-breasted Grosbeak tended to be more common in heavily cut woodlots than in selectively cut or uncut woodlots. In heavily cut woodlots, it nested lower and had more concealed nests. This appeared to be maladaptive, with these nests having lower nest success. L.A. Smith et al. (2006, 2007) considered heavily cut woodlots ecological traps, attracting more birds most of which failed in their reproductive attempt. Approximately 94% of the cuts in some regions of Ontario are heavy diameter-limit cuts, and this could be contributing to its decline. Wyatt and Francis (2020) concluded that forest maturation may reduce nesting opportunities and that it is often found in higher densities in postharvest forests. In Quebec, it may occur in strip-cuts 5 years after harvesting. Reforestation and maturation of second-growth forests may limit breeding opportunities (Pelletier and Dauphin in Gauthier and Aubry 1996; Toussaint in Robert et al. 2019). In New York clear-cuts, the Rose-breasted Grosbeak reached its highest abundance 7-10 years after cutting and declined slowly throughout mid- and late succession (Keller et al. 2003). In the same state, it represented 1.86% of birds in uncut forests, 1.50% when 25% of harvestable trees were removed, 1.68% when 50% of trees were removed, 3.11% when 75% were removed, and 4.70% when 100% were removed. It tended to increase with increasing intensity of logging (Webb et al. 1977). In Pennsylvania, it was equally abundant pre- and postcutting of clear-cuts in aspen and mixed oak stands but densities tended to be higher in cuts (Yahner 1993, 2003). In the same state, there was no difference in its abundance in stand improvement cuts whether snags were retained or harvested (Stribling et al. 1990). In Minnesota, it responded positively to tree removal when basal area was reduced to 7-10 m^2 per ha (Hanowski et al. 2002). In Saskatchewan, Cumming and Diamond (2002) studied the Rose-breasted Grosbeak in 4 age-classes of forest: mature (50-60 years old), rotation age (80-90 years), old (100-110 years), and very old (more than 140 years). It was absent in mature and rotation age forests and occurred in 20-49% of old stands and less than 20% of very old stands. It was significantly more abundant in post-rotation-age stands and was therefore likely to decline if older stands disappeared from the landscape. They recommended that some stands 120 or more years old should be maintained. In Alberta, it colonized deciduous stands when 75-100% of trees were retained. It experienced no other increases, decreases, extirpations, or colonization in any other forest type or level of tree retention (Harrison et al. 2009). In Alberta, Tittler et al. (2001) studied the effects of retaining some residual trees in clear-cuts in aspen-spruce–jack pine forests. There was no significant difference in its abundance in control and treatment plots prior to cutting, but it was significantly more abundant in control than treatment plots after cutting. Tree retention in cut-blocks did not affect its abundance. In the Yukon, Sinclair et al. (2003) reported that its primary habitat was being rapidly lost due to clear-cutting of mixed white spruce and balsam poplar stands.

In West Virginia, the Rose-breasted Grosbeak exhibited no response to well pads, access roads, or pipelines (Farwell et al. 2019). In Alberta and the Northwest Territories, it was significantly more abundant along seismic lines and pipelines than in forest interior adjacent to these facilities. It was significantly less abundant within 50 m of well pads than in forest interior. It was significantly more abundant at quiet well pads than at noisy compressor stations (Bayne et al. 2008, 2016).

In Pennsylvania and New Jersey over 15 years, hemlock declined from representing 56% of the total basal area to 46% due to the hemlock woolly adelgid; the amount of woody understorey

increased. The Rose-breasted Grosbeak responded positively to hemlock decline, probably due to the increase in the shrub and sapling layer (Toenies et al. 2018).

DesGranges et al. (1987) studied the response of the Rose-breasted Grosbeak to die-backs of sugar maple. Healthy stands had 35% more foliage and 57% more insects than die-back stands. It was 20% less abundant in die-back stands.

Blake et al. (1992) examined the effects of drought on the Rose-breasted Grosbeak in Wisconsin and Michigan. It was negatively affected by wet Mays and positively by dry Junes.

In Minnesota, Hanowski et al. (1996) concluded that very low frequency electromagnetic fields associated with a transmission line had no measurable effect on the Rose-breasted Grosbeak.

The Rose-breasted Grosbeak is a popular cage bird in its wintering range and habitat loss may be occurring there as well (Wyatt and Francis 2020). Males were formerly highly prized as ornaments for ladies' hats and abundant numbers were shot (Beal 1897a).

Price (2004) predicted that the breeding range of the Rose-breasted Grosbeak might contract in southern Ontario if the average summer temperature increased by 2°C.

Status

The range of the Rose-breasted Grosbeak appears to have increased in southern Ontario from a restricted area along the southern border to the southern half of the province, but this may be a result of better coverage by observers. Range expansions and contractions are likely related to changes in habitat, particularly clearing of forests followed by increased availability of edge and second-growth habitat, as well as its adaptation to suburban habitats (Wyatt and Francis 2020). McIlwraith (1894) reported that it bred regularly along the southern border. In Elgin County, it was a common resident in 1891 and 1954; by 2000, it was uncommon but widespread (Lancaster et al. 2004). In the Kingston area, it has been reported since the mid-19th century (Weir 2008). Sheppard et al. (1936) reported that it was observed only during migration in Niagara Region where it was a rare migrant in the Niagara Falls area. It was suspected that some birds might have remained to breed in the more secluded portions of the region. Baillie and Harrington (1937) considered it fairly common throughout southern Ontario, breeding north to the transcontinental railway and probably west to Lake of the Woods. The first atlas demonstrated that its range included all the Carolinian and Great Lakes–St. Lawrence forest regions with some intrusions into the Boreal Forest Region north to Red Lake, Sioux Lookout, and Lake Abitibi. There was 1 record from the Hudson Bay Lowland near Moosonee. It was widespread south of the Boreal Forest Region except in Essex County which has very limited forest cover. It was concluded that the historical range was probably the same, with early observers overlooking it. Highest abundance appeared to occur along the southern edge of the Canadian Shield from Owen Sound to Kingston (Eagles in Cadman et al. 1987). James (1991) considered the Rose-breasted Grosbeak common in the south, uncommon in the north to Sioux Lookout and Cochrane, rare north to Pickle Lake and Moosonee, and a vagrant at Winisk.

The second atlas demonstrated that there had been no significant change in the distribution of the Rose-breasted Grosbeak since the first atlas. It was a little more widespread in the extreme southern Boreal Forest Region, particularly at the latitude of Lake Nipigon. It was observed in some

new blocks in the Boreal Forest Region but was apparently absent in some previously occupied blocks. It disappeared from many squares on Manitoulin Island and in Algoma District, but was present in many more squares in Essex County. Its probability of observation declined significantly province-wide and in the Carolinian and Great Lakes–St. Lawrence forest regions. It was most abundant in southern Ontario from Algonquin Park south to Lake Simcoe, Peterborough, and Kingston east to Pembroke and Cornwall. It was also abundant on the Bruce Peninsula and the Norfolk Sand Plain. It was least abundant in extreme southwestern Ontario, Toronto, and Manitoulin Island (Wyatt in Cadman et al. 2007).

Wyatt and Francis (2020) noted that the Breeding Bird Survey (BBS) for the United States showed no change for the Rose-breasted Grosbeak for 1966-2000, but that this masked a significant increase 1966-79 and a significant decrease 1980-2000. In Canada, there was a significant increase of 7.3% per year 1966-79 and a significant decrease of 4.4% per year 1980-2000, with a net decrease of 2.1% per year 1966-2000. L.A. Smith et al. (2007) reported that the Ontario population decreased at a rate of 2% per year 1966-2004. Moore et al. (2010) reported that BBS data indicated that it decreased in North America at a rate of 0.8% per year 1968-2005, 1.9% in Canada, and 2.3% in Ontario. BBS results indicate that it decreased at annual rates of 0.284% in Canada and 1.05% in Ontario 1970-2021. The trends 2011-21 were annual increases of 0.199% in Canada and 0.0793% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings are incapable of flight when they leave the nest. Semicaptive birds at Erindale could fly when they were 12 days old. Young in southwestern Ontario were incapable of flight 2-5 days after leaving the nest and moved only short distances from it. After the first week, they began to forage for themselves and were capable of short flights. Fledglings became increasingly mobile as they aged and moved significantly higher up into the canopy. Those 0-5 days out of the nest occurred at heights similar to or lower than nests, typically less than 5 m from the ground, but within a week were usually more than 10 m up. They also moved further from the nest as they aged. Fledglings 0-5 days out of the nest averaged 48.5 m from the nest. By 6-11 days, they were 136.3 m from the nest and they were 228.1m from it 12-18 days out of the nest. Fledglings were usually independent 18 days after leaving the nest, at the age of 28-30 days. The Erindale young started feeding themselves when they were 28 days old and the adults stopped feeding them when they were 30 days old (Ivor 1944; Moore et al. 2010). Austin (1968) reported that young could not fly well until they were 20 days old. Family groups remain together until autumn migration (Wyatt and Francis 2020).

Both adults and young inhabited clear-cuts 1-10 years old in Pennsylvania, Minnesota, Virginia, and West Virginia. In Pennsylvania, the Rose-breasted Grosbeak was not netted in mature forests adjacent to clear-cuts. In Minnesota, adults nested in clear-cuts as young as 7 years old, so these birds may simply have remained in the breeding area during the postfledging period. In other areas, birds may have moved from forests to clear-cuts after the young were independent (Marshall et al. 2003; Stoleson 2013; Streby et al. 2011b). In Michigan, it was much more abundant during the postfledging period in mature riparian than mature upland forests. Both forest types had a similar overstorey, but riparian woodlots had a shrubby understorey of alders and honeysuckles (Akresh et al. 2009).

Nest sites tended to have more understorey cover than random locations in southwestern Ontario. There was no difference in the shrub cover of nests and fledgling locations 0-5 days out of the nest. Of those that survived a week out of the nest, 17 of 28 (60.7%) moved to a different forest treatment than where the nest was located. Treatments included uncut forests and those thinned by selective harvesting and heavy diameter-limit cuts. The mean age of dispersal was 14.2 days postfledging (range 7-21 days). Six of 17 fledglings (35.3%) crossed open gaps to a different forest fragment, with a median gap distance of 20 m (range 20-50 m; Moore et al. 2010).

McAtee (1908) reported that fledglings ate as much as 85% plant material, but did not elaborate further. It is most likely that this was predominantly fruit.

Moore et al. (2010) determined that there were no significant differences in daily nest survival or fledgling survival in 3 forest management treatments: unharvested woodlots and selectively thinned and heavy diameter-limit cuts. Twenty-six of 42 fledglings (61.7%) survived the 3-week fledgling period. Eighty-six percent of deaths occurred in the first week after leaving the nest, mostly in the first 5 days. Fledgling survival to independence was similar between years and sexes. The recruitment rate per female per season was 0.22 and 0.37 for the best- and worst-case scenarios, with predation by mammals and birds the most significant cause of mortality. Fledglings became less vulnerable to predation as they aged because they became more mobile and begged less. Young fledglings appeared to rely primarily on camouflage, often remaining perfectly still until approached within 1 m. Adults actively defended fledglings and gave alarm calls when potential predators approached. Older fledglings moved vertically into denser and elevated vegetation layers, probably limiting the suite of predators that they were vulnerable to. Forest management appeared to have little effect on fledgling survival even though the forest treatments varied significantly for a suite of vegetational parameters. Low regional forest cover rather than selective logging is likely contributing to population declines of the Rose-breasted Grosbeak.

MIGRATION

The Rose-breasted Grosbeak is a medium- to long-distance migrant that winters in Central and South America. Ontario birds have been recovered in Honduras, El Salvador, Guatemala, Columbia, Venezuela, and southern Mexico after travelling as far as 3,790 km. Although there are few recoveries, there appear to be no differences in the distance travelled by the sexes. Autumn migration is more protracted than spring migration. It migrates nocturnally; during the day it may be seen singly, in pairs, or in loose conspecific flocks. It may also occur in mixed flocks, particularly with warblers in late summer and autumn (Brewer et al. 2018; Collier 1989; Francis and Cooke 1990; Tozer 2012; Wyatt and Francis 2020).

Weir (2008) reported that the sexes arrived simultaneously in spring at Kingston. At Prince Edward Point, the earliest and latest arrival dates were 1 and 13 May for males and 5 and 12 May for females. The mean arrival date of 17.1 May for males was significantly earlier than the mean arrival date of 18.2 May for females. In every year, the mean arrival date of males was earlier, although the difference was slight in some years. Older birds also returned earlier than yearlings. Average arrival was 15.5 May for older males and 18.1 May for yearling males. Early females appeared to include a higher percentage of adults than later arrivals. There was a significant tendency for brighter males to arrive earlier but there was considerable variation in arrival dates of birds with similar brightness.

If few yearling males obtain territories, there is little advantage in arriving early. The earlier arrival of brighter yearling males suggests that they may be more likely to obtain territories (Francis and Cooke 1990). At Long Point, mean capture dates were 9.7 May for older males, 13.1 May for yearling males, and 10.0 May for females of unknown age. Older males arrived significantly earlier than yearling males (Stewart et al. 2002). Wyatt and Francis (2020) reported that 50% of birds arrived at each location in spring within a 6-14 day period. They reported median capture dates at Long Point of 11 May for adult males, 13 May for yearling males, and 14 May for females. In New York, older males showed a strong tendency to arrive earlier than yearling males. This tendency was most pronounced among older returning males that had previously bred in the area (Yunick 1996b).

Some studies examined whether climate change affected migration timing of the Rose-breasted Grosbeak. In New York, Zelt et al. (2017) compared its spring arrival and autumn departure dates in 1888-1939 to 1967-2012. It arrived slightly earlier and left slightly later in the later period, but not significantly. In Massachusetts, the mean arrival date was 9 May 1851-1973 and 6 May 1988-2007, a significant difference. Arrival times were less responsive to temperature than to the flowering periods of plants (Ellwood et al. 2010).

In southern Ontario, average arrival is in the first week of May and the earliest migrants arrive in mid-April. The peak of migration is in the second and third weeks of May and migrants leave by the end of May (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). In the southern Shield, the Rose-breasted Grosbeak typically arrives in the second week of May with the earliest records in late April (Mills 1981; Tozer 2012).

In the southern Shield, birds are migrating by at least the second week of August, with sightings well into September and the latest observations in late September or very early October (Mills 1981; Tozer 2012). In the south, migration begins in early to mid-August with numbers increasing later in the month. Most depart in late September or early October, with late records to December and early January (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). At Long Point, there was no difference in the timing of autumn migration of the sex or age classes, with 50% of birds passing through within a 10-20-day period. The median capture date was 20 September for adult males, 15 September for juvenile males, 13 September for adult females, and 15 September for juvenile females. The middle 50% of birds passed through between 8 and 21 September, with 90% occurring between 18 August and 27 September (Wyatt and Francis 2020).

The Rose-breasted Grosbeak uses a variety of habitats during migration, mostly forested and shrubby areas, especially where there is an abundance of fruit. These include upland and lowland deciduous and mixed forests, treed islands, shrubby margins of forests and wetlands, and shrub thickets. In Mississippi after trans-Gulf migration, it used mostly shrub thickets less than 5 m tall, but also pine forests and shrubby dune ridges (Campbell et al. 2001; Wyatt and Francis 2020). In Wisconsin and Minnesota, spring migrants were significantly more abundant in upland than riparian forests. Upland forests were dominated by sugar maple or oaks. Riparian forests were characterized by silver maple, green ash, and white elm (Kirsch et al. 2013). It was also significantly more abundant in upland than riparian forests during spring migration in Pennsylvania. Upland forests had 74% canopy closure compared with 83% for riparian forests and 39% shrub coverage compared with 19% in riparian forests (Rodewald and Matthews 2005). During spring migration in Pennsylvania, it

was significantly more abundant in shrubby habitats than in forests (Smith and Hatch 2006). During autumn migration in Pennsylvania, Rodewald and Brittingham (2002, 2004) determined that there were no significant differences in its abundance in forest interior, forest edges, forest-agricultural edges, suburban forests, pole-stage forests, and shrub-sapling-stage forests.

The earliest spring migrants often visit bird feeders where they prefer black oil sunflowers. Autumn migrants and postfledging-period birds may also eat sunflowers at feeders and feed them to their fledglings (Lancaster et al. 2004; Tozer 2012). In early spring, the Rose-breasted Grosbeak may visit hummingbird feeders to drink sugar water (personal observation). During spring migration, it eats leaf buds of ash and presumably other tree species (Fitch 1958). During autumn migration in Muskoka and Parry Sound districts, small groups eat elderberries and fruits of hophornbeam (Mills 1981).

The Rose-breasted Grosbeak commonly strikes television towers, lighthouses, and other structures during migration. During 1960-2000, 152 were killed in spring and 104 in autumn at the Long Point lighthouse (Wyatt and Francis 2020). From 1972 to 1982, 45 were killed at the Lennox generating station chimneys; 14 were killed on a single night on 6 September (Weir 2008). Loss et al. (2014) determined that it was 24.1 times more likely to strike a low-rise building than average and 16.2 times more likely to strike a high-rise. It was not among the top 20 species overall or for striking 1-3-storey residences.

James (1991) considered the Rose-breasted Grosbeak a common migrant in Ontario. Hussell et al. (1992) reported a significant decline of 2.4% per year at Long Point Bird Observatory (LPBO) 1961-88. Annual trends by period were: 1961-70, –2.0%; 1970-79, –4.9%; and 1979-88, –4.6%. LPBO data for 1961-97 indicated a marginally significant decline of about 1% per year in spring but a similar increase in autumn (Wyatt and Francis 2020).

WINTER

James (1991) reported that the Rose-breasted Grosbeak was an occasional rare winter resident in the south north to Sudbury and at Thunder Bay. One overwintered successfully in the Kingston area at a feeder, and there are winter records from Elgin County and Niagara Region (Black and Roy 2010; Lancaster et al. 2004; Weir 2008).

Blue Grosbeak

Passerina caerulea

BREEDING SEASON

Habitat Requirements

In Ontario, the Blue Grosbeak has been observed during the breeding season in open anthropogenic habitats. These include a grove of roadside trees, on wires above a grassy field, in common reed in a ditch along a road, and in semiopen shrubby and woodland habitat. It probably bred somewhere within these areas, but this was not confirmed (Woodliffe 2022).

The Blue Grosbeak's habitat requirements are very similar to those of the Indigo Bunting. The Blue Grosbeak nests in old fields, forest edges, transmission-line corridors, open areas with slash left after logging, hedgerows, stream edges, deserts, mesquite savannahs, saltcedar stands, multi-aged southern pine forests, and roadsides. It also nests in orchards, shrubbery around houses and gardens, and sunflower patches. In the west, it requires dense vegetation near water and nests in shrubs along watercourses, ditches, and canals. In the east, presence of water may not be essential and it prefers upland areas to lowlands. It tends to avoid treed and shrub swamps and forest interior. Its general habitat structure is characterized by dense ground cover, low to moderate shrub density, few trees, and an open canopy (Austin 1968; Lowther and Ingold 2020; Stabler 1959; Taber in Austin 1968). In Arkansas, it was a typical species of early tree succession areas, but was not numerous. It was absent in burned and unburned broomsedge fields and treed plots. It occurred in clonal persimmon plots in the early tree phase with 17% cover, 301 trees per ha, a stem density of 796 per ha, and sparse ground cover (Shugart and James 1973). In Utah, Arizona, and Nevada, its average habitat characteristics were 24.5% canopy cover, 28.8% shrub density, 27.6 trees 7.6-15.2 cm diameter at breast height in a 0.04-ha circle, and 35.6% ground cover (Whitmore 1977). In Arizona, it nested in a 20-ha riparian stand of cottonwood and willow with a patchy understorey of saltcedar, cattails, and bulrushes (Rosenberg et al. 1982).

In the Atlantic states, the nest is usually in a low shrub or vine in a thicket. Where it is more common, nests are often in fruit trees or cultivated plants around houses (McAtee 1908). In Colorado, the first nest of a pair was 76 cm from the ground and was attached to sumac and wolfberry. The nest for the second brood was 17 m away, 97 cm from the ground in a sparse clump of skunkbush sumac (Stabler 1959). In California, nests along ditches were fastened to 2-3 upright shoots at heights of 15 cm to 1.5 m. Some nests were in dense patches of small willow saplings. Occasionally, nests were in peach orchards 2.4-3.7 m from the ground. One nest was 6 m up in a willow at the end of a horizontal branch overhanging a ditch full of water. Another was 4.6 m up in a poplar in a residential yard (Taber in Austin 1968). Four other California nests were all in young black willows along the edge of a tidal bay 0.9-2.1 m from the ground (Bleitz 1956). In the east, the Blue Grosbeak usually nests in a shrub or small tree 0.9-2.4 m from the ground, but it also nests in tall herbaceous species and vines. In Virginia, it preferred to nest in second-growth saplings such as oaks and locusts and these seemed to be their natural nesting sites. Species that it has nested in

include grapevines, pines, alders, sweetgum, mulberries, blackberries, oaks, pear, cherries, willows, locusts, red maple, and a variety of ornamental shrubs. Most nests are 1-2 m from the ground but one was 7.6 m up in an oak. Nests may be as low as 15 cm from the ground (Austin 1968).

The Blue Grosbeak vigorously defends a territory against intruding conspecifics but tolerates other species. In Georgia, 1 pair had a territory of 6.2 ha during nest building and incubation but defended only 5.3 ha during the nestling stage (Odum and Kuenzler 1955). In another area in Georgia, territories averaged 1.2 ha. Territories averaged 5.2 ha in Alabama with a range of 0.8-8.73 ha (Lowther and Ingold 2020).

No information is available on natal philopatry or adult site fidelity.

Limiting Factors

No information appears to be available on how long it takes to build a nest and how much time elapses between nest completion and egg laying. Eggs are laid at the rate of 1 a day. Hatching takes place over 2 days, so it is probable that incubation begins before the clutch is complete. The incubation period is 11-13 days and the nestling period is 9-13 days (Austin 1968; Lowther and Ingold 2020; Stabler 1959).

The Blue Grosbeak commonly raises 2 broods in the south but only one in the northern portion of its range. In Colorado, 1 pair raised 2 broods in nests 17 m apart. The second clutch was completed about a month after the first clutch was completed. Clutches of 2-5 eggs have been reported. Most clutches contain 4 eggs; 2- and 5-egg clutches are rare (Austin 1968; Lowther and Ingold 2020; McAtee 1908; Stabler 1959; Taber in Austin 1968).

The age at first breeding is unknown but it is probable that yearlings are capable of breeding. The Blue Grosbeak is probably monogamous but no detailed studies have been done on this aspect of its breeding biology. Extra-pair copulations are a significant component of its mating system. In Alabama, 29 of 55 nestlings (52.7%) were extra-pair and 14 of 20 broods (70%) contained extra-pair young (Lowther and Ingold 2020).

In Tennessee, 1 pair foraged by one or both birds flying to a weed-top perch and sitting motionless for a few seconds. Then they either made low short flights and hovered over or adjacent to the herbaceous vegetation, plucking insects from leaves or stems, or flew to the ground and hopped among the grasses until they made a capture. The male often followed the female from place to place as she hunted and accompanied her when she returned with an insect even if he had

not made a kill himself (Alsop 1979). It is possible that the male was guarding the female against extra-pair copulations rather than participating in foraging. In Arizona, the Blue Grosbeak foraged by hovering and gleaning from foliage (Rosenberg et al. 1982). It spends considerable amounts of time foraging on the ground, often in and around plowed fields and pastures. On the ground, it searches one spot thoroughly before hopping to another location. It may also perch on roadside wires to hover and glean on vegetation, or flycatch from the ground and shrubs (Austin 1968; Lowther and Ingold 2020).

Males exhibit no strong tendency to feed nestlings. In Tennessee, Blue Grosbeaks fed their nestlings preying mantises almost exclusively. All mantids delivered to young were very large, in excess of 75 mm. The females removed the head and wings from all carcasses and all or most of the legs before delivering them to the nest. Young were fed 96% mantids with the only other food being grasshoppers. Grasshoppers were the most common large insects in the fields where the birds were hunting, ranging in size from 20 to 50 mm. The mantids' large size (mostly 75-100 mm but some larger) in addition to their slow movements and their tendency to remain motionless when approached probably made them desirable prey (Alsop 1979). McAtee (1908) reported that nestlings and recently fledged young ate 99.08% animal food and 0.92% vegetable matter. The animal food consisted of 74.1% grasshoppers, 10.7% caterpillars, 10% snails, and a single each of weevil, long-horned beetle, robber fly, and bristle fly. The vegetation consisted of blackberry remains and seeds of crabgrass, yellow foxtail, green foxtail, wild rice, dropseed grass, and smartweed. Lowther and Ingold (2020) stated that nestlings ate mostly orthopterans, especially short-horned grasshoppers. They are also fed owlet moth caterpillars, especially those of the small mocis moth.

In Arizona, 9 adults had consumed 48% cicadas and 52% grasshoppers by volume and 50% cicadas and 50% grasshoppers by frequency. Most prey was 21-30 mm long. Young fledged in July when cicadas were most abundant (Rosenberg et al. 1982). McAtee (1908) analyzed the contents of 51 stomachs collected from April to September. The diet consisted of 67.6% animal matter and 32.4% vegetable matter. The animal matter was mostly insects (65.7% of the entire diet) plus some snails and spiders. Grasshoppers were the most important animal food, comprising 27.2% of the diet, especially short-horned grasshoppers and crickets. Thirty-two of the 51 Blue Grosbeaks had eaten nothing else. Caterpillars and adult moths formed 9.77% of the diet, including caterpillars of the white-lined sphinx moth which constituted 40% of the May diet in Texas, and many other sphinx moths. Beetles were also important in the diet. June beetles comprised the entire diet of some birds. It also ate dung beetles, 7.18% weevils, leaf beetles, metallic wood-boring beetles, click beetles, and long-horned beetles; it rarely consumed ground beetles. It ate leaf-footed bugs, stink bugs, treehoppers, and cicadas. It rarely ate flies (including robber flies), wasps, ants, sawfly larvae, snails, and spiders. Vegetation it consumed included 14.25% grain, 18.05% weed seeds, 0.06% fruit, and 0.04% miscellaneous. Wild blackberries were the only fruit that it consumed. Seeds were the preferred vegetable food, but it did not eat a great variety. They were mostly foxtails and bindweeds. One bird fed largely on the seeds of wild rice. It did not specifically seek grain and only 1 bird had eaten grain exclusively. Lowther and Ingold (2020) reported that it also ate seeds of panic grasses, dropseeds, oats, corn, and alfalfa.

The Blue Grosbeak is a common host of the Brown-headed Cowbird. It sometimes ejects cowbird eggs and may bury them in the nest. The cowbird usually removes a grosbeak egg from the nest. All 7 nests found at 1 California site were parasitized. Five cowbirds and only 2 grosbeaks fledged from these nests. Zero of 6 nests were parasitized at another California site. Other parasitism rates include 3 of 5 nests (60%) in Arizona, 20 of 33 nests (60.6%) and 4 of 5 nests (80%) in Oklahoma, and 4 of 17 nests (23.5%) in South Carolina. One cowbird and 1 grosbeak fledged from 1 nest. Four of each species fledged from 6 nests that contained 13 grosbeak and 14 cowbird eggs (Bleitz 1956; Lowther and Ingold 2020).

Habitat loss does not appear to be a significant limiting factor for the Blue Grosbeak. It is expected to benefit from abandonment of agricultural land (Lowther and Ingold 2020). The current trend is to convert shrubby land to agricultural fields or other land uses, so the amount of suitable habitat for it may be decreasing in Ontario.

The Blue Grosbeak is widespread but scarce throughout its range. This may be due to competition with the Indigo Bunting and other species in the same genus (Lowther and Ingold 2020).

The Blue Grosbeak commonly nests along roads and is occasionally killed by vehicles (Lowther and Ingold 2020).

Status

James (1991) considered the Blue Grosbeak an occasional rare straggler in the south to Lake Nipissing. It was a vagrant in the north at Vermilion Bay and Rossport. It was first reported in the province in 1913 and there were at least 11 records in the decade before 1991. At that time, there was no evidence of breeding in the province.

The first indication that the Blue Grosbeak might breed in Ontario was in 1995. A pair was observed west of Blenheim along the Lake Erie shoreline. They were observed mate feeding, copulating, and carrying nesting material. Both sexes were observed carrying food but did not always go to a specific spot, so nesting was not positively confirmed. The male remained in the area until early September. He returned in 1996 and stayed for several weeks, but no females were present (Woodliffe 2022).

Breeding evidence for the Blue Grosbeak was obtained in 4 atlas squares in 2024: 3 in Essex County and 1 in Middlesex-Elgin. One pair was seen near Leamington and a pair with at least 1 fledgling was observed in Windsor. The latter record is the first confirmation of breeding in the province (Bumelis 2024), although no nests have been found yet.

Ontario is well north of the Blue Grosbeak's normal breeding range. Its range is extending northward with strays found in spring and autumn into Connecticut, Massachusetts, and Wisconsin. It has recently been confirmed nesting in New York. The Breeding Bird Survey indicates an annual increase of 1.0% 1966-2006. During this period, there was significant positive growth at the periphery of its range in Illinois, Maryland, and Colorado and also in its core range in Kentucky, Tennessee, and California (Lowther and Ingold 2020).

POSTFLEDGING PERIOD

When fledglings become independent, they leave the adults and assemble in small flocks composed of a few families. The adults join them later with the young from their second broods. Shortly afterwards, in early September, they depart southward on their autumn migration (Austin 1968).

During the postfledging period, juveniles and adults move to grain fields, roadside weed patches, and rice fields to forage. Favourite foods at this time include cultivated and wild oats and cultivated rice when it is in the milk stage (Austin 1968; Taber in Austin 1968).

An immature male banded in September in Alabama was recaptured in the same location the following August (Lowther and Ingold 2020). This suggests that there is some site fidelity to postfledging habitat.

Domestic cats are a known threat to Blue Grosbeak fledglings (Lowther and Ingold 2020).

MIGRATION

The Blue Grosbeak is a nocturnal migrant that occasionally strikes television towers. It arrives in the Gulf Coast states in the first week of April and migration continues through the second week of May. During spring migration, individuals may occur far north of the breeding range. Spring overshoots occur mostly in April and May. Males arrive in spring ahead of females and form feeding flocks before the females arrive (Austin 1968; Lowther and Ingold 2020). In South Dakota, autumn migration extends from mid-August to mid-September, but may continue through October in other areas (Lowther and Ingold 2020).

Spring migration habitat is similar to the breeding habitat. Autumn migrants gather in habitats similar to those used during the postfledging period. These include grasslands, rice fields, and grain fields (Lowther and Ingold 2020).

Most Ontario migration records are of spring overshoots. These occur mostly in May, but spring birds have been detected from 18 April to 7 June (Burrell and Charlton 2015; Cranford 2010). Spring birds are seen predominantly in the south, particularly in Essex County, but they may occur anywhere in the south and have been documented in Algonquin Park, Sault Ste. Marie, and Thunder Bay District (Cranford 2013).

Beginning in the late 1990s, 2-4 records of the Blue Grosbeak were documented annually in Ontario and accepted by the Ontario Bird Records Committee. It is likely that additional birds were observed but not reported to the committee. By 2021, 112 records had been accepted, including 48 in the southern portion of the province in the previous 20 years. At this time, it was concluded that there was no longer a need to report Blue Grosbeaks observed in the south (Riley et al. 2021). Nonetheless, it is not a regular migrant in Ontario. Most birds are spring overshoots and almost none of these breed or exhibit normal migration patterns.

Indigo Bunting

Passerina cyanea

BREEDING SEASON

Habitat Requirements

In Ontario, 52.7% of Indigo Bunting nests were in open woodlots or in wooded areas at clearings, edges, roads, paths, and shorelines; 28.0% were in shrubby fields and pastures, fencerows, savannahs, and orchards; 15.1% were on road and railway rights-of-way; 3.2% were in residential gardens; and 1.1% were in a cottage area of a provincial park. It preferred deciduous stands (21 nests) to mixed (12 nests) and coniferous (2 nests) stands. Only 3 nests were reported in closed woods. Almost all nest sites had dense undergrowths of saplings or shrubs, herbaceous species, or vines (Peck and James 1987).

In Algonquin Park, the Indigo Bunting preferred shrubby areas such as recently logged areas (MacLulich 1938). Martin (1960) found that it was common in plots bordering woods but did not

record it in forests. In Muskoka and Parry Sound districts, it nested in brushy pastures, along hydro corridors, and at edges of woods, streams, and ponds (Mills 1981).

In the Great Lakes–St. Lawrence Forest Region south of the Canadian Shield in Durham Region, the Indigo Bunting nested in a black spruce bog surrounded by a red maple–poplar swamp, an open wet forest with rank growth of ferns and raspberries, and in beech–sugar maple, sugar maple, and beech woodlots (Speirs and Orenstein 1975).

In the Carolinian Forest Region, the Indigo Bunting favoured shrubby hillsides in Niagara Region and was partial to nesting in raspberry bushes (Sheppard et al. 1936). In Elgin County, it usually nests in woodland edges or shrubby pastures, but occasionally in rural residential yards that contain suitable stands of trees and shrubs (Lancaster et al. 2004). At Point Pelee, it nested in 2 wooded areas where ash represented 18% and 38% of the crown cover. Average diameter at breast height (DBH) of ash trees in these stands were 26.5 and 41.1 cm (Dodds and Otis 2009).

In Ontario south of the Shield, abundance of the Indigo Bunting was negatively correlated with the amount of forest 100 m from edge, forest size, the amount of forest cover within 2 km, and the amount of regional forest cover. These relationships were not significant at the 0.05 level but the relationship with core area of forest interior was significant at the 0.10 level (Austen et al. 2001).

The Indigo Bunting is an early successional species associated with shrubby thickets and forest edges. It nests in both dry and damp areas but tends to avoid very wet areas. Highest densities often occur in shrubby and weedy habitat between forests and fields. It commonly nests at edges of forests, in fields regenerating 6-30 years after cultivation is abandoned, gaps in forest canopies created by tree falls or insect infestations, young clear-cuts and burns, shrubby roadsides, shrubby areas along streams, railway and hydro line rights-of-way, hedgerows, oak savannahs, brushy prairies, shrubby swamps, along irrigation ditches, and borders of agricultural fields. It seldom nests in conifer plantations except in the southern portion of its range, in treed swamps, and grazed pastures and rarely nests in corn and soybean fields. It avoids urban and suburban areas, intensively grazed and cultivated areas, closed-canopy forests with limited woody undergrowth, and hayfields (Alterman et al. 2005; Baily 1954; Bielefeldt and Rosenfield 1994; Carey 1982; Carey and Nolan 1979; Cox et al. 2012; Davis and Mack 1995; Faanes and Andrew 1983; Fitch 1958; Graber and Graber 1963; Hoffman 1989a; Keller et al. 2003; Kopachena and Crist 2000; Lehnen and Rodewald 2009a; Lent and Capen 1995; Morgan 1976; Mossman 1988; Mossman and Hoffman 1989; Mossman et al. 1991;

Novak et al. 2016; Payne 2020; Payne and Payne 1993; Shugart and James 1973; Taber and Johnston in Austin 1968; Taylor and Taylor 1979; Westneat 1989; Yahner 2003; Yahner et al. 2002). Although it nests in sites dominated by saplings, it is more numerous in shrubby areas (Payne 2020). In addition to areas with low woody vegetation, males require tall perches for singing posts. These are often at the top of a tall tree, particularly if the top is dead, but males often sing from utility wires along roadsides. Perches are usually adjacent to edges between wooded and open habitats (Davis and Mack 1995; Kopachena and Crist 2000; Payne 2020).

Some studies examined the habitat requirements of the Indigo Bunting at the landscape scale. In the eastern United States, 57% of detections of the Indigo Bunting on Breeding Bird Survey (BBS) routes were in fragmented habitats (Donovan and Flather 2002). In Quebec, it inhabits the deciduous forest zone where forests are dominated by sugar maple–bitternut hickory or sugar maple–basswood communities. Forests in this region are fragmented and there is much edge habitat. The demarcation between areas of high and low probability of observation is clear and corresponds to the transition between deciduous and mixed forests (Barden in Robert et al. 2019; Labonté and Dauphin in Gauthier and Aubry 1996). In North Dakota, it inhabited landscapes that were 42-75% forested; no areas were more than 75% forested (Cunningham and Johnson 2019). In Indiana, Ford et al. (2001) studied the Indigo Bunting in a forested landscape and an agricultural corridor. They found more nests in the corridor landscape. It was the only species they studied that had better nest survival rates and a higher number of fledglings per nest attempt in the agricultural landscape. In Pennsylvania, it was equally abundant in landscapes with 40% and 15% forest cover (Keller and Yahner 2007). In North Carolina, it was negatively correlated with elevation and the amount of canopy cover at the 200-m scale, and residential development at the 1,000-m scale. It required a disturbed landscape but was adverse to development (Gilbert and Ferguson 2019).

Some studies suggested that the Indigo Bunting requires water in the vicinity of its territory. In Utah, all nests reported by Whitmore (1975) were along streams or irrigation areas. In Texas, it was associated with water, with 94% of territories containing water. Thirty percent of territories were associated with livestock ponds, 58% with permanent creeks, and 12% with intermittent creeks (Kopachena and Crist 2000). Nonetheless, it has nested in a wide variety of upland sites lacking any water (Taber and Johnston in Austin 1968). There is no evidence that presence of water is essential in Ontario.

The Indigo Bunting highly prefers deciduous stands and its probability of occurrence declines with increasing coverage by conifers. It prefers young stands to mature stands and open-canopy stands with an undergrowth of deciduous shrubs and saplings to closed-canopy forests. In the southeastern United States, it nests in pine and pine-hardwood stands in early successional areas where it is abundant in both middle-aged and young shrubby stands (Conner et al. 1983). In Texas, it was most often associated with low-elevation mesic woodlands and uniform early successional growth typical of moist bottomlands that had been cleared. It occurred predominantly along edges created by clearing forests for pastures and hayfields. In Kansas, it was more abundant in young forests than in cropland, old fields, or mature hardwood forests (Kopachena and Crist 2000). In northeastern upland hardwoods, it was detected in 15% of plots in mature undisturbed forests compared with 47% of disturbed and successional stands (Noon et al. 1979). In northeastern poplar–

white birch stands, Back (1979) reported it in 3-year-old burns and sapling-pole-stage stands, but not in more mature stands. In deciduous woodlots in Illinois, it was positively correlated with the density of shrubs (Blake and Karr 1987). In Pennsylvania, Haney (1999) reported it in 9.1% of old-growth forests, 94.6% of woodlots statewide, and 93.1% of forests in the Appalachian Plateau. In North Carolina, it was negatively correlated with the percent coverage of forest canopy (Lumpkin and Pearson 2013). In bottomland hardwoods in South Carolina, it occurred only in early successional stands dominated by black willow, alders, and other shrubs (Buffington et al. 1997). In Wisconsin upland forests, it was a species of more open xeric woods and was 5 times more abundant in the most xeric continuum than the most mesic continuum. It occurred in 3 other woodlots where there were occasional openings in the canopy due to fallen trees (Bond 1957).

Considerable information is available on the microhabitat preferences of the Indigo Bunting. In Indiana, Carey and Nolan (1979) observed differences in habitat where it occurred at high and low densities in old fields. Low-density areas had been out of cultivation for 25-30 years and were characterized by dense stands of deciduous trees mostly more than 7 m tall with large eroded areas with little ground cover. High-density areas had been cut over or cultivated 3-5 years previously and some were mowed during the study. The vegetation was a lush cover of forbs and grasses with scattered blackberries, roses, and small saplings. In Utah, it was associated mostly with hedgerows among alfalfa fields. Habitat within 0.04 ha around male song perches consisted of 0.5 species of trees, 3.24 shrub density, 14-76 cm canopy height, 67.1% ground cover, 0.09 tree 7.6-15.2 and 15.2-22.9 cm diameter at breast height (DBH), 0.14 tree 22.9-38.1 cm DBH, and 0.29 tree larger than 38.1 cm DBH (Whitmore 1975). In Texas pine forests, it was positively associated with increasing percentage of sapling pines and negatively with increasing density of pole-sized trees, foliage at 7-15 m, the number of tree species, and percent canopy closure. It tolerated tall vegetation as long as it was sparse and patchy. It was not negatively affected by the absence of tall trees (Conner et al. 1983). Conover et al. (2009) studied its response to borders between wooded field margins and row-crop fields. It occurred in low density in fields with no borders, had highest density in fields with 10-m borders, and moderate density in fields with borders 30 m or more wide. In borders, the Indigo Bunting represented 8% of all birds and was fifth in abundance. In Texas, Kopachena and Crist (2000) sampled a diameter of 229 m around song perches, an area of 4.1 ha. Mean habitat characteristics included 2.91 isolated trees, 5.67 tree stands, tree stand size 9,119 m^2, size of largest open area 14,004 m^2, size of largest stand of trees 14,706 m^2, and 228.7 m of edge around the largest stand of trees. The area consisted of 48.9% open habitat, 16.1% early second growth, 16.4% late second growth, and 16.0% mature forest. Perches frequently occurred on or near edges of extensive woodlands. Perches occurred at lower elevations and were mostly on level ground; they were on lower slopes when they were on a slope. In Pennsylvania, nest sites had higher densities of woody stems than random sites (Schill and Yahner 2009). In Texas, it occurred more often in sites with low canopy cover and nested in areas with greater concealment than random sites. Nest concealment at 1.5-2.0 m above ground where most nests were placed was important in influencing nest success, with nest concealment greater around successful sites (Novak et al. 2016). The Indigo Bunting was largely a hedgerow species in the mid-Atlantic states. It was positively correlated with slope, percent ground cover, and the amount of forest cover within 2 km. It was negatively correlated with foliage density 0.3-1.0 m from the ground and the number of dead trees larger than 3 cm DBH (Robbins et al. 1989).

In Iowa, it nested mostly in woody vegetation. All nests with woody support were surrounded by dense forb growth. It was positively correlated with saplings, grasses, forbs, vines, horizontal patchiness of vegetation, and vertical stratification of vegetation. It was negatively correlated with deciduous trees. Dense herbaceous cover was a prerequisite for nesting (Stauffer and Best 1980). In Vermont, it was associated with clear-cuts, dense understorey, and deciduous vegetation. Its mean habitat values were 86.6% ground cover by green vegetation, 10.8% ground cover by slash, 13.9% canopy closure, canopy height 2.9 m, 0.0 m^2 BA of trees, 0.5 cm DBH of deciduous trees, 0 conifer, and 0 snag (Thompson and Capen 1988).

In Arkansas, nests in areas with shorter shrubs and trees and with few large trees were more likely to be successful. Increased cover by vines was also an indicator of nest success. Nests lower to the ground with increased cover of shrubs 0.5-1.0 m tall were more likely to be successful. Nests in areas with more vegetation were more successful; grapevines often provided excellent cover (Alterman et al. 2005). In Missouri, higher nests were less likely to be depredated than lower nests. Few other microhabitat variables were important in defining predation rates (Burhans et al. 2002).

The Indigo Bunting is an edge species. Bond (1957) agreed with this assessment but also observed it well within upland forests even where there was no reduction in forest cover. In Missouri, 60% of nests were within 20 m of edge, significantly more than the 45% of habitat at this distance from edge; 25% were 21-40 m from edge, similar to availability; and 15% were more than 40 m from edge, less than availability. It selected areas within 20 m of edge and avoided areas more than 40 m from edge. Predation rates were significantly lower within 20 m of edge indicating that edge habitat was not acting as an ecological trap (Woodward et al. 2001).

The Indigo Bunting is not an area-sensitive species. Studies on its area-sensitivity have been conducted in woodlands rather than shrublands. The fact that it commonly nests in hedgerows indicates that it is not area sensitive. In Illinois, it was positively correlated with woodlot size in 1 year but forest size had no effect in another year (Blake and Karr 1987). In Pennsylvania, it was equally abundant in woodlots less than 2 ha, 6-20 ha, 40-150 ha, and larger than 1,500 ha (Keller and Yahner 2007). There was no difference in its probability of detection in riparian woodlots 50-800 m in width in Maryland and Delaware (Keller et al. 1993). In the mid-Atlantic states, it was negatively correlated with woodlot size (Robbins et al. 1989).

Indigo Buntings have been documented roosting in dense raspberry bushes during the breeding season (Payne 2020).

Ontario nests were in shrubs, trees (mostly saplings), herbaceous plants, and vines. Deciduous shrubs, trees, and vines were greatly preferred (27 species, 97.2% of nests) over coniferous shrubs and trees (4 species, 2.8% of nests); 11 nests were in nonwoody species. Sixty-five nests were in raspberry bushes, 12 were in maples, 8 were in hazels, 7 were in hawthorns, 5 were in dogwoods, 5 were in elms, 4 were in apple trees, and 6 were in ferns. Most were in upright forks with fewer supported between vertical stalks and canes. Three were at the ends of boughs saddled on a branch or woven around a sapling trunk. Many, and especially those in raspberries, were near the top of the shrubs, well hidden just below the uppermost leaves. Nests were 0.2-6 m from the ground, with most 0.6-1 m up (Peck and James 1987). Mills (1981) reported a nest in alders in Muskoka or Parry Sound district.

In other areas, choice of the nest plant appears to be determined by the canopy cover over the nest and rigidity and branching form of the plant. The most frequently used species have forking stems that support the nest below a continuous layer of leaves. Later nests are often in forbs with rigid stems such as goldenrods, stinging nettle, thistles, milkweeds, giant ragweed, great burdock, joe-pye-weed, cow parsnip, and purple loosestrife. In Michigan, nests were found in more than 40 plant species but 50% of nests were in black raspberry and gray dogwood. Other species it has nested in include multiflora rose, staghorn sumac, red cedar, common juniper, bracken fern, Allegheny blackberry, spreading dogbane, bedstraws, poison ivy, prickly-ash, oaks, greenbrier, wild grape, Virginia creeper, mountain laurel, spicebush, spotted knapweed, garlic mustard, autumn olive, privet, barberry, buttonbush, hackberry, sweetgum, Jerusalem artichoke, hophornbeam, gooseberry, and black walnut. Of 41 Iowa nests, 42% were in forbs, 39% in shrubs, and 20% in deciduous saplings. Most nests are 0.3-1.0 m from the ground with less than 10% 10 m or higher in trees. There are no reports of nests being reused (Baily 1954; Morgan 1976; Payne 2020; Phillips 1951; Stauffer and Best 1980; Taber and Johnston in Austin 1968).

In Kansas, males with nests in cornfields sang from a roadside utility wire, with each claiming about 10 m of wire. The closest neighbouring territory on a wire was 40 m (Davis and Mack 1995). In Michigan, territories averaged 1.4 ha (range 0.4-8 ha). The smallest were along shrubby and weedy edges of woods and in old fields. The largest were in shrub swamps (Payne 2020). A territory in Kansas was 1.1 ha. The distance between pairs of 32 singing males averaged 153.6 m (range 33.5-396 m; Fitch 1958).

Natal philopatry rates are low, with most birds banded as nestlings nesting far from the natal site. Of more than 2,600 nestlings in Michigan, 138 (about 5.3%) returned to breed as yearlings or adults. Two nestlings were recovered as adults in the breeding season 52 km and 350 km from the natal area. Of more than 150 returning nestlings in Michigan, fewer than 10% bred within 1-2 km of the natal site (Payne 2020; Payne and Payne 1993). Of 155 young in Ohio, only 2 (1.3%) were recovered as adults and only 1 (0.6%) returned to its natal area (Lehnen and Rodewald 2009b).

It appears as though most surviving adults return to the same area to breed in subsequent years. In Indiana, 50% of females returned (Carey 1982). Return rates of males were 62% in fields with high-density populations and 28% in low-density fields. In high-density fields, 67.3% of males were adults; 73.5% of the males in low-density fields were yearlings (Carey and Nolan 1979). In Ohio, 82 of 280 adults (29.3%) were recovered in a subsequent year and 81 (98.8% of returning birds) returned to the same site (Lehnen and Rodewald 2009b). At 2 sites in Michigan, 42.4% and 62.1% of males returned in a subsequent year. Ninety-six percent of adult males and 71% of yearling males returned to the same territory. Females were significantly more likely to disperse to a new territory in a subsequent season than males. The return of her mate was the best predictor of whether a female would settle at the same territory or disperse, with most dispersal related to changes in males. The Indigo Bunting breeds in local groups of territories with several neighbours within 200 m. Social familiarity with song within the group may be a reason for males to return to their previous site. The greater incidence of dispersal by females may be because they are unlikely to benefit from prior familiarity of other females (Payne 2020; Payne and Payne 1993).

Limiting Factors

Eggs have been found in Ontario nests from the last week of May until the third week of August, with most present in the last 3 weeks of June. A nestling in pinfeathers on 4 September indicated an even later egg date (Peck and James 1987, 1998b). In Algonquin Park, nest construction occurs from late May to late June, eggs are present from early June to late July, nestlings are present from late June to late July, and dependent fledglings have been seen from early July to early September (Tozer 2012).

Females settle on males' territories 1-2 days after they arrive. The pair spends 0-6 days in selecting a nest site (mean 3.4 days). The first nest of the season takes 4-10 days to build, but later nests are built in as little as 2 days. The first egg is usually laid the day after the nest is complete, but as many as 3 days may elapse before egg-laying begins. In Indiana, the time spent from nest-site searching to laying of the first egg varied from 5-34 days (average 15.8 days). Longer periods were associated with early nesting yearling females and abundance of cowbirds. When cowbirds were abundant, nesting was delayed to avoid the peak laying period of the parasite. Eggs are laid on consecutive days. Incubation begins with the laying of the last egg. The incubation period in 2 Ontario nests was 12 days. Incubation periods of 12-13 days are typical, occasionally 11 days in summer and 14 days during cool weather. The nestling period is typically 9-12 days but may be as short as 8 days if the young are disturbed and as long as 14 days during cold weather (Carey 1982; Morgan 1976; Payne 2020; Peck and James 1987; Taber and Johnston in Austin 1968).

The Indigo Bunting typically raises 2 broods, rarely 3. Females nest repeatedly after both failed and successful nestings. In Michigan, 56.5% of females fledged 1 brood, 12.8% fledged 2, and 0.1% fledged 3 broods. These proportions were considered minima because females may breed elsewhere in the same season. Clutches of 2-6 eggs were reported in Ontario, with only a single 6-egg clutch found. Three eggs was the most common clutch size (average 3.31 eggs). The clutch size is typically 3-4 eggs, less often 1-2 eggs; single-egg clutches are usually abandoned. Smaller clutches may have had an egg removed by a cowbird. Larger clutches are more common later in the season (Payne 2020; Peck and James 1998b; Phillips 1951; Taber and Johnston in Austin 1968).

Both sexes are capable of breeding when they are 1 year old. Yearling females breed regularly and nest repeatedly during the season. About half of yearling males breed and almost all older males breed. In Michigan, 55% of yearling and 90% of adult males were mated and 49% and 85% nested respectively. Yearling males have lower reproductive success than adults. Yearlings that are unsuccessful in attracting a mate sometimes move to a new territory. Yearling males with blue plumage have better reproductive success than brown yearlings. Matching songs of neighbouring males raised the breeding success of browner males by 50% to equal that of blue males that did not song-match. Song-matching by blue yearling males increased their success to equal that of adult males (Payne 1982, 2020).

Carey and Nolan (1979) defined 4 types of mating systems for the Indigo Bunting in Indiana: polygyny, when a male was mated simultaneously to 2 or more females; season-long monogamy, when a male mated with a single female for the entire season; successive monogamy, when a male mated with 2 or more females but with no overlap in the period of association; and short-term monogamy, when a male was mated to a single female for less than the entire breeding season. Of

141 males, 10% were polygynists, 28% were season-long monogamists, 11% were successive monogamists, 37% were short-term monogamists, and 13% were unmated. The percentage of birds that were polygynists was significantly higher than expected. The proportion of polygynists changed annually from 3% to 15%, with no apparent reason for the changes. Eighty-five percent of males that were polygynous, season-long monogamists, and successive monogamists were adults. Yearlings predominated in the short-term monogamy (58% of males) and unmated (95%) categories. Polygynous males were the most productive and short-term monogamists were the least productive. Females mated to polygynous males were as productive as those mated to long-term monogamists and much more productive than those mated to other monogamous types of males. Females settled first in territories of polygynists and last in territories of short-term monogamists. In Michigan, 15% of males were polygynous. Most polygynous males had 2 mates but 2 had 3 mates and 1 had 4 mates. Of yearling polygynists, 84.2% matched a neighbour's song. The rate of polygyny was similar for adult and yearling males, and song-matching did not influence the rate of polygyny for adult males (Payne 1982). In Michigan, polygyny was associated with a decrease in male parental care (Westneat 1988a). Pairs usually remain together for the breeding season. Less often, the female disperses to another territory and mates with another male. Some females nest with 3 different mates within a season. Females are more likely to move to another territory when they are successful than unsuccessful in their first nesting attempt. Some take their fledglings with them and mate with another male after the brood is independent. Occasionally pairs move together and renest as far as 1 km from the original territory (Payne 2020). When both members of a pair return in a subsequent year, the proportion of them that remate is significantly higher than expected. At 2 Michigan sites, 50.7% and 49.0% of returning pairs reunited. Rematings may be due to a mutual attraction by both sexes to a common breeding site or to active mate selection. Sixteen Michigan pairs bred together for 3 or more years, including 2 pairs for 4 years and 1 pair for 5 years (Payne 2020; Payne and Payne 1993).

Extra-pair copulations are a common mating strategy. Nesting in neighbourhoods of 8-14 males facilitates extra-pair copulations. Both sexes spend considerable time foraying off their territories. Although some of this time may be spent foraging, most appears to be used to solicit extra-pair copulations, typically within 200 m of the home territory. Females solicit extra-pair copulations on their male's territory and those of other males, and may be forced by intruding males. Most off-territory forays occur when females are fertile. In Kentucky, 36 of 88 nestlings (40.9%) were extra-pair; 29.0% of Michigan broods had at least 1 extra-pair young. In another study, 41.5% of young were not matched genetically with the putative father, but all matched with the female. In 3 broods, all young were extra-pair. One study found that yearlings were less likely to be cuckolded than adults; another study found the opposite. Yearlings achieve fewer extra-pair copulations than adults (Carter et al. 2018; Payne 2020; Payne and Payne 1989, 1993; Payne and Westneat 1988).

Intraspecific nest parasitism is rare and occurs in less than 1% of nests. Single 6-egg clutches have been reported in Ontario and Michigan and these suggest laying by 2 females (Payne 2020).

The Indigo Bunting feeds on the ground on fallen seeds, takes grass seeds from plants, and forages in low shrubs, herbaceous species, and trees from ground level to a height of 15 m. It takes seeds from standing grasses and forbs, shuffling along the stem to the seed head. It gleans insects

and spiders from leaves while perching on small branches or moving through the canopy. It feeds on dandelion seeds in lawns, in cornfields on the pollen in the tassels, and in soybean fields on small insects. In summer, it feeds in open wetlands on reed canary grass seeds, with males from several territories visiting without conflict. It takes seeds from the surface of the ground without scratching with its feet. Upon arrival in spring, it feeds on twigs and leaves of flowering deciduous trees and also on leaf buds, young leaves, and pollen of trees. During autumn migration, it feeds in the tops of shrubs and trees and more often on the seeds of standing grasses and forbs. It is an opportunistic feeder, eating small seeds, insects, and berries as they become available (Payne 2020).

In Michigan, only 1.5% of males fed the nestlings in their first 4 days and all were adult males. Overall, 20.6% of males fed nestlings at least once; 18.8% of Kentucky males fed young. No polygynous males fed young. Nestlings are fed spiders, bees, mayflies, butterflies, moths, caterpillars, and harvestmen (Morgan 1976; Ritchison and Little 2014; Taber and Johnston in Austin 1968; Westneat 1988a, 1988b).

During the breeding season, adults eat small spiders and insects and occasionally berries and seeds. The predominant insects consumed include grasshoppers, caterpillars, bugs, and beetles. Aphids and cicadas are the main bugs consumed. Beetles that it eats include weevils, click beetles, and locust borers. Grass and forb seeds that it eats include those of thistles, dandelions, goldenrods, big bluestem, oats, common reed grass, Johnson grass, vetches, clovers, asters, and sorghum. Berries that it consumes include strawberries, blueberries, blackberries, and mulberries. The Indigo Bunting has eaten dog biscuits, cankerworms during an outbreak in an orchard, and mosquitoes. During autumn migration, the diet consists mostly of grass seeds (Holt 1918; Payne 2020; Taber and Johnston in Austin 1968).

The Indigo Bunting is a common host of the Brown-headed Cowbird. It deserts all nests when the cowbird egg is laid prior to bunting eggs, but otherwise accepts eggs. The proportion of parasitized nests decreases as the season advances. More than half of bunting nests are initiated after the peak of cowbird laying. In Michigan, 23% of May nests were parasitized, 26% were parasitized in June, 9% were parasitized in July, and 0% were parasitized in August. Parasitized nests fledge about 1.5 fewer young than unparasitized nests. Nests with 1 cowbird nestling are more likely to fledge buntings than those with 2 cowbird nestlings, and parasitized nests are more likely to be depredated. Nests with less tree canopy, more tall snags nearby, and closer to trees are more likely to be parasitized. In Ontario, 51 of 193 nests (26.4%) were parasitized. Parasitism rates reported in Indiana include 5 of 7 nests (71.4%), 53 of 126 nests (42.1%), and 22 of 63 nests (34.3%). In the latter study, the parasitism rates before and after 15 June were 46.3% and 13.6% respectively. Other parasitism rates include 6 of 14 nests (42.9%) in Ohio, 3 of 82 nests (3.7%) in Arkansas, 13 of 55 nests (23.6%) in river floodplains and 142 of 295 nests (48.1%) in old fields in Missouri, 18 of 109 nests (16.5%) in Georgia and South Carolina, 3 of 15 nests (20.0%) in Texas, 411 of 1,725 nests (19.5%) in Michigan, 8 of 10 nests (80.0%) in Wisconsin, 18 of 60 nests (30.0%) in West Virginia, 12 of 68 nests (17.6%) in Mississippi, and 6 of 30 nests (20.0%) in Quebec (Alterman et al. 2005; Brittingham and Temple 1996; Burhans et al. 2010; Carey 1982; Chapa-Vargas and Robinson 2013; Hackemack et al. 2016; Kilgo and Moorman 2003; Labonté and Dauphin in Gauthier and Aubry 1996; Morgan 1976; Novak et al. 2016; Payne 2020; Peck and James 1998b; Phillips 1951).

The Indigo Bunting benefitted from early deforestation and forest fragmentation, but the amount of suitable habitat is declining. Habitat loss is occurring due to hedgerow removal, roadside maintenance, natural succession of old fields, urbanization, and planting coniferous plantations (Hanberry and Thompson 2019; Labonté and Dauphin in Gauthier and Aubry 1996; Taber and Johnston in Austin 1968).

Forest management improves habitat for the Indigo Bunting. In Pennsylvania hardwoods, it was absent in uncut forests and increased significantly immediately after clear-cutting (Yahner 1993, 2003). In Pennsylvania bottomland hardwoods, it was absent prior to clear-cutting; 2 years after cutting it represented 70% of all birds present. At least 1 growing season was required for establishment of early successional grasses and forbs (Harrison and Kilgo 2004). In New York clear-cuts, it was in a guild of species that was most abundant 5-7 years after clear-cutting and that declined significantly thereafter to become almost absent 24-25 years after cutting (Keller et al. 2003). It also benefits from partial harvests. Vanderwel et al. (2007) reported that it increased by 50% when 10% of trees were removed from boreal forests, including in Ontario. In southwestern Ontario, Holmes et al. (2004) did not find it in woodlots with no recent history of harvesting. It and the cowbird were the best indicators of heavy diameter-limit cuts. In New York upland forests, it was absent in uncut woods and occurred in low abundance in stands where 25-75% of merchantable trees had been removed (Webb et al. 1977). In Indiana, it was significantly more abundant 2-4 years after creating openings of 0.02-0.4 ha in a 2,000-ha forest (Robinson and Robinson 1999). In stand improvement cuts in Pennsylvania, it was more abundant in snag-retention treatments. These had significantly greater woody plant material 0-1.5 m above ground (Stribling et al. 1999).

The Indigo Bunting appears to avoid housing. In Waterloo Region, neotropical migrants consistently decreased in diversity and abundance as the number of houses within 100 m of forest edge increased, regardless of woodlot size (Friesen et al. 1995). In Chicago, it was strongly negatively correlated with distance to edge and the amount of coverage by urban development (Schneider and Miller 2014). In North Carolina, it was negatively correlated with the number of buildings within 200 m (Lumpkin and Pearson 2013).

Fires within forests tend to be beneficial, with the Indigo Bunting responding positively to fire in the Great Smokey Mountains (Rose and Simons 2016). In Georgia, it was associated with high-intensity burns that resulted in 20-50% canopy mortality and severe to total midstorey mortality. It was most abundant 3-6 years after fire when there was decreased canopy cover and an increase in shrub density (Klaus et al. 2010).

In Delaware, the Indigo Bunting was equally abundant in areas with low, moderate, and high populations of deer (Tymkiw et al. 2013).

In West Virginia, the Indigo Bunting was significantly more abundant adjacent to shale gas infrastructure (roads, pipelines, and well pads), particularly linear features, than distant from these features. As the forest was fragmented, its population expanded to follow the new construction and concentrated near pipelines and access roads (Farwell et al. 2019).

Near Missouri lead mines, the probability of a female fledging a young decreased from 57% to 23% in areas with elevated lead concentrations in the soil. Most nest failures were due to predation,

suggesting that lead affected birds' behaviour and activity at the nest, or affected nest-site quality (Thompson et al. 2024).

In North Carolina, the Indigo Bunting was negatively correlated with the average daily mean temperature, suggesting that it may be sensitive to climate change (Lumpkin and Pearson 2013).

Status

The Indigo Bunting is much more common now than it was prior to European settlement. It would have been confined to openings and edges in the extensive forest cover, such as wetland borders, areas cleared by First Nations, savannahs, burns, and alvars. The opening of the eastern forests coupled with tree planting and fire suppression in the west allowed it to greatly expand its range and population (Wells 1958). Baillie and Harrington (1937) considered it fairly common and well distributed north to Lake Nipissing and Ottawa, breeding throughout this range but more common along the southern edge of the province. They concluded that it probably bred at Sioux Lookout, Thunder Bay, and in the Sudbury area. The first atlas confirmed that it nested from the southern border throughout the Great Lakes–St. Lawrence Forest Region, with minor intrusions into the extreme south of the Boreal Forest Region. It was scarce in Nipissing and Parry Sound districts except in disturbed areas. Highest densities occurred in southwestern Ontario and in Rainy River District (Rising in Cadman et al. 1987). James (1991) considered it common in the south and rare in the north to Red Lake, Nipigon, and Timmins.

The second atlas revealed no significant change in the distribution of the Indigo Bunting. Overall, the population was stable, but its probability of observation declined significantly south of the Canadian Shield. The decline may have been due to agricultural intensification. It was most abundant in the Carolinian Forest Region and along the southern edge of the Shield (McLaren in Cadman et al. 2007).

The range and population of the Indigo Bunting increased throughout most of the 20th century, but the Breeding Bird Survey (BBS) indicated a decline in the last quarter of the century (Payne 2020). BBS results indicate that it increased at annual rates of 0.466% in Canada and 0.588% in Ontario 1970-2021. The trends 2011-21 were annual decreases of 1.41% in Canada and 2.1% in Ontario. All results were highly reliable (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings perch a few metres from the nest for the first few hours after leaving the nest and are capable of flying upward into a tree within hours of leaving the nest. Sometimes they return to the nest to roost at night, especially if they left the nest before they were 10 days old. Brood division may occur, with each adult responsible for particular individuals. A maximum of 50% of males feed the fledglings; polygynous males rarely provide care to fledglings. Males that do not feed usually follow the female and fledglings, but some remain on their territory and mate with another female. Young reach independence 14-25 days after fledging. Once they are independent, juveniles often flock together, with or without adults (Payne 2020; Westneat 1988a, 1988b).

Both adult and juvenile Indigo Buntings commonly occur in clear-cuts in hardwood stands during the postfledging period, but little is known of its use of other habitat types. In Pennsylvania, it was common in clear-cuts and absent in adjacent mature forests. In Missouri clear-cuts, it was

most abundant the second year after cutting and was significantly less abundant 7-15 years postharvest. In West Virginia clear-cuts, adult captures were correlated with vertical complexity of vegetation, herbaceous ground cover, and arthropod richness and biomass. The herbaceous ground cover was probably a source of seeds. Juveniles were positively correlated with caterpillars and negatively with basal area, vertical vegetation complexity, understorey stem density, herbaceous ground cover, and arthropod richness and biomass (Marshall et al. 2003; McDermott and Wood 2010; Porneluzi et al. 2014; Stoleson 2013; Streby et al. 2011b; Vitz and Rodewald 2005).

MIGRATION

The Indigo Bunting is a complete migrant, wintering from Florida to northern South America. It is a nocturnal migrant that may continue to fly after daylight. During autumn migration in Louisiana, it made northeastern morning flights, probably to account for wind drift during the nocturnal migration. It is solitary during nocturnal flights but may occur in flocks during the daytime. In Mississippi during spring migration, birds stopped over for an average of 2.8 and 3.5 days in 2 years. In New Jersey, the mean autumn stopover duration was 10.1 days (maximum 29 days). In Ontario, birds fly directly to the breeding areas, so spring flocks are rarely seen (Brewer et al. 2018; Curry 2006; Kuenzi et al. 1991; Payne 2020; Seewagen and Newhouse 2018; Yaukey 2010).

In New York, Zelt et al. (2017) compared Indigo Bunting arrival and departure dates for 1898-1939 and 1967-2012. There was little climate change in the first period and significant warming in the second. It arrived significantly earlier in the later period but there was no difference in its autumn departure date. Ellwood et al. (2010) did a similar study in Massachusetts for 1851-1973 and 1988-2007 and observed no response to increasing temperatures. In Indiana, older males arrived 19-21 days earlier in spring than yearling males and 15-18 days earlier than females (Carey and Nolan 1979). In Michigan, there was no difference in the mean arrival time of adult and yearling males but the first arrivals were adults (Payne 1982). In Missouri, adult males arrived earlier than yearling males and females, but adult males with less blue colour and yearlings with more blue arrived at the same time (Quay 1987). At Long Point, mean capture dates were 18.6 May for adult males, 17.5 May for yearling males and 18.5 May for males of unknown age. Although adult males arrived a bit later, the difference was not significant (Stewart et al. 2002).

In southern Ontario, most Indigo Buntings arrive in mid-May, the peak of migration is in the last 2 weeks of May, and the earliest migrants occur in late April. One was observed at a feeder in late March in Elgin County (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008). Average arrival in the southern Shield is mid- to late May (Mills 1981; Tozer 2012).

In the southern Shield, autumn migration begins in mid-August and all birds are gone by late September (Mills 1981; Tozer 2012). In the south, the main departure is in mid- to late September with stragglers to mid-October; one was reported on a Christmas Bird Count (Black and Roy 2010; Curry 2006; LaForest 1993; Lancaster et al. 2004; Weir 2008).

The Indigo Bunting is occasionally a late autumn vagrant to northern Ontario north of the normal breeding range. There are 20 records of birds in the north from 20 September to 24 November. All 3 November records were of birds at feeders that had probably been artificially induced to linger. Almost all were associated with human-influenced areas such as weedy or

disturbed areas in towns, feeders in towns, or campgrounds in provincial parks. Three were found at natural sites: 2 on shorelines and 1 on an island (Wormington 1986).

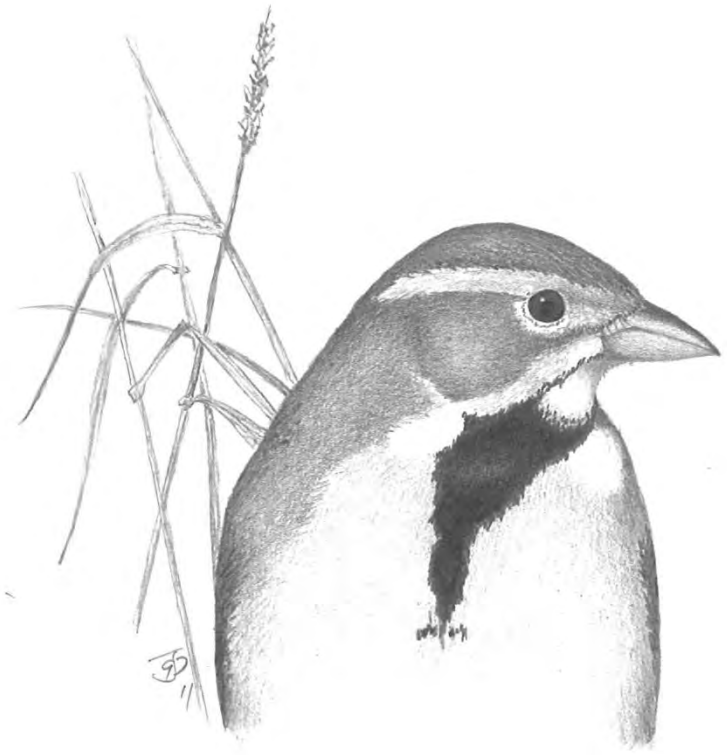
During migration, the Indigo Bunting inhabits open grasslands, shrubs, leafy trees, and tall standing grasses with seeds (Payne 2020). During spring migration in Pennsylvania, Smith and Hatch (2008) observed it significantly more often in shrubs than in forest. During autumn migration in Pennsylvania, it confined its habitat use to shrub-sapling-stage forests and forest-agricultural edges. It was not detected in older or suburban forests or in forest-interior habitat (Rodewald and Brittingham 2004).

The Indigo Bunting is occasionally killed at communication towers and other tall structures during migration. Three were killed at the Lennox generating station chimneys 1972-82 (Payne 2020; Weir 2008).

James (1991) considered the Indigo Bunting an uncommon migrant and an autumn wanderer north to Winisk and Moosonee.

Dickcissel

Spiza americana



BREEDING SEASON

Habitat Requirements

Peck and James (1987) reported that 1 Ontario Dickcissel nest was in a timothy field and another was in a shrubby farm field. During an invasion in 1988, most nests were in old or abandoned fields of grasses, forbs, and shrubs; 1 was in a hayfield (Peck and James 1998b). During the 2017 invasion, breeding birds were reported in grasslands, hayfields, and sites where tallgrass prairie habitat restoration had taken place. All were open areas dominated by grasses with some shrubs, taller forbs, or overhead wires that provided singing perches (Woodliffe 2018).

The Dickcissel is an obligate grassland species that nests in tallgrass prairies, old fields and meadows, hayfields, reclaimed surface mines planted to grasses, lightly grazed pastures, weedy field borders, roadsides, fencerows and hedgerows, Conservation Reserve Program lands, and grassed waterways. It occasionally nests in no-till row crops, shrubby areas, and marshes. Old fields, meadows, and hayfields are highly preferred over tallgrass prairie, its historical habitat. These are occupied first and birds tend to colonize prairies only after old fields are at carrying capacity. The

more heterogeneous vegetation structure in old fields provides better nesting habitat than prairies and supports a higher density and more polygynous males. Predation rates may be higher in old fields because these may have a higher density of predators. It prefers hayfields that contain alfalfa to those dominated by grasses. Habitats that contain forbs are superior. The forbs increase vegetation structure, provide nest sites and cover for nests, and are used as singing perches. When grasslands are sprayed to kill weeds, density of the Dickcissel declines significantly. Perches are an essential component of the habitat. Ideal nesting habitat may be unoccupied if there are no suitable singing perches. Tall forbs, shrubs, fence posts, and overhead wires along roads are suitable perches (Askins et al. 2007; Dechant et al. 2002k; Finck 1984; Fitch 1958; Fretwell 1977; Fretwell and Calver 1969; Graber and Graber 1963; Graves et al. 2010; Gross in Austin 1968; Harmeson 1974; K.L. Mitchell et al. 2012; Mulvihill 1988; Patterson and Best 1996; Swanson 1996; Temple 2020; Walk et al. 2010; Winter 1999; Zimmerman 1971, 1982, 1984; Zimmerman and Finck 1989).

At the landscape level, the Dickcissel is negatively affected by urbanization. McLaughlin et al. (2014) found that it did not avoid grasslands embedded in urban landscapes, but its density declined significantly with the intensity of surrounding urban areas. In Illinois at the 400-m scale, it was positively associated with agricultural land (Glass and Eichholz 2023).

The Dickcissel occurs in a wide range of habitats, but prefers areas with tall (25-150 cm) and dense (90-100%) cover, greater than 50% forb coverage, and more than 10 elevated song perches per ha. Occupied areas in Wisconsin had less than 1% woody cover, 74% herbaceous cover, 17% litter cover, 9% bare ground, 63 cm maximum vegetation height, 19 cm vegetation height-density, and 5-8 cm litter depth. Mean nest-site characteristics in Iowa were similar to those of the Red-winged Blackbird: 67 cm vertical cover, 98 cm height of live vegetation, 48% grass cover, 54% forb cover, and 94% total cover. Vegetation within territories and at nest sites is either taller or denser than unoccupied areas. Nest sites with taller vegetation, greater visual obstruction, greater coverage by grasses, and smaller amounts of bare soil have higher nest success. When Dickcissel densities are high, all but the least suitable vegetation is included within territories. At low densities, only optimum habitats are occupied. It is positively correlated with grass cover, litter cover and depth, and vegetation height and density. It is strongly negatively correlated with bare ground. Although shrubs and small trees may be used as nest sites and perches, all studies except one in Ohio determined that it was negatively correlated with coverage by woody vegetation (Chapman et al. 2004; Dechant et al. 2002k; Graves et al. 2010; Hatchett et al. 2013; McLaughlin et al. 2014; Monroe

et al. 2019; Patterson and Best 1996; Powell et al. 2008; Rotenberry and Wiens 1980; Swanson 1996; Winter 1999; Zimmerman 1971).

The Dickcissel does not avoid grassland edges adjacent to cropland or roads, with nests reported as close as 3 m to a cropland edge (Lituma and Buehler 2016). It appears to avoid edges with treed habitats, with the median distance of nests 400 m from a wooded edge in Illinois compared with 100 m for cropland edges (Walk et al. 2010). Proximity to wooded areas appears to reduce habitat suitability (Temple 2020). It may also avoid edges in urban landscapes where its occurrence was negatively correlated with the edge-to-interior ratio (McLaughlin et al. 2014).

Most studies concluded that the Dickcissel is not area sensitive and not significantly affected by habitat fragmentation (Dechant et al. 2002k; Herkert 1994a; McLaughlin et al. 2014; Swanson 1996). It has nested in grasslands as small as 1 ha and in strip habitats such as roadsides, fencerows, and grassed waterways. In Illinois, it nested in grassed waterways 7-28 m wide rather than hedgerows 1-3 m wide (Dechant et al. 2002k). Some studies found relationships between its abundance and patch size. In Kentucky and Tennessee, Giocomo et al. (2008) found most nests in fields larger than 150 ha. Temple (2020) reported that it preferred fields larger than 10 ha and had denser populations in larger fields. In Missouri, its density was unaffected by patch size but its nesting success decreased with decreasing patch size. Nest success may vary by the type of predators present, possibly explaining why patch size does not affect nesting success in some areas (Winter and Faaborg 1999). Zuckerberg et al. (2018) found that the direct and indirect effects of temperature and precipitation on nesting success were moderated by grassland patch size. The positive effects of precipitation in the previous year were strongest in small patches but had little effect in large patches. Warm temperatures reduced nesting success in small patches but increased nesting success in large patches.

In Ontario, 23 nests were elevated and 2 were on the ground. Elevated nests were in 5 species of forbs and 6 species of deciduous trees and shrubs. One ground nest was at the base of a forb and the other was concealed among timothy stalks. Nests were 0.08-1 m above ground, with most 0.3-0.6 m up (Peck and James 1998b). Coady (2007) reported a 2005 nest in Bronte Provincial Park that was 0.96 m above ground in a 2-m-tall hawthorn.

Typically 75% or more of nests are elevated. Early nests may be in grasses when forbs are still short and below the grasses. Deciduous shrubs and saplings are often used as nest sites. Nests are in a crotch or clump of the supporting vegetation but not tied to it in any manner. They are surrounded by green vegetation and well shaded (average 96%) with overhead vegetation. In Oklahoma, 36.2% of elevated nests were in white elm, 7.4% in Osage orange, 6.3% in hackberry, 4.2% in evening-primrose, 3.2% in mulberry, 2.1% in plum, and 1.1% in each of dogwood, coralberry, juniper, blackberry, heath aster, fleabane, sunflower, giant ragweed, and thistle. In Illinois, it highly selected old field aster for nesting, but nesting success was lower in asters than in dead vegetation. It has also nested in greenbrier, alfalfa, rose, green milkweed, grama grass, smooth brome, willow, wild crabapple, oak, cherry, and apple. Nests have been reported as high as 4.3 m from the ground but most are less than 1 m up. Replacement nests tend to be higher above ground in vegetation with greater average height, visual obstruction, and forb coverage, and somewhat lower grass coverage. Vegetation at random sites exhibited the same trends. Nests are only used once but may

be built on top of an old nest (Dechant et al. 2002k; Fretwell 1977; Gross in Austin 1968; Harmeson 1974; Overmire 1962; Patterson and Best 1996; Temple 2020; Walk et al. 2004).

The male defends a territory that includes the nest site and foraging area; females are not aggressive. Males abandon their territories toward the end of the breeding season, often before their mates have finished nesting. Males may make distant flights, possibly to scout for better habitat. In Kansas prairies, which are suboptimal habitat, males were on their territories significantly less than old-field males, spending more time in distant flights. Old-field males spent more time in territorial displays and less time in distant flights. Territory size is affected by habitat quality, density of Dickcissels, and mating status. Territories in suboptimal habitat are significantly larger than those in optimal habitat. Territory size decreases with increasing density. In Kansas, the minimum territory size that could support a pair was 0.36 ha but smaller territories have been reported elsewhere. This minimum territory size limited the density that could be reached. Unmated males have significantly smaller territories than mated males, but there is no difference in territory sizes of monogamous and polygynous males regardless of how many mates they have. In Kansas, mean territory sizes were 0.72 ha for unmated males, 0.85 ha for monogamous males, and 0.95 ha for polygynous males. Overall mean territory sizes in 2 years were 0.50 and 0.71 ha (maximum 0.98 ha). In Illinois, territories ranged from 0.16 to 0.95 ha for mated males. In tallgrass prairies, territories averaged 1.4 ha in Iowa and 1.5 ha in Oklahoma. Overall, territories are typically 0.3-1.1 ha with extremes of 0.15-1.5 ha. Territory sizes tend to decline with the season (Dechant et al. 2002k; Finck 1984; Fitch 1958; Harmeson 1974; Schartz and Zimmerman 1971; Temple 2020; Verheijen et al. 2019; Zimmerman 1966, 1971).

No information is available on natal philopatry, but it is probably extremely low or nonexistent.

Males exhibit site fidelity in the core of the range but there is considerably less fidelity to peripheral and sporadically occupied areas. These sites are typically not inhabited in subsequent years even if conditions have not changed (Temple 2020). In Kansas, an average of 49% of territorial males returned in the next year; no females returned. Sixty-nine percent of returning males switched territories. Those that switched spent an average of 7.5 weeks on their territories, significantly less than for males that remained on their previous territories (10.3 weeks). Fidelity to the territory of the previous year was related to the number of mates that they attracted and perhaps to the number of young that they produced (Zimmerman and Finck 1989). Also in Kansas, 16 of 197 males (8.1%) and 1 of 146 females (0.7%) returned (Verheijen et al. 2017). In Illinois, 5 of 25 females (20.0%) were resighted the next year. Two that emigrated following nest failure were seen the following year 1.1 and 5 km from their previous nests (Walk et al. 2004).

Limiting Factors

Eggs have been found in Ontario nests from the first week of June until the last week of July, mostly in mid-July. The female builds the nest in 2-4 days and begins laying 1-2 days later. Eggs are laid on consecutive days. The incubation period at 4 Ontario nests was 9-10 days, shorter than reported elsewhere, suggesting that incubation began before the clutch was complete. Incubation is 11.5-13 days elsewhere with an average of 12.0 days in Kansas. The nestling period is 7-10 days, mostly 9-10 days (Gross in Austin 1968; Harmeson 1974; Peck and James 1998b; Temple 2020; Winter 1999; Zimmerman 1971, 1983).

The Dickcissel is typically single-brooded, consistent with its long-term care of fledglings. At least 2 cases of double broods have been reported. It has been speculated that early breeders in the southern portion of the range may move northward to nest again later in the season, but this has not been confirmed. Replacement nests may be common. Almost all females that remained at an Illinois site continued to nest until they fledged young. After nest failure, 62% of females emigrated, 36% renested, and 2% ceased nesting. Emigrants were detected 13-32 km away and some may have renested at distant locations. Dispersal distances from initial to subsequent nests in the same area were 22-806 m (mean 222 m). First eggs were laid in replacement nests an average of 8.5 days after nest loss (range 4-15 days). At another site, 85.7% of females that lost their nests in good habitat renested. Only 17% of those in low-quality habitat renested (Harmeson 1974; Temple 2020; Walk et al. 2004). Clutches of 3-5 eggs have been reported in Ontario (average 3.83 eggs); 4 eggs was the most common clutch size. Elsewhere, clutches of 3-6 eggs have been reported, with most clutches containing 4 eggs. In some cases, clutch size is smallest early in the season when food resources are scarce. In other areas, clutch size decreases regularly as the season progresses. Clutch size was about 0.75 eggs smaller in replacement than first clutches in Illinois, but subsequent nests fledged as many young because nesting success was higher. Two 7-egg clutches have been reported and at least 1 of these (0.3% of nests) was a result of intraspecific nest parasitism. Similarly, a 9-egg clutch must have been due to more than 1 female laying in the same nest (Giocomo et al. 2008; Gross in Austin 1968; Harmeson 1974; Peck and James 1998b; Peer 2010; Temple 2020; Walk et al. 2004).

Both sexes are capable of breeding as yearlings but some males are unsuccessful in attracting a mate; all females breed. Unmated yearling males are common and these birds tend to have the lowest-quality territories. Unmated males may retain their territories for less than 2 weeks and these represent 13.6-33.3% of the male population. Vegetation in bachelors' territories is shorter, less dense, and covers less of the area than territories of mated males. Females may be attracted to a bachelor's territory but do not remain long if the habitat is inferior (Fretwell 1977; Schwartz and Zimmerman 1971; Temple 2020; Zimmerman 1966; Zimmerman and Finck 1989).

The Dickcissel is commonly polygynous in the core of its range and considerably less so at its periphery. In Kansas, males in prairies were all monogamous; more than 50% of males in old fields were polygynous. The female-to-male sex ratio was higher in old fields. Females selected habitats with greater vegetation structure and vegetation volume. Polygyny is adaptive for females because it allows them all to nest and select higher-quality habitats. Females mated to polygynous males also have higher reproductive success. Most polygynous males are bigamists but a few have 3 mates. Some males had as many as 8 mates in a season. The nests of females mated to a polygynous male are asynchronous, with an average of 8.8 days between the laying of the first egg by the first and second females. The male is highly attentive to the female until she starts brooding, thereby precluding him from attracting another mate at that time (Finck 1984; Fretwell 1977; Fretwell and Calver 1969; Harmeson 1974; Schultz and Zimmerman 1971; Zimmerman 1966, 1971; Zimmerman and Finck 1989).

The Dickcissel forages for arthropods on the ground in dense foliage of grasses, forbs, and low shrubs. It takes seeds from the ground and ripe seed heads. In Kansas, it spent most of its time foraging in forbs where arthropods were most abundant, lesser time in grass where insects were

38% less abundant, and the least amount of time in wheat where insects were 53% less abundant than in forbs. In wheat fields, it fed on wheat rather than insects (Schwartz and Zimmerman 1971; Temple 2020).

In the core of the range, males rarely feed nestlings, usually only later in the season after territoriality declines or during droughts or other periods when food is scarce and the nestlings are at risk of starving. Provisioning rates are significantly higher when the male helps. Male provisioning may be more common at the periphery of the range where there are fewer opportunities for attracting additional mates (Finck 1984; Maddox and Bollinger 2000; K.L. Mitchell et al. 2012; Schwartz and Zimmerman 1971). Nestlings are preferentially fed grasshoppers, with the nestling diet consisting of 86% and 91% orthopterans in 2 years. The Dickcissel ate caterpillars according to their availability and spiders, beetles, flies, bugs, and hymenopterans less than their availability (K.L. Mitchell et al. 2012). In Illinois, the nestling diet was highly selective for orthopterans, and caterpillars were eaten more than their availability. Beetles and hymenopterans were consumed less than their availability (Temple 2020). One brood was fed garden orbweavers (Judd 1901).

During the breeding season, adults feed on orthopterans, lepidopterans, termites, flies, hymenopterans, and spiders. They also eat seeds of grasses, willows, smartweeds, and pinks. During migration and winter, the diet consists almost entirely of grass seeds (Temple 2020). At 1 Kansas site, the Dickcissel fed extensively on grasshoppers, profitable prey because of their large size (Schwartz and Zimmerman 1971). Thirty-three Illinois birds ate 68% vegetable and 32% animal matter. The vegetation included 32% waste wheat and oats and 36% weed seeds, especially those of foxtails, smartweeds, and knotweeds with lesser amounts of chickweeds. Orthopterans comprised 28% of the diet: 26% short-horned grasshoppers and 2% crickets. Birds also ate cankerworms in an infected orchard (Gross in Austin 1968). Judd (1901) analyzed the contents of 152 stomachs collected during the breeding season. The diet consisted of 70% animal and 30% vegetable matter. Insect food included 41% orthopterans, 15% beetles, 8% lepidopterans, 2% hymenopterans, and 1% flies and bugs. From June to August, 50% of the diet consisted of short-horned and long-horned grasshoppers and crickets. Two percent of the diet consisted of spiders and a few small snails. The vegetable matter consisted of seeds of millet, foxtails, panic grasses, and oats. Wiens and Rotenberry (1979) reported the Oklahoma diet over 3 years to consist of 2%, 22%, and 1% beetles; 30%, 6%, and 32% orthopterans; and 32%, 33%, and 2% lepidopterans. In 2 years, short-horned grasshoppers were most important in the diet; beetles (mostly weevils) were most important in the third year. Caterpillars contributed a third of the diet biomass in 2 years and odonates comprised a similar amount in the other year. Seeds, largely of grasses, consistently constituted 25-33% of the diet. It also consumed bees, ground and long-horned beetles, assassin and jewel bugs, flies, and spiders.

The Dickcissel is a common host of the Brown-headed Cowbird. It usually accepts parasitic eggs but may occasionally abandon heavily parasitized nests. Nest survival is not reduced by parasitism, but the clutch size is reduced due to egg removal by cowbirds. In the core of its range, parasitism rates are very high and nest loss may be considerable. In the periphery of its range, parasitism rates are low and the effects of parasitism are negligible. In Kansas, the Dickcissel was the preferred host because it nested later into the season than other hosts and can raise as many as 5 cowbird fledglings. In Kansas, nests had lower parasitism rates in annually burned and ungrazed pastures

than in pastures managed with patch-burn grazing. Parasitism rates appear to be higher when nests are closer to woody vegetation, in nests placed higher in vegetation, in lower density Dickcissel populations, and in populations nesting with Red-winged Blackbirds because of the blackbirds' effective mobbing of cowbirds. Parasitism rates of 0-92% have been reported. At the periphery of the range, parasitism rates tend to be 0-5% or a maximum of 10%. In the core of the Dickcissel range, which corresponds to the highest cowbird densities, parasitism rates are 31-33% in old-field habitats and 50-70% in prairies, with a maximum of 92%. In Ontario, 1 of 25 nests (4.0%) was parasitized (Burhans et al. 2010; Dechant et al. 2002k; Fretwell 1977; Galligan et al. 2006; Giocomo et al. 2008; Jensen and Cully 2005; Monroe et al. 2019; Overmire 1962; Patterson and Best 1996; Peck and James 1998b; Peer et al. 2000; Rivers et al. 2010; Temple 2020; Verheijen et al. 2022; Walk et al. 2010; Winter 1999; Zimmerman 1983).

The most significant limiting factor for the Dickcissel is control programs in South America where it is considered an agricultural pest. It is hunted and eaten throughout its winter range. In Venezuela, it is killed illegally by spraying roosts with lethal organochlorine and organophosphate pesticides. Some roosts support 10-30% of the global population. Its decline in North America has been attributed mostly to winter control (Temple 2020).

Only about 4% of tallgrass prairie remains, the Dickcissel's original habitat. It has adapted well to anthropogenic habitats such as pastures, hayfields, and old fields, but these are also disappearing due to conversion to row crops. Fields planted to switch grass for agrofuel production have the potential to support it, but these are managed to maximize biomass and homogeneity of the vegetation, typically making them unsuitable (Askins et al. 2007; Robertson et al. 2012; Temple 2020; Walk et al. 2010).

Hay mowing is a significant source of mortality. This is exacerbated by the recent tendency to plant monocultures of alfalfa which are mowed earlier and more frequently than traditional clover-timothy fields. Mowing may retard natural succession and maintain habitat but annual mowing and mowing during the breeding season results in very high mortality. Low productivity and low annual return rates are associated with mowed alfalfa fields, suggesting that these are population sinks. In Arkansas, all nests were destroyed in fields mowed 26-31 May but the effects of haying 17-26 June were trivial. In Iowa, all birds left fields after mowing and did not recolonize them until the vegetation was 20 cm tall. Densities in unmowed fields increased after other fields were mowed. In Illinois tallgrass prairies, it preferred areas that were mowed in July every 2-3 years. In Iowa, it increased in monotypic reed canary grass when blocks less than 2 ha were mowed to 10 cm then disked. This resulted in an increase in litter and forb cover and arthropod biomass and abundance (Benson et al. 2013; Dechant et al. 2002k; Frawley and Best 1991; Gross in Austin 1968; Luscier and Thompson 2009; Patterson and Best 1996; Swanson 1996; Temple 2020). Wolcott et al. (2023) recommended that grassland management be deferred until August to protect both nests and fledglings.

Burning is a common management practice to prevent woody growth in grasslands. Fire also eliminates accumulated litter and standing dead vegetation. The Dickcissel largely avoids habitats in the year that they are burned, but it may be common the next year (Askins et al. 2007; Dechant et al. 2002k; K.L. Mitchell et al. 2012; Powell et al. 2008; Verheijen et al. 2019). In Illinois, it responded

positively to prescribed burns in undisturbed grasslands. Nest density and survival also increased with forb coverage (Glass and Eichholz 2023).

Light to moderate grazing may provide suitable habitat by controlling woody growth and making grasslands more heterogeneous. Heavy grazing is detrimental, resulting in vegetation that is too short and sparse. It may also make nests more susceptible to predation and parasitism (Dechant et al. 2002k; Kim et al. 2008; Renken and Dinsmore 1987; Swanson 1996; Verheijen et al. 2019).

The Dickcissel is strongly affected by drought. Densities decline significantly in the core of the range during drought, with birds often moving to the periphery of the range. During droughts, food is scarce with some nestlings starving and brood sizes being smaller (Kim et al. 2008; Patterson and Best 1996; Suedkamp Wells et al. 2008; Temple 2020; Verheijen et al. 2019).

In Texas, Hatchett et al. (2013) reported that wind farms had no effects on the Dickcissel. Proximity to a wind turbine did not affect nest density, nest-site characteristics, or nest success.

Price (2004) predicted that the Dickcissel's breeding range might expand in southern Ontario if the average summer temperature increased by 2°C.

Status

Historically, the Dickcissel was probably confined to the tallgrass prairies in the central portion of the continent. It spread north and east following extensive deforestation and conversion of land to pastures and hayfields. A disjunct population nested along the Atlantic coast from the early 1800s, but declined and disappeared by 1900, when the breeding range was probably similar to historical conditions. It began to reappear in the east in the 1920s and its range gradually extended northward and eastward from the prairies. Even in the core of its range, populations fluctuate markedly in response to precipitation, being abundant in years of normal precipitation and uncommon during droughts. At the periphery of its range, it is a sporadic breeder, often common in some years and completely absent in other years. Invasions into peripheral areas are often associated with droughts in the core of the range (Fretwell 1977; Gross 1956; Hurley and Franks 1976; Temple 2020).

Ontario is at the periphery of the Dickcissel's range. It is absent or rare in most years but there are occasional invasions to southern Ontario when it may be locally rare or uncommon (James 1991). Breeding was first documented at Point Pelee in 1884 where it was present in all suitable habitat as far as 4.8 km into the mainland (Saunders 1885). Baillie and Harrington (1937) considered it a very rare breeder in the extreme southwest, but with rare records east to Ottawa. Only 2 breeding records were obtained during the first atlas (Eagles in Cadman et al. 1987). An invasion occurred in 1988, with more than 30 nests documented at Point Pelee, Pelee Island, Wheatley, Sarnia, Port Colborne, and Richmond Hill. This occurred during a drought year on the prairies, with breeding evidence obtained as far north as Manitoulin Island and Rainy River District (Austen et al. 1994; Coady 2007; Peck and James 1998b). Breeding evidence was also obtained in 1989, 1990, 1992, and 2000 before the second atlas. During the second atlas, breeding evidence was obtained in 11 squares in southwestern Ontario, mostly in Essex and Chatham-Kent, with at least 43 individuals reported in 2005 (Read and Sutherland in Cadman et al. 2007). From 2010 to 2017, there was a noticeable increase north and northeast of its core range and the area it occupied increased significantly by

2017. In that year, it was reported in 21 Ontario municipalities from Rainy River to Algoma in the north, to Prince Edward County in the east, and most municipalities southwest of there. A total of 410 birds were reported at 129 sites. The invasion did not appear to be drought related and was probably a result of a general range expansion (Woodliffe 2018).

Breeding Bird Survey (BBS) data indicate that the Dickcissel declined steeply by more than 30% 1966-78. Its population has been stable since 1976 at approximately 66% of its 1966 population (Temple 2020). BBS results indicate that it increased at annual rates of 0.892% in Canada and 0.0748% in Ontario 1970-2021. Trends for 2011-21 were annual increases of 2.02% in Canada and 0.789% in Ontario. All results were of low reliability (A.C. Smith et al. 2023).

POSTFLEDGING PERIOD

Fledglings 1-3 days out of the nest selected areas that were more concealed with denser vegetation than random sites, but vegetation at nest sites was denser. Those 4-11 days out of the nest used even denser vegetation that was comparable to nest sites. Survival rates were positively correlated with vegetation density at the nest site and during the first 3 days out of the nest, but not for older fledglings. Most mortality occurs within a week of leaving the nest. In Nebraska and Iowa over 2 years, fledglings moved an average of 3.7 m and 6.5 m from the nest in the first day, 93.1 m and 123.2 m by day 7, and 141.8 m and 355.3 m by day 15. The maximum distances moved were 401 m and 1,060 m. In Illinois, fledglings remained within 50 m of the nest for the first 6 days and moved out to 150 m by day 27. In Missouri, daily movements by juveniles were fairly constant, increasing at a slow rate until 28 days postfledging. Large movements of more than 600 m started then with the longest movements of 1.8-2.4 km occurring 32-38 days after fledging. The mean time when fledglings first moved more than 300 m was 17.7 days. Three weeks after fledging, average daily movements were 172.6 m. Young have been found as far as 1.6 km from the nest 10 days after fledging. The average home range size of fledglings was 48.8 ha. Home ranges were larger when vegetation was shorter and less variable and were nearly 2 times larger in a drought year (Berkeley et al. 2007; Jones et al. 2017; Suedkamp Wells et al. 2007, 2008; Temple 2020).

Fledglings gradually move from dense grass and forb cover to more open habitats such as corn and soybean fields and wetlands. Grasslands were used at a rate (64%) more than their availability. Crop fields (34%) and wetlands (2%) were used less than their availability. Fledglings that left the natal fields were still being fed by adults, so it is uncertain whether they were selecting habitat or simply following the adults (Berkeley et al. 2007).

Females are largely responsible for feeding the fledglings, although a few males assist. They are fed mostly caterpillars and grasshoppers. Fledglings may be dependent on adults for as long as 4 weeks after fledging. One female fed a juvenile 43 days after it fledged. Soon after independence, juveniles join postbreeding flocks of adults and form premigratory flocks that may consist of several hundred birds in the core of the range (Berkeley et al. 2007; Gross in Austin 1968; Suedkamp Wells et al. 2008; Temple 2020; Walk et al. 2004; Wilhelm 1994).

MIGRATION

During migration, the Dickcissel inhabits large open fields and wetlands where there are abundant seeds to feed on, especially sorghum, rice, and grasses. Flocks often visit grain fields to feed. Nocturnal roosts may be in open fields, bare croplands, marshes, dense stands of grasses, and along

weedy margins of drainage ditches. In late autumn and winter, it may visit bird feeders where it commonly associates with the House Sparrow (Blomme 1989; Gross in Austin 1968; Temple 2020).

The Dickcissel is a rare migrant in Ontario that occasionally wanders north to Thunder Bay and Fort Albany. Some birds remain in the south until early winter (James 1991).

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SCIENTIFIC NAMES OF SPECIES MENTIONED IN THE TEXT

Acorn *Quercus*
Adelgid *Adelgid*
    balsam woolly *A. piceae*
    hemlock woolly *A. tsugae*
Admiral, red *Vanessa atalanta*
Agalinis *Agalinis*
Alcid ALCIDAE
Alder *Alnus*
    black *A. glutinosa*
    green *A. alnobetula*
    grey *A. incana*
Alderfly SIALIDAE
Alewife *Alosa pseudoharengus*
Alfalfa *Medicago sativa*
Algae ALGAE
    green CHLOROPHYTA
Almond *Prunus amygdalus*
Alyssum *Lobularia*
    sweet *L. maritima*
Amaranth *Amaranthus*
    redroot *A. retroflexus*
Amphibian AMPHIBIA
Amphipod AMPHIPODA
Anemone *Anemonoides*
    wood *A. quinquefolia*
Animal ANIMALIA
Annelid ANNELIDA
Anole *Anolis*
    brown *A. sagrei*
Ant FORMICIDAE
    carpenter *Camponotus*
    fire *Solenipsis invicta*
Ant-lion MYRMELEONTIDAE
Anthracnose *Apiognomonia*
    sycamore *A. veneta*
Aphid APHIDAE
    birch *Euceraphis*
    woolly ERIOSOMATINAE
Apple *Malus pumila*
Apricot *Prunus armeniaca*
Arachnid ARACHNIDA
Arbutus *Epigaea*
    trailing *E. repens*
Armyworm NOCTUIDAE
Arrow-grass *Triglochin*
    common *T. maritima*
Arrowhead *Sagittaria*
    broad-leaved *S. latifolia*
Arrowwood *Viburnum*
    northern *V. recognitum*
    southern *V. dentatum*
Arthropod ARTHROPODA
Artichoke *Cynara*
Artichoke, Jerusalem *Helianthus tuberosus*
Arum, arrow *Peltandra*
    green arrow *P. virginica*
Ash *Fraxinus*
    black *F. nigra*
    green *F. pennsylvanica*
    pumpkin *F. profunda*
    white *F. americana*
Asparagus *Asparagus officinale*
Aspen *Populus*
    large-toothed *P. grandidentata*
    trembling *P. tremuloides*
Aster ASTERACEAE
    heath *Symphyotrichum pilosum*
    large-leaved *Eurybia macrophylla*
    old field PORTERIANI
    Pringle's *Symphyotrichum pilosum* var. *pringlei*
Avens, mountain *Dryas integrifolia*

Bacteria BACTERIA
Baldcypress *Taxodium distichum*
Balm, horse *Collinsonia*
Banana *Musa*
Barberry *Berberis*
    Japanese *B. thunbergii*
Barley *Hordeum vulgare*
Basswood *Tilia americana*
Bat CHIROPTERA
    hoary *Lasiurus cinereus*
    little brown *Myotis lucifugus*
    red *Lasiurus borealis*

Bayberry *Myrica pensylvanica*
Beaked-rush *Rhynchospora*
Bean FABACEAE
Bear *Ursus*
    polar *U. maritimus*
Bearberry *Arctostaphylos uva-ursi*
Bearberry, alpine *Arctous alpina*
Beaver *Castor canadensis*
Bedstraw RUBIACEAE
Bee APOIDEA
    bumble *Bombus*
    carpenter XYLOCOPINAE
    honey *Apis*
    sweat HALICTIDAE
Beech *Fagus grandifolia*
Beech, blue *Carpinus carolinus*
Beet *Beta vulgaris*
Beetle COLEOPTERA
    Asian longhorned *Anoplophora glabripennis*
    bark SCOLYTINAE
    bean leaf *Certoma trifurcata*
    bess PASSALLIDAE
    black margined loosestrife *Galerucella calmariensis*
    blister MELIDAE
    brown leaf *Phyllobius oblongus*
    carrion SILPHIDAE
    cedar *Sandalus niger*
    checkered CLERIDAE
    click ELATERIDAE
    clown HISTERIDAE
    Colorado potato *Leptinotarsa decemlineator*
    crawling water HALIPLIDAE
    darkling TENEBRIONIDAE
    dung SCARABAEINAE
    eastern larch *Dendroctnus simplex*
    ebony THYREOCORIDAE
    elm leaf *Xanthogaleruca luteola*
    flat bark CUCUJIDAE
    flea ALTICINI
    glowworm PHENGODIDAE
    ground CARABIDAE
    Japanese *Popillia japonica*
    June MELOLONTHINAE
    lady COCCINELLIDAE
    leaf CHRYSOMELIDAE
    long-horned CERAMBYCIDAE
    marsh SCIRTIDAE
    metallic wood-boring BUPRESTIDAE
    minute brown scavenger LATHRIDIIDAE
    mountain pine *Dendroctonus ponderosae*
    picnic NITIDULIDAE
    pill BYRRHIDAE
    potato *Leptinotarsa*
    predaceous diving DYTISCIDAE
    rainbow scarab *Phanaeus vindex*
    rose chafer CETONIINI
    rove STAPHYLINIDAE
    scarab SCARABAEIDAE
    skin DERMESTIDAE
    soldier CANTHARIDAE
    spruce *Dendroctonus rufipennis*
    stag LUCANIDAE
    tiger CICINDELIDAE
    tumbling flower MORDELLIDAE
    viburnum leaf *Pyrrhalta viburni*
    water-scavenger HYDROPHILIDAE
    whirligig GYRINIDAE
    willow flea *Crepidodera aurata*
Beggartick *Bidens*
    nodding *B. cenua*
Bellwort *Uvularia*
    perfoliate *U. perfoliata*
Bentgrass *Agrostis*
    creeping *A. stolonifera*
Bergamot *Monarda*
    wild *M. fistulosa*
Bilberry *Vaccinium*
    bog *V. uliginosa*
Bindweed CONVOLVULACEAE
    black *Fallopia convolvulus*
    field *Convolvulus arvensis*
Birch *Betula*
    bog *B. nana*
    dwarf *B. glandulosa*
    gray *B. populifolia*
    river *B. nigra*
    silver *B. pendula*
    swamp *B. pumila*

sweet *B. lenta*
white *B. papyrifera*
yellow *B. lutea*
Bishop's cap *Mitella*
naked *M. nuda*
Bison *Bison bison*
Bittern *Botaurus*
Least *B. exilis*
Bittersweet *Celastrus*
American *C. scandens*
Asiatic *C. orbiculatus*
Blackberry *Rubus*
Allegheny *R. allegheniensis*
Bladdernut *Staphylea trifolia*
Blanketflower *Gaillardia*
Blazing-star *Liatris*
Blight, chestnut *Cryphonectria parasitica*
Bloodroot *Sanguinaria canadensis*
Blueberry *Vaccinium*
highbush *V. corymbosum*
lowbush *V. angustifolium*
velvetleaf *V. myrtilloides*
Bluebird *Sialia*
Mountain *S. curricoides*
Bluegrass *Poa*
annual *P. annua*
Canada *P. compressa*
Kentucky *P. pratensis*
Bluejoint *Calamagrostis*
Canada *C. canadensis*
Bluestem POACEAE
big *Andropogon gerardii*
little *Schizachyrium scoparium*
Boatman, water CORIXIDAE
Bobcat *Lynx rufus*
Bogbean *Menyanthes trifoliata*
Bog-rush *Schoenus*
Boneset *Eupatorium*
Borage BORAGINACEAE
Borer, currant-tip *Psenocerus supernotatus*
Borer, emerald ash *Agrilus planipennis*
Borer, European corn *Ostrinia nubialis*
Borer, European oak *Agrilus sulcocollis*
Borer, locust *Megacyllene robiniae*
Borer, sugar maple *Glycobius speciosus*
Bristletail THYSANURA
Brome *Bromus*
downy *B. tectorum*
smooth *B. inermis*
Broom *Cytisus*
Scotch *C. scoparius*
Broomsedge *Andropogon*
Virginia *A. virginicus*
Bti *Bacillus thuringiensis israelensis*
Buckeye *Aesculus*
Ohio *A. glabra*
Buckthorn *Rhamnus*
common *R. cathartica*
glossy *R. frangula*
Buckwheat *Fagopyrum sagittatum*
Buckwheat, false climbing *Fallopia scandens*
Budworm TORTRICIDAE
black-headed *Acleris variana*
jack pine *Choristoneura pinus*
spruce *Choristoneura fumiferana*
western spruce *Choristoneura occidentalis*
Buffalo-berry *Shepherdia canadensis*
Bufflehead *Bucephala albeola*
Bug HEMIPTERA
ambush PHYMATINAE
ash-gray leaf PIESMATIDAE
assassin REDUVIIDAE
box elder *Boisea*
chinch BLISSIDAE
damsel NABIDAE
ebony THYREOCORIDAE
harlequin *Murgantia histrionica*
jewel SCUTELLERIDAE
lace TINGIDAE
leaf PHYLLIDAE
leaf-footed COREIDAE
mealy PSEUDOCOCCIDAE
milkweed LYGAEINAE
plant MIRIDAE
seed LYGAEIDAE
shield ACANTHOSOMATIDAE
shore SALDIDAE
soldier *Podisus maculiventris*

- soft-winged HOMOPTERA
- spittle CERCOPIDAE
- squash *Anasa*
- stink PENTATOMIDAE
- stilt BERYTIDAE
- swallow *Oeciacus vicarius*
- tarnished plant *Lygus lincolnaris*
- true HEMIPTERA

Bugleweed *Lycopus*
Bugloss *Echium*
- viper's *E. vulgare*

Bulrush CYPERACEAE
- American three-square *Schoenoplectus americana*
- dark green *Scirpus atrovirens*
- hard-stemmed *Schoenoplectus acutus*
- red *Blysmus rufus*
- river *Schoenoplectus fluviatilus*
- saltmarsh *Bolboschoenus maritimus*
- soft-stemmed *Schoenoplectus tabenaemontani*
- tufted *Trichophorum cespitosum*

Bumble Bee *Bombus*
- arctic *B. polaris*

Bunchberry *Cornus canadensis*
Burdock *Arctium*
- lesser *A. minus*

Burnet *Sanguisorba*
- Canadian *S. canadensis*

Bur-reed *Sparganium*
- big *S. eurycarpum*

Bush, beauty *Kolkwitzia amabilis*
Bush, creosote *Larrea tridentata*
Bush-clover *Lespedeza*
- round-headed *L. capitata*

Butter-and-eggs *Linaria vulgaris*
Buttercup *Ranunculus*
Butterfly LEPIDOPTERA
- admiral, red *Vanessa atalanta*
- black swallowtail *Papilo polyxenes*
- brush-footed NYMPHALIDAE
- cabbage white *Pieris rapae*
- copper LYCAENINAE
- gossamer-winged LYCAENIDAE
- hackberry emperor *Asterocampa celtis*
- lady *Vanessa*
- monarch *Danaus plexippus*
- mourning cloak *Nymphalis antiopa*
- sulphur PIERIDAE
- swallowtail PAPILIONIDAE
- white PIERIDAE

Butternut *Juglans cinerea*
Buttonbush *Cephalanthus occidentalis*
Buttonweed *Diodia virginiana*

Cabbage *Brassica oleracea*
Cabbage, skunk *Symplocarpus foeditus*
Cactus CACTACEAE
- prickly-pear *Opuntia*

Caddisfly TRICOPTERA
- giant casemaker PHRYGANEIDAE
- long-horned LEPTOCERIDAE
- net-spinning HYDROPSYCHIDAE

Calla *Calla*
- wild *C. palustris*

Campion *Silene*
Cane, switch *Arundinaria tecta*
Canker, beech bark *Neonectria faginata*
Cankerworm GEOMETRIDAE
- fall *Alsophila pometaria*
- spring *Paleacrita vernata*

Canola *Brassica campestris*
Caragana *Caragana*
Caribou *Rangifer tarandus*
Carnation *Dianthus caryophyllus*
Carp *Cyprinus carpio*
Carrot, *Daucus*
- wild *D. carota*

Cat FELIDAE
- domestic *Felis catus*

Catalpa *Catalpa*
Catchfly *Silene*
Caterpillar LEPIDOPTERA
- cherry sphynx *Sphinx drupiferatum*
- eastern tent *Malacosoma americanum*
- forest tent *Malacosoma disstria*
- geometer GEOMETRIDAE
- hackberry emperor *Asterocampa celtis*
- owlet NOCTUIDAE
- rosy maple moth *Dryocampa*

- saddled prominent *Heterocampa guttivitta*
- spring cankerworm *Paleacrita vernata*
- tent *Malacosoma*
- winter moth *Operophtera brumata*

Catnip *Nepeta cataria*
Cattail *Typha*
- broad-leaved *T. latifolia*
- hybrid *T.* x *glauca*
- narrow-leaved *T. angustifolia*

Cattle *Bos taurus*
Cedar CUPRESSIDAE
- Atlantic white *Chamaecyparis thyoides*
- red *Juniperus virginiana*
- white *Thuja occidentalis*

Centipede CHILOPODA
Cestode CESTODA
Chafer, shining leaf RUTELINAE
Cherry *Prunus*
- black *P. serotina*
- pin *P. pensylvanica*
- sand *P. pumila*
- sweet *P. avium*

Chestnut, American *Castanea dentata*
Chestnut, horse *Aesculus hippocastanum*
Chickadee *Poecile*
- Carolina *P. carolinensis*

Chicken *Gallus gallus*
Chicory *Cicorium intybus*
Chickweed CARYOPHYLLACEAE
- common *Stellaria media*
- mouse-ear *Cerastium*

Chipmunk SCIURIDAE
- eastern *Tamias striatus*

Chokeberry *Aronia*
Chokecherry *Prunus virginianus*
Cicada CICADIDAE
- 17-year *Magicicada septendecim*

Cicely, sweet *Osmorhiza*
Cinquefoil POTENTILLEAE
- creeping *Potentilla reptans*
- marsh *Comarum palustre*
- shrubby *Dasiphora*
- silvery *Potentilla argentea*
- sulphur *Potentilla recta*

Clam PELECYPODA
- Venus VENERIDAE

Clematis *Clematis*
Cloudberry *Rubus chamaemorus*
Clover FABACEAE
- bur *Medicago polymorpha*
- hop *Trifolium aureum*
- low hop *Trifolium campestre*
- red *Trifolium pratense*
- sweet *Melilotus*
- white *Trifolium repens*
- white sweet *Melilotus albus*
- yellow sweet *Melilotus officinalis*

Club, devil's *Oplopanax horridus*
Club, Hercules' *Zanthoxylum clava-herculis*
Clubmoss LYCOPODIACEAE
- flat-branched tree- *Dendrolycopodium obscurum*

Cockle *Agrostemma*
- corn *A. githago*

Cocklebur *Xanthium*
- rough *X. strumarium*

Cockroach BLATTIDAE
Coconut *Cocos nucifera*
Coffee *Coffea*
Coffee-tree *Gymnocladius*
- Kentucky *G. dioica*

Cohosh, blue *Caulophyllum*
Coltsfoot, sweet *Petasites*
Columbine *Aquilegia*
Coneflower ASTERACEAE
- cutleaf *Rudbeckia laciniata*
- cultivated *Echinacea*

Conjunctivitis *Mycoplasma*
- mycoplasmal *M. gallisepticum*

Coralberry *Symphoricarpos orbiculatus*
Coralroot *Corallorhiza*
Cordgrass *Sporobolus*
- marsh hay *S. pumilus*
- prairie *S. michauxianus*
- saltmarsh *S. alterniflorus*

Cormorant *Nannopterum*
Corn *Zea mays*
- field *Zea mays indentata*
- sweet *Zea mays sacharata*

Corvid CORVIDAE
Corydalis *Corydalis*
golden *C. aurea*
Cotoneaster *Cotoneaster*
Cotton *Gossypium*
Cottongrass *Eriophorum*
Cottontail *Sylvilagus*
Cottonwood *Populus*
Cow *Bos taurus*
Coyote *Canis latrans*
Crab CANCERIDAE
fiddler OCYODIDAE
Crabapple *Malus*
flowering *Malus*
sweet *M. coronaria*
Crabgrass *Digitaria*
hairy *D. sanguinalis*
smooth *D. ischaemum*
Cranberry *Vaccinium*
American *V. macrocarpon*
bog *V. oxycoccos*
highbush *V. opulus* var. *americanum*
mountain *V. vitis-idaea*
small *V. oxycoccus*
Crane *Grus*
Sandhill *G. canadensis*
Crayfish DECAPODA
Creeper, trumpet *Campsis*
Creeper, Virginia *Parthenocissus quinquefolia*
Cricket GRYLLIDAE
tree OECANTHINAE
Crossbill *Loxia*
Cassia *L. sinesciuris*
Croton *Croton*
Crowberry *Empetrum*
Crustacean CRUSTACEA
Cuckoo *Coccyzus*
Yellow-billed *C. americanus*
Cucumber, wild *Echinocystis lobatus*
Currant *Ribes*
golden *R. aureum*
northern red *R. triste*
red *R. rubrum*
skunk *R. glandulosum*
swamp *R. lacustre*
Cutgrass *Leersia*
rice *L. oryzoides*
Cutworm NOCTUIDAE
Cypress CUPRESSACEAE

Daisy *Leucanthemum*
oxeye *L. vulgare*
Damselfly ZYGOPTERA
narrow-winged CALOPTERYGIDAE
spread-winged LESTIDAE
Dandelion *Taraxacum*
common *T. officinale*
Darner AESCHNIDAE
green *Anax junius*
Deer *Odocoileus*
white-tailed *O. virginianus*
Devil's club *Oplopanax horridus*
Dewberry *Rubus*
Disease, Dutch elm *Ceratocystis ulmi*
Dobsonfly CORYDALIDAE
Dock *Rumex*
curly *R. crispus*
greater water *R. britannica*
Dodder *Cuscuta*
Dog *Canis familiaris*
Dogbane *Apocynum*
hemp *A. cannabinum*
Dogwood *Cornus*
flowering *C. florida*
gray *C. racemosa*
red-osier *C. sericea*
rough-leaved *C. drummondii*
silky *C. amomum*
Douglas-fir *Pseudotsuga*
Dove COLUMBIDAE
Mourning *Zenaida macroura*
Dragonfly ANISOPTERA
spiketail *Cordulegaster*
skimmer LIBELLULIDAE
Dragon's Mouth *Arethusa bulbosa*
Dropseed *Sporobolus*
ensheathed *S. vaginiflorus*
overlooked *S. neglectus*

prairie *S. heterolepis*
sand *S. cryptandus*
tall *S. asper*
Duck ANATIDAE
Wood *Aix sponsa*
Duckweed LEMNACEAE

Eagle ACCIPITRIDAE
Bald *Haliaeetus leucocephalus*
Golden *Aquila chrysaetos*
Earthworm LUMBRICIDAE
common *Lumbricus terrestris*
Earwig *Forficula auricularia*
Egret ARDEIDAE
Great *Ardea alba*
Eider *Somateria*
Elderberry *Sambucus*
common *S. canadensis*
red *S. pubens*
Elk *Cervus canadensis*
Elm *Ulmus*
Chinese *U. parvifolia*
red *U. rubra*
Siberian *U. pumila*
white *U. americana*
Ericaceous ERICACEAE
Eucalyptus *Eucalyptus*
Euonymus *Euonymus*
Evening-primrose *Oenothera*
Everlasting *Anaphalis*
pearly *A. margaritacea*

Falcon *Falco*
Peregrine *F. peregrinus*
Prairie *F. mexicanus*
Feathergrass *Nassella*
Mexican *N. tenuissima*
Fennel *Foeniculum vulgare*
Fern PTERIDOPHYTA
bracken *Pteridium aquilinum*
Christmas *Polystichum acrostichoides*
cinnamon *Osmunda cinnamomea*
hay-scented *Dennstaedtia punctilobula*
marsh *Thelypteris palustris*
polypody *Polypodium*
royal *Osmunda regalis*
sensitive *Onoclea sensibilis*
Fern, sweet *Comptonia peregrina*
Fescue *Festuca*
meadow *F. pratensis*
red *F. rubra*
Fig *Ficus*
Fir *Abies*
balsam *A. balsamea*
Fraser *A. fraseri*
Firefly LAMPYRIDAE
Fireweed *Chamaenrion angustifolium*
Fish PISCES
Fishfly CHAULIODINAE
Flag, northern blue *Iris versicolor*
Flatsedge *Cyperus*
yellow *C. esculentus*
Flax *Linum*
Flea SIPHONAPTERA
bird CERATOPHYLLIDAE
Flea, sand HIPPIDAE
Fleabane *Erigeron*
daisy *E. strigosus*
Flicker *Colaptes*
Northern *C. auratus*
Fly DIPTERA
anthomyiid ANTHOMYIIDAE
big-headed PIPUNCULIDAE
black SIMULIIDAE
blow CALLIPHORIDAE
brachyeran BRACHYERA
brine *Ephydra hians*
bristle TACHNIDAE
crane TIPULIDAE
dance EMPIDIDAE
deer TABANIDAE
dung SCATHOPHAGIDAE
flesh SARCOPHAGIDAE
flower SYRPHIDAE
frit CHLOROPIDAE
fruit DROSOPHILIDAE
golden-backed snipe *Chrysopilus thoracicus*
goldenrod gall *Eurosta solidaginis*

- green bottle *Lucilia*
- horse TABANIDAE
- house MUSCIDAE
- hump-backed PHORIDAE
- leaf-miner AGROMYZIDAE
- limoniid crane LIMONIIDAE
- long-legged DOLICHOPODIDAE
- march BIBIONIDAE
- marsh SCIOMYZIDAE
- nematoceran NEMATOCERA
- picture-winged OTITIDAE
- robber ASILIDAE
- root-maggot ANTHOMYIIDAE
- salt-marsh *Tabanus*
- seaweed FUCELLIA
- shore EPHYDRIDAE
- snipe RHAGIONIDAE
- soldier STRATIOMYIDAE
- stiletto THEREVIDAE

Flycatcher TYRANNIDAE
- Scissor-tailed *Tyrannus forficatus*
- Southwestern Willow *Empidonax traillii extimus*

Forget-me-not *Myosotis*
- spring *M. verna*

Forsythia *Forsythia*

Fox CANIDAE
- arctic *Alopex lagopus*
- red *Vulpes vulpes*

Foxtail POACEAE
- giant *Setaria faberi*
- green *Setaria viridis*
- meadow *Alopecurus pratensis*
- yellow *Setaria pumila*

Frog RANIDAE
- green *Lithobates clamitans*
- leopard *Lithobates pipiens*
- western chorus *Pseudacris triseriata*
- wood *Lithobates sylvatica*

Froghopper CERCOPOIDEA

Frostweed *Verbesina virginica*

Fungus FUNGI
- beech bark canker *Neonectria faginata*
- bracket POLYPORACEAE
- dogwood anthracnose *Discila desructiva*
- mycorrhizal GLOMEROMYCOTA

Gale, sweet *Myrica gale*

Gapeworm *Syngamus trachea*

Geranium *Geranium*
- spotted *G. maculatum*

Gnat DIPTERA
- dark-winged fungus SCIARIDAE
- fungus SCIAROIDEA

Goldeneye *Bucephala*

Goldenrod ASTERACEAE
- broad-leaved *Solidago flexicaulis*
- Canada *Solidago canadensis*
- early *Solidago juncea*
- flat-topped *Euthamia graminifolia*
- gray *Solidago nemoralis*
- rough-stemmed *Solidago rugosa*
- stiff-leaved *Solidago rigida*
- tall *Solidago altissima*

Goldfinch *Spinus*
- Lesser *S. psaltria*

Goldfish *Carassius auritus*

Goose ANSERINAE
- Ross's *Anser rossii*
- Snow *Chen caerulescens*

Gooseberry *Ribes*
- prickly *R. cynosbati*

Goosefoot AMARANTHACEAE

Gourd CUCURBITACEAE

Grackle *Quiscalus*
- Boat-tailed *Q. major*

Grain POACEAE

Grape *Vitus*
- fox *V. labrusca*
- frost *V. vulpina*
- riverbank *V. riparia*
- wild *Vitis*

Grass POACEAE
- American manna *Glyceria grandis*
- arctic spear *Poa alpina*
- barnyard *Echinochloa*
- beach *Elymus arenarius*
- Chinese silver *Miscanthus sinensis*
- creeping alkali *Puccinellia phryganodes*

crested wheat *Agropyron cristatum*
fescue *Festuca*
goose *Eleusine indica*
grama *Bouteloua*
Indian *Sorgastrum nutans*
intermediate wheat *Thinopyrum intermedium*
Johnson *Sorgum halepense*
June *Koeleria*
love *Eragrostis*
lyme *Leymus arenarius*
manna *Glyceria*
marram *Ammophila breviligulata*
melic *Melica racemosa*
mountain bunch *Festuca viridula*
mountain-rice STIPEAE
muhly *Muhlenbergia*
needle *Stipa*
oldfield three-awn *Aristida oligantha*
old witch *Panicum capillare*
orchard *Dactylus glomerata*
panic *Dichanthelium*
poverty *Danthonia*
poverty oat *Danthonia spicata*
quack *Elymus repens*
reed *Glyceria*
reed canary *Phalaris arundinaceae*
reed manna *Glyceria maxima*
river *Chionachne cyathapoda*
rye *Elymus*
sand *Triplasis*
satin *Muhlenbergia*
slough *Beckmannia syzigachne*
spinifex *Spinifex*
squirrel-tail *Hordeum jubatum*
sweet *Anthoxanthum*
switch *Panicum virgatum*
tall wheat *Thinopyrum obtusiflorum*
thickspike wheat *Elymus lanceolatus*
western wheat *Elymus smithii*
wheat *Elymus*
windmill *Chloris*
witch *Elymus repens*
Grass, blue-eyed *Sisyrinchium*
Grasshopper ORTHOPTERA
long-horned TETTIGONIIDAE
short-horned ACRIDIDAE
Greenbrier *Smilax*
Gromwell *Lithospermum*
Groundsel *Senecio*
Grouse PHASIANIDAE
Ruffed *Bonasa umbellus*
Grub COLEOPTERA
Guelder-rose *Viburnum opulus*
Gull LARIDAE
Bonaparte's *Chroicocophalus philadelphia*
American Herring *Larus smithsonianus*
Ring-billed *Larus delawarensis*
Gum, black *Nyssa sylvatica*

Hackberry *Celtis*
common *C. occidentalis*
sugar *C. laevigata*
Hare LEPORIDAE
Harrier *Circus*
Northern *C. hudsonius*
Harvestmen OPILIONES
Hawk ACCIPITRIDAE
Cooper's *Auster cooperii*
Ferruginous *Buteo regalis*
Red-tailed *Buteo jamaicensis*
Sharp-shinned *Auster striatus*
Swainson's *Buteo swainsoni*
Hawkweed *Hieracium*
orange *H. auranticum*
Hawthorn *Crataegus*
common *C. monogyna*
Hazel *Corylus*
American *C. americana*
beaked *C. cornuta*
Hazelnut *Corylus*
Heath ERICACEAE
Hemlock *Tsuga canadensis*
western *T. heterophylla*
Hemp *Cannabis*
Heron ARDEIDAE
Black-crowned Night *Nycticorax nycticorax*
Great Blue *Ardea herodias*
Green *Butorides virescens*

Herring CLUPEIDAE
Hickory *Carya*
- bitternut *C. cordiformis*
- mockernut *C. tomentosa*
- pignut *C. glabra*
- shagbark *C. ovata*
- shellbark *C. laciniosa*

Histoplasmosis *Histoplasma*
Hobblebush *Viburnum lantanoides*
Holly AQUIFOLIACEAE
- American *Ilex opaca*
- mountain *Nemopanthus mucronata*
- winterberry *Ilex verticillata*

Hollyhock *Alcea pallida*
Honeysuckle CAPRIFOLIACAEAE
- American fly *Lonicera canadensis*
- amur *Lonicera maackii*
- Bella *Lonicera* x *bella*
- Japanese *Lonicera japonica*
- Morrow's *Lonicera morrowii*
- tartarian *Lonicera tatarica*
- winter *Lonicera fragrantissima*

Hop *Humulus*
- common *H. lupulus*

Hophornbeam *Ostrya virginiana*
Hornet VESPIDAE
- bald-faced *Dolichovespula maculata*

Horse *Equus ferus*
Horsetail *Equisetum*
- field *E. arvensis*
- marsh *E. palustre*
- rough *E. hyemale*
- water *E. fluviatile*

Horseweed *Erigeron canadensis*
Hound's-tongue *Cynoglossum*
Huckleberry *Gaylussacia*
- black *G. baccata*

Human *Homo sapiens*
Hummingbird TROCHILIDAE
- Ruby-throated *Archilochus colubris*

Hymenopteran HYMENOPTERA

Ibis THRESKIORNITHIDAE
- White *Eudocimus albus*

Insect INSECTA
- scale COCCOIDEA

Invertebrate INVERTEBRATA
Iris *Iris*
Ironweed *Vernonia*
Isopod ISOPODA
Ivy, Boston *Parthenocissus tricuspidata*
Ivy, English *Hedera helix*
Ivy, poison *Toxicodendron*

Jack-in-the-pulpit *Arisema triphyllum*
Jaeger *Stercorarius*
Jay CORVIDAE
- Steller's *Cyanocitta stellari*

Jewelweed *Impatiens*
- spotted *I. capensis*

Joe-pye-weed *Eutrochium*
- spotted *E. maculatum*

Juneberry *Amelanchier*
- Canada *A. canadensis*
- downy *A. arborea*
- roundleaf *A. sanguinea*
- smooth *A. laevis*

Juniper *Juniperus*
- Chinese *J. chinensis*
- common *J. communis*

Katydid TETTIGONIIDAE
Kestrel *Falco*
- American *F. sparverius*

Kingfisher *Megaceryle*
- Belted *M. alcyon*

Kittiwake *Rissa*
Knapweed *Centaurea*
- spotted *C. stoebe*

Knotweed *Polygonum*
- prostrate *P. aviculare*

Lacewing NEUROPTERA
- brown HEMEROBIIDAE
- green CHRYSOPIDAE

Lady's slipper *Cypripedium*
- pink *C. acaule*
- showy *C. reginae*

Lady's-thumb *Persicaria maculosa*
Lamb *Ovis*
Lamb's-quarters *Chenopodium album*
Lanternfly FULGORIDAE
Larch *Larix*
    European *L. decidua*
Laurel *Kalmia*
    bog *K. polifolia*
    mountain *K. latifolia*
    sheep *K. angustifolia*
    swamp *K. polifolia*
Leafhopper CICADELLIDAE
Leafminer, black locust *Macrosaccus robiniella*
Leafroller TORTRICIDAE
    aspen *Epinotia criddleana*
    oblique-banded *Choristoneura roseaceana*
Leatherleaf *Chamaedaphne calyculata*
Leech HIRUDINEA
    smooth turtle *Placobdella parasitica*
Legume FABACEAE
Lemming MURIDAE
Lepidopteran LEPIDOPTERA
Lettuce ASTERACEAE
    cultivated *Lactuca sativa*
    prickly *Lactuca serriola*
    wild *Lactuca*
Lice, bark PSOCODEA
Lice, bird PHTHIRAPTERA
Lice, book PSOCODEA
Lice, chewing MALLOPHAGA
Lice, jumping plant PSYLLIDAE
Lichen LECANOROMYCETES
    beard *Usnea*
    cup *Cladonia*
    reindeer *Cladonia*
    star-tipped reindeer *Cladina stellaris*
Lilac *Syringa vulgaris*
Lily LILIACEAE
    glacier *Erythronium grandiflorum*
Lily, corn *Veratrum californicum*
Linden TILIACEAE
Lizard SQUAMATA
Lobster NEPHROPOIDEA
Locust (animal) LOCUSTINAE
    Rocky Mountain *Melanoplus spretus*
Locust (plant) FABACEAE
    black *Robinia pseudo-acacia*
    honey *Gleditsia tricanthos*
Longspur *Calcarius*
    Chestnut-collared *C. ornatus*
Loon *Gavia*
    Common *G. immer*
Loosestrife, purple *Lythrum salicaria*
Loosestrife, swamp *Decodon verticillatus*
Loosestrife, whorled *Lysimachia quadrifolia*
Lousewort *Pedicularis*
Lupine *Lupinus*
Lynx *Lynx canadensis*

Maggot DIPTERA
    larch cone *Strobilomyia laricis*
Magnolia MAGNOLIACEAE
Mallard *Anas platyrhynchos*
Mallow MALVACEAE
    dwarf *Malva neglecta*
Mammal MAMMALIA
Mangrove RHIZOPHORACEAE
Mantis *Mantus*
    preying *M. religiosa*
Maple *Acer*
    amur *A. ginnala*
    black *A. nigrum*
    Manitoba *A. negundo*
    mountain *A. spicatum*
    Norway *A. platinoides*
    red *A. rubrum*
    silver *A. saccharinum*
    striped *A. pensylvanicum*
    sugar *A. saccharum*
Marigold *Calthra*
    marsh *C. palustris*
Marshelder *Cyclachaenea xanthiifolia*
Marten *Martes americana*
Mayapple *Podophyllum peltatum*
Mayflower *Maianthemum*
    Canada *M. canadensis*
Mayweed *Matricaria*
Mayfly EPHEMEROPTERA

- burrowing EPHEMERIDAE
- stream HEPTAGENIIDAE

Meadow-rue *Thalictrum*
Meadowsweet *Spiraea*
Mealworm *Tenebrio*
Mecopteran MECOPTERA
Megalopteran MEGALOPTERA
Melon CUCURBITACEAE
Mercury, three-seeded *Acalypha*
Merganser MERGINI
- Common *Mergus merganser*
- Hooded *Lophodytes cucullatus*

Merlin *Falco columbarius*
Mesquite *Neltuma*
Midge CHIRONOMIDAE
- biting CEROTOPOGONIDAE
- gall CECIDOMYIIDAE
- hackberry thorn gall *Celticesis spiniformis*

Milkweed *Asclepias*
- common *A. syriaca*
- green *A. viridis*
- swamp *A. incarnata*

Milkwort *Polygala*
- field *P. sanguinea*
- fringed false *P. paucifolia*

Millet *Panicum miliaceum*
Millipede DIPLOPODA
Milo *Sorghum bicolor*
Minnow CYPRINIDAE
Mint LAMIACEAE
Mistletoe *Arceuthobium*
Mite ACARI
- fowl *Ornithonyssus*
- northern fowl *Ornithonyssus sylviarum*
- water *Hydrachna*

Mole TALPIDAE
Mollusc MOLLUSCA
- bivalve BIVALVIA

Monarch *Danaus plexippus*
Monocot LILIOPSIDA
Moonseed *Menispermum*
- Canada *M. canadense*

Moose *Alces alces*
Morning-glory CONVOLVULACEAE
Mosquito CULICIDAE
- common house *Culex pipiens*

Moss BRYOPHYTA
- haircap *Polytrichum*
- feather HYPNALES
- juniper haircap *Polytrichum juniperinum*
- red-stemmed feather *Pleurozium schreberi*
- Spanish *Tillandsia usneoides*
- sphagnum *Sphagnum*
- waxyleaf *Dicranum polysetum*

Moth LEPIDOPTERA
- armyworm *Spodoptera*
- browntail *Euproctis chrysorrhoea*
- cabbage looper *Tichoplusa ni*
- cattail borer *Bellura obliqua*
- cecropia *Hyalophora cecropia*
- clearwing SESIIDAE
- clothes TINEIDAE
- codling *Cydia pomonella*
- corn earworm *Heliothus zea*
- crambid snout CRAMBIDAE
- elm spanworm *Ennomos subsignaria*
- eastern tent caterpillar *Malacosoma americanum*
- ermine YPONOMEUTIDAE
- fall armyworm *Spodoptera frugiperda*
- five-spotted hawk *Manduca quinquemaculatus*
- forest tent caterpillar *Malacosoma disstria*
- geometer GEOMETRIDAE
- gypsy *Lymantria dispar*
- lappet LASIOCAMPIDAE
- leafroller TORTRICIDAE
- linden looper *Erannis tiliaria*
- luna *Actius luna*
- owlet NOCTUIDAE
- pine needleminer *Exoteleia pinifoliella*
- plume PTEROPHORIDAE
- prometheus *Callosamia promethea*
- prominent NOTODONTIDAE
- ragweed borer *Epiblema strenuana*
- rosy maple *Dryocampa rubicunda*
- saddled prominent *Heterocampa guttivitta*
- small mocis *Mocis latipes*
- snout PYRALIDAE
- sphinx SPHINGIDAE

- tiger ARCTIINAE
- tussock LYMANTRIIDAE
- twirler GELECHIIDAE
- underwing EREBIDAE
- white-lined sphinx *Hyles lineata*
- white-marked tussock *Orgyia leucostigma*
- winter *Operophtera brumata*

Mould FUNGI
- slime MYXOMYCETES

Mountain-ash *Sorbus*
- American *S. americana*
- European *S. acuparia*
- showy *S. decora*

Mouse MURIDAE
- deer *Peromyscus maniculatus*
- house *Mus musculus*
- white-footed *Peromyscus leucopus*

Mulberry *Morus*
- white *M. alba*
- red *M. rubra*

Mullein *Verbascum*
- common *V. thapsus*
- moth *V. blattaria*

Mushroom FUNGI
Muskrat *Ondatra zibethicus*
Mustard BRASSICACEAE
- black *Brassica nigra*
- field *Brassica rapa*
- garlic *Allaria petiolata*
- tall tumble *Sisymbrium altissum*

Myriapod MYRIAPODA
Myrtle *Myrtus communis*

Nannyberry *Viburnum lentago*
Nematode NEMATODA
Nettle URTICACEAE
- stinging *Urtica dioica*

Neuropteran NEUROPTERA
Newt *Notophthalmus*
Niger *Guizotia abyssinica*
Nighthawk *Chordeiles*
- Common *C. minor*

Nightshade SOLANACEAE
- bittersweet *Solanum dulcamara*

Nimblewill *Muhlenbergia schreberi*
Ninebark *Physocarpus opulifolius*

Oak *Quercus*
- black *Q. velutina*
- bur *Q. macrocarpa*
- cherrybark *Q. pagoda*
- chestnut *Q. prinus*
- chinquapin *Q. muhlenbergii*
- dwarf chinquapin *Q. prinoides*
- Hill's *Q. ellipsoides*
- overcup *Q. lyrata*
- pin *Q. palustris*
- red *Q. rubra*
- scarlet *Q. coccinea*
- scrub *Quercus*
- shingle *Q. imbricaria*
- Shumard *Q. schumardii*
- swamp chestnut *Q. michauxii*
- swamp white *Q. bicolor*
- white *Q. alba*

Oak, poison *Toxicodendron*
Oat *Avena sativa*
Oat, wild *Avena fatua*
Odonate ODONATA
Oligochaete OLIGOCHAETA
Olive *Elaeagnus*
- autumn *E. umbellata*
- Russian *E. angustifolia*

Onion *Allium*
Opossum *Didelphis*
Orache *Atriplex*
Orange *Citrus sinensis*
Orange, mock *Philadelphus*
Orange, Osage *Maclura pomifera*
Orbweaver ARANEIDAE
- garden *Argiope*
- long-jawed TETRAGNATHIDAE

Orthopteran ORTHOPTERA
Osprey *Pandion haliaetus*
Otter *Lutra*
- river *L. canadensis*

Owl STRIGIDAE
- American Barn *Tyto alba*

Barred *Strix varia*
Boreal *Aegolius funereus*
Great Horned *Bubo virginianus*
Oyster OSTREIDAE

Pansy *Viola* x *wittrockiana*
Parsnip APIACEA
cow *Heracleum lanatum*
water *Sium sauve*
wild *Pastinaca sativa*
Paspalum *Paspalum*
Pawpaw *Asimina triloba*
Pea *Pisum sativum*
Pea, partridge *Chamaecrista fasiculata*
Pea, seaside *Lathyrus japonicus*
Peach *Prunus persica*
Peanut *Arachis hypogaea*
Pear *Pyrus communis*
Pecan *Carya illinionensis*
Peeper *Pseudacris*
spring *P. crucifer*
Pellitory *Parietaria*
Pennsylvania *P. pensylvanica*
Pepper PIPERACEAE
Pepperbush *Clethra*
sweet *C. alnifolia*
Pepperweed *Lepidium*
Perch, yellow *Perca flavescens*
Persimmon *Diospyros*
Pheasant *Phasianus*
Ring-necked *P. colchicus*
Phlox POLEMONIACEAE
Pig *Sus*
Pigeon COLUMBIDAE
Rock *Columba livia*
Pigweed *Amaranthus*
smooth *A. hybridus*
Pimpernel *Lysmachia*
scarlet *L. arvensis*
Pine *Pinus*
interior lodgepole *P. contorta var. latifolia*
jack *P. banksiana*
Japanese black *P. thunbergii*
loblolly *P. taeda*
lodgepole *P. contorta*
mountain *P. mugo*
pitch *P. rigida*
ponderosa *P. ponderosa*
red *P. resinosa*
scotch *P. sylvestris*
shortleaf *P. echinata*
Virginia *P. virginianus*
white *P. strobus*
Pink CARYOPHYLLACEAE
Pinkweed *Persicaria pensylvanica*
Pipit *Anthus*
Sprague's *A. spragueii*
Pitcher Plant *Sarracenia purpurea*
Plant PLANTAE
Plantain *Plantago*
English *P. lanceolata*
Planthopper FULGOROMORPHA
achilid ACHILIDAE
fulgorid FULGORIDAE
Plum *Prunus*
American *P. americana*
domestic *P. domesticus*
wild *Prunus*
Pokeweed *Phytolacca americana*
Polychaete POLYCHAETA
Pondweed, bushy *Najas flexilis*
Poplar *Populus*
balsam *P. balsamifera*
black *P. nigra*
white *P. alba*
Poppy PAPYVERACEAE
Porcupine *Erethizon dorsatum*
Potato *Solanum tuberosus*
Prairie dog *Cynomys*
black-tailed *C. ludovicianus*
Prickly-ash *Xanthoxylum*
northern *X. americanum*
Privet *Ligustrum*
Pronghorn *Antilocapra americana*
Prune *Prunus domesticus*
Pseudoscorpion PSEUDOSCORPIONIDAE
Psyllid, hackberry gall *Pachypsylla*
Pumpkin *Pepo*

Purslane *Portulaca*
Pussytoes *Antennaria*
plantain-leaved *A. plantaginifolia*
Pyrrhuloxia *Cardinalis sinuatus*

Quail ODONTOPHORIDAE

Rabbit LEPORIDAE
jack *Lepus*
Raccoon *Procyon lotor*
Radish, wild *Raphanus raphanistrum*
Ragweed *Ambrosia*
common *A. artemisiifolia*
giant *A. trifida*
Ragwort *Senecio*
Rail RALLIDAE
Raisin *Vitis*
Raisin, northern wild *Viburnum cassinoides*
Raisin, wild *Viburnum cassinoides*
Raspberry *Rubus*
black *R. occidentalis*
red *R. idaeus*
purple-flowered *R. odoratus*
Rat RODENTIA
cotton *Sigmodon*
Redbud *Cercis canadensis*
Redpoll *Acanthis flammea*
Common *A.f. flammea*
Hoary *A.f. hornemanni*
Redtop *Agrostis alba*
Reed POACEAE
common *Phragmites australis*
Reedgrass *Calamagrostis*
northern *C. inexpansa*
Reptile REPTILIA
Rhododendron *Rhododendron*
Rice POACEAE
cultivated *Oryza sativa*
wild *Zizania*
Rocket, yellow *Barbarea vulgaris*
Rodent RODENTIA
Rootworm *Diabrotica*
corn *Diabrotica*
northern corn *Diabrotica barberi*
Rose *Rosa*
Carolina *R. carolina*
multiflora *R. multiflora*
prairie *R. arkansana*
prickly *R. acicularis*
Rosebay *Rhododendron*
Lapland *R. lapponicum*
Rosemary *Andromeda*
bog *A. glaucophylla*
Rush JUNCACEAE
Baltic *Juncus balticus*
saltmarsh *Juncus gerardi*
soft *Juncus effusus*
Rye POACEAE
cultivated *Secale cereale*
Virginia wild *Elymus virginicus*
wild *Elymus*
Ryegrass *Lolium*
perennial *L. perenne*
tall *L. arundinaceum*

Safflower *Carthamus tinctorius*
Sagebrush *Artemesia tridentata*
Salamander CAUDATA
Allegheny Mountain dusky *Desmognathus ochrophaeus*
dusky *Desmognathus*
Jefferson *Ambystoma jeffersonianum*
red-backed *Plethodon cinereus*
Salsify *Tragopogon*
yellow *T. dubius*
Saltcedar *Tamarix ramosissima*
Saltgrass *Distichlis spicata*
Sandpiper SCOLOPACIDAE
Solitary *Tringa solitaria*
Spotted *Actitis macularius*
Upland *Bartramia longicauda*
Sandwort *Arenaria*
pine-barren *A. caroliniana*
Sapsucker *Sphyrapicus*
Yellow-bellied *S. varius*
Sarsaparilla *Aralia*
bristly *A. hispida*
wild *A. nudicaulis*

Saskatoon *Amelanchier alnifolia*
Sassafras *Sassafras alba*
Sawfly TENTHREDINIDAE
  argid ARGIDAE
  birch leafminer *Fenusa pumila*
  larch *Pristophora erichsonii*
  pine *Diprion pini*
  pitch pine *Neodiprion*
  willow *Nematus ventralis*
Saxifrage *Saxifraga*
  prickly *S. tricuspidata*
Scale, pine needle *Chionaspis pinifoliae*
Scorpion SCORPIONES
Scorpionfly MECOPTERA
Screech-Owl *Megascops*
  Eastern *M. asio*
Seal PHOCIDAE
Sedge CYPERACEAE
  awl-fruited *Carex stipata*
  beaked *Carex rostrata*
  bulrush *Carex scirpoidea*
  chaffy *Carex paleacea*
  creeping *Carex chordorrhiza*
  few-seeded *Carex oligosperma*
  fox *Carex vulpinoidea*
  Hoppner's *Carex subspathacea*
  lake *Carex lacustris*
  meager *Carex exilis*
  Pennsylvania *Carex pensylvanica*
  prairie *Carex prairea*
  tussock *Carex stricta*
  water *Carex aquatilis*
  wheat *Carex atherodes*
  woolly-fruited *Carex lasiocarpa*
Seed, canary *Phalaris canariensis*
Selfheal *Prunella*
Shad *Dorosoma*
  gizzard *D. cepedianum*
Sheep OVALIDAE
Shiner CYPRINIDAE
  common *Luxilus cornutus*
  emerald *Notropis atherinoides*
  golden *Notemigonus crysoleucas*
Shorebird CHARADRIIFORMES
Shrew SORICIDAE
  masked *Sorex cinereus*
  short-tailed *Blarina brevicauda*
Shrimp NATANTIA
  fairy *Branchineta*
Silverberry *Elaeagnus commutata*
Silverweed *Argentina*
Skeletonizer HETEROCERA
Skimmer LIBELLULIDAE
  twelve-spotted *Libellula pulchella*
Skink SCINCIDAE
Skipper HESPERIIDAE
  European *Thymelicus lineola*
  tawny-edged *Polites thermistocles*
Skunk *Mephitis*
  striped *M. mephitis*
Slug STYLOMMATOPHORA
Smartweed POLYGONACEAE
  arctic *Koengia alpina*
  pale *Persicaria lapathifolium*
  water *Persicaria amphibia*
Snail GASTROPODA
  freshwater HYGROPHILA
  land STYLOMMATOPHORA
  mud LITTORINIMORPHA
  pond LYMNAEIDAE
Snake COLUBRIDAE
  common garter *Thamnophis sirtalis*
  DeKay's brown *Storeria dekayi*
  rat *Elaphe*
  red-bellied *Storeria occipitomaculata*
  ribbon *Thamnophis sauritus*
Snakefly RAPHIDIOPTERA
Snakeroot *Sanicula*
  black *S. canadensis*
Snipe *Gallinago*
  Wilson's *G. delicata*
Snowball bush *Viburnum opulus*
Snowberry *Symphoricarpus albus*
Solomon's-seal LILIACEAE
  false *Maianthemum racemosum*
  starry false *Maianthemum stellatum*
Sorghum *Sorghum bicolor*
Sorrel, sheep *Rumex acetosella*

Sow thistle *Sonchus*
perennial *S. arvensis*
Soybean *Glycine max*
Sparrow PASSERELLIDAE
Baird's *Centronyx bairdii*
Brewer's *Spizella breweri*
Ipswich *Passerculus sandwichensis princeps*
Sagebrush *Artemisiospiza nevadensis*
Saltmarsh *Ammospiza caudacuta*
Sphagnum *Sphagnum*
Spicebush *Lindera benzoin*
Spider ARANEIDAE
crab THOMISIDAE
garden orbweaver *Argiope*
ghost ANYPHAENIDAE
jumping SALTICIDAE
nursery web PISAURIDAE
orbweaver ARANEIDAE
sac CLUBIONIDAE
sun jumping *Heliophanus*
wolf LYCOSIDAE
Spiderwort *Tradescantia*
Spikenard *Aralia racemosa*
Spikerush *Eleocharis*
Spiketail *Cordulegaster*
Spiraea *Spiraea*
Spittlebug CERCOPOIDEA
meadow *Philaenus spumarius*
Sprangletop *Scolochoa festucacea*
Springbeauty *Claytonia*
Virginia *C. virginica*
Springtail COLLEMBOLA
snow *Hypogastrura nivicola*
Spruce *Picea*
black *P. mariana*
blue *P. pungens*
Engelmann *S. engelmannii*
Norway *P. abies*
red *P. rubens*
sitka *P. sitchensis*
white *P. glauca*
Spurge EUPHORBIACEAE
flowering *Euphorbia corollata*
Squash *Curcubita*
Squashberry *Viburnum edule*
Squirrel SCIURIDAE
flying *Glaucomys*
gray *Sciurus carolinensis*
ground *Spermophilus*
northern flying *Glaucomys sabrinus*
red *Tamiasciurus hudsonicus*
southern flying *Glaucomys volans*
thirteen-lined ground *Ictidomys tridecimlineatus*
Star, blazing *Liatris*
dense *L. spicata*
Starflower *Lysimachia*
Stargrass *Hypoxis*
yellow *H. hirsuta*
Steeplebush *Spiraea tomentosa*
Stickleback GASTEROSTEIDAE
threespine *Gasterosteus aculeatus*
Stilt *Himantopus*
Black-necked *H. mexicanus*
Stitchwort *Stellaria*
St. John's-wort *Hypericum*
common *H. perforatum*
Fraser's marsh *H. fraseri*
Stonefly PLECOPTERA
winter TAENIOPTERYGIDAE
Stork's-bill *Erodium*
Strawberry *Fragaria*
Strider, water GERRIDAE
Sumac *Rhus*
fragrant *R. aromatica*
poison *R. vernix*
shining *R. copallinum*
skunkbush *R. trilobata*
smooth *R. glabra*
staghorn *R. typhina*
winged *R. copallina*
Sundew *Drosera*
Sunflower *Helianthus*
giant *H. giganteus*
Swallowtail PAPILIONIDAE
black *Papilo polyxenes*
Sweetflag *Acorus americanus*
Sweetgrass *Anthoxanthum*
Sweetgum *Liquidambar styraciflua*

Swift *Chaetura*
    Chimney *C. pelagica*
Switchgrass *Panicum virgatum*
Sycamore *Platanus occidentalis*

Tadpole AMPHIBIA
Tamarack *Larix laricinia*
Tanager *Piranga*
    Summer *P. rubra*
Tapeworm CESTODA
Tea, Labrador *Ledum groenlandicum*
Tea, marsh Labrador *Rhododendron tomentosum*
Tea, New Jersey *Coenanthus americanus*
Teasel *Dipsacus*
Termite TERMITOIDAE
Tern LARIDAE
    Common *Sterna hirundo*
    Forster's *Sterna forsteri*
Thistle ASTERACEAE
    bull *Cirsium vulgare*
    Canada *Cirsium arvense*
    field *Cirsium discolor*
    nodding *Carduus nutans*
    perennial sow *Sonchus arvensis*
    sow *Sonchus*
    swamp *Cirsium douglasii*
Thistle, Russian *Salsola kali*
Three-awn *Aristida*
    oldfield *A. oligantha*
Thrasher *Toxostoma*
    Curve-billed *T. curvirostre*
Thrip THYSANOPTERA
Thrush TURDIDAE
    Bicknell's *Catharus bicknelli*
Tick ACARINA
    cattle IXODIDAE
    winter *Dermacentor albipictus*
Tick-trefoil *Desmodium*
Thrip THYSANOPTERA
Timothy *Phleum pratense*
Toad *Bufo*
Tobacco *Nicotiana*
Tomato *Solanum lycospersicum*
Towhee *Pipilo*
    Spotted *P. maculatus*
Tree, arbutus *Arbutus menziesii*
Tree, cucumber *Magnolia acuminata*
Tree, tulip *Liriodendron tulipifera*
Treefrog *Pseuacris*
Treehopper MEMBRACIDAE
Tree-of-heaven *Ailanthus altissima*
Trefoil *Lotus*
    bird's-foot *L. corniculatus*
Trout SALMONIDAE
Tumbleweed *Salsola tragus*
Turnip *Brassica rapa*
Turtle CHELYDRIDAE
    map *Graptemys*
Tussockgrass *Nassella*
Twinflower *Linnaea borealis*

Vervain *Verbena*
    blue *V. hastata*
    hoary *V. stricta*
    white *V. urticifolia*
Vertebrate VERTEBRATA
Vetch *Vicia*
    American *V. americana*
    common *V. sativa*
    tufted *V. cracca*
Viburnum *Viburnum*
    maple-leaved *V. acerifolium*
Vine, matrimony *Lycium barbarum*
Violet *Viola*
Viper's-bugloss *Echium*
Vireo *Vireo*
    Black-capped *V. atricapilla*
    Least Bell's *V. bellii pusillus*
    Plumbeous *V. plumbeus*
    Western Warbling- *V. swainsoni*
Vole MURIDAE
    meadow *Microtus pennsylvanicus*
    red-backed *Myodes gapperi*
Vulture *Cathartes*
    Turkey *C. aura*

Walkingstick HETERONEMIIDAE
Walnut *Juglans*
  black *J. nigra*
Warbler PARULIDAE
  Brewster's *Vermivora chrysoptera* x *cyanoptera*
  Golden-cheeked *Setophaga chrysoparia*
  Kentucky *Geothlypis formosa*
  Lawrence's *Vermivora chrysoptera* x *cyanoptera*
  MacGillivray's *Geothlypis tolmiei*
  Yellow-throated *Setophaga dominica*
  Worm-eating *Helmitheros vermivorum*
Wasp HYMENOPTERA
  braconid BRACONIDAE
  chalcid CHALCIDOIDEA
  cuckoo CHRYSIDIDAE
  ichneumonid ICHNEUMONIDAE
  mud-dauber SCELIPHRINI
  paper *Polistes*
  parasitic SCOLIOIDEA
  scoliid SCOLIIDAE
  spider POMPILIDAE
  thread-waisted SPHECIDAE
Watermelon *Citrullus colocynthis*
Waterfowl ANATIDAE
Waterlily NYMPHAEACEAE
  white *Nymphaea odorata*
Waterweed *Elodea*
  Canadian *E. canadensis*
Wax myrtle *Morella cerifera*
Weasel *Mustela*
Webworm, fall *Hyphantria cunea*
Weevil CURCULIONIDAE
  acorn *Curculio*
  alfalfa *Hypera postica*
  brown leaf *Phyllobius oblongus*
  Canada thistle bud *Larinus carlinae*
  clover leaf *Hypera punctata*
  clover root *Sitona lepidus*
  cotton boll *Anthonomus grandis*
  imported long-horned *Calomycterus setarius*
Whale CETACEA
Wheat *Triticum aestivum*
Wheatear *Oenanthe*
  Northern *O. oenanthe*
Whimbrel *Numenius phaeopus*
Whip-poor-will *Antrostomus*
  Eastern *A. vociferus*
Whiteface *Leucorhinia*
  crimson-ringed *L. glacialis*
Whitlow-grass *Draba*
Willow *Salix*
  arctic *S. arctica*
  beaked *S. bebbiana*
  black *S. nigra*
  bog *S. pedicellaris*
  crack *S. fragilis*
  hoary *S. candida*
  limestone *S. calcicola*
  meadow *S. petiolaris*
  net-leaved *S. reticulata*
  peach-leaved *S. amygdaloides*
  purple *S. purpurea*
  pussy *S. discolor*
  sandbar *S. exigua*
  short-fruit *S. brachycarpa*
  tea-leaved *S. planifolia*
  weeping *S. babylonica*
Willowherb *Epilobium*
  great *E. hirsutum*
Wilt, oak *Bretziella fagacearum*
Wintercress *Barbarea*
Wintergreen *Gaultheria procumbens*
Wiregrass *Aristida*
Wireworm ELATERIDAE
Witch-hazel *Hamamelis virginiana*
Wolf *Canis*
  gray *C. lupis*
Wolfberry *Lycium*
Woodchuck *Marmota monax*
Woodcock *Scolopax*
  American *S. minor*
Woodfern *Dryopteris*
  spinulose *D. carthusiana*
Woodlouse, pill ARMADILLIDIIDAE
Wood-nymph C*ercyonis*
  common *C. pegala*
Woodpecker PICIDAE
  Black-backed *Picoides arcticus*

- Downy *Dryobates pubescens*
- Hairy *Dryobates villosus*
- Pileated *Dryocopus pileatus*
- Red-bellied *Melanerpes carolinus*
- Red-headed *Melanerpes erythrocephalus*

Wood-rush *Luzula*
Wood-sorrel *Oxalis*
Woolgrass *Scirpus cyperinus*
Worm, dew *Lumbricus terrestris*
Worm, horsehair NEMATOMORPHA
Worm, marine POLYCHAETA
Worm, ribbon NEMERTEA
Wormwood *Artemesia*

Yarrow *Achillea*
Yellowjacket VESPIDAE
Yellowlegs *Tringa*
- Lesser *T. flavipes*

Yew *Taxus*
- American *T. americanus*
- Japanese *T. cuspidata*